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The bivalve *Glycymeris planicostalis* as a high-resolution paleoclimate archive for Rupelian (Early Oligocene) of Central Europe

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Abstract

Current global warming is likely to result in a unipolar glaciated world with unpredictable repercussions on atmospheric and oceanic circulation patterns. These changes are expected to affect seasonality as well as the frequency and intensity of decadal climate oscillations. To better constrain the mode and tempo of the anticipated changes, climatologists require high-resolution proxy data of time intervals in the past, e.g. the Early Oligocene during which boundary conditions were similar to those predicted for the near future. As demonstrated by the present study, pristinely preserved shells of the long-lived bivalve mollusk *Glycymeris planicostalis* from the late Rupelian of the Mainz Basin, Germany, provide an excellent archive to reconstruct changes of sea surface temperature on seasonal to inter-annual time scales. Their shells grew uninterruptedly during winter and summer and therefore recorded the full seasonal temperature amplitude that prevailed in the Mainz Basin 30 Ma ago. Absolute sea surface temperature data were faithfully reconstructed from $\delta^{18}O_{shell}$ values assuming a $\delta^{18}O_{water}$ signature that was extrapolated from coeval sirenian tooth enamel. Extreme values ranged between 12.3 and 22.0 °C and agree well with previous estimates based on planktonic foraminifera and shark teeth. However, summer and winter temperatures varied greatly on inter-annual time-scales. Winter and summer temperatures averaged over 40 annual increments of three specimens equaled 13.6 ± 0.8 °C and 17.3 ± 1.2 °C, respectively. Unless many samples are analyzed, this variability is hardly seen in foraminiferan tests. Our data also revealed decadal-scale oscillations of seasonal extremes which have – in the absence of appropriate climate archives – never been identified before for the Oligocene. This information can be highly relevant for numerical climate studies aiming to predict possible future climates in a unipolar glaciated or, ultimately, polar ice-free world.

1 Introduction

Current CO_2-induced global warming is likely to result in a unipolar glaciated world ultimately followed by one substantially without polar ice caps (e.g. Raper and Braithwaite, 2006). In light of these predicted boundary conditions, climate is expected to change profoundly, particularly at higher latitudes. According to numerical climate models, reduced meridional gradients will lead to substantial changes in atmospheric and oceanic circulation patterns (e.g. Cai and Chu, 1998; Hansen et al., 2004), thereby affecting seasonality as well as the frequency and intensity of decadal climate oscillations (e.g. Marshall et al., 2001; Solomon et al., 2007). In turn, this will alter surface temperature patterns, storm intensities and precipitation rates (Hurrell, 1995; Dai et al., 1997; Barbosa, 2009), all of which present a major challenge to densely populated coastal areas and coastal ecosystems, particularly in Central Europe (Ottersen et al., 2001; Stenseth et al., 2002).

To date, the mode and tempo of the environmental change anticipated for the near future have remained poorly constrained (e.g. Vellinga and Wood, 2002; Hátún et al., 2005). A promising avenue toward a better understanding of future climates is to investigate the short-term climate variability of time intervals in the past during which boundary conditions were similar to those predicted for the coming millennia. The last time a unipolar glaciated world occurred in Earth history was during the Early Oligocene when atmospheric CO_2 levels were slightly higher than today (Zachos et al., 2008) and the paleogeographic configuration on a global scale was at least broadly similar to the present-day situation (Lefebvre et al., 2013). Thus, the Oligocene world can serve as a natural laboratory for studying the possible effects of anthropogenic global warming. As yet, however, the Oligocene has remained a relatively poorly studied epoch of Earth history, which is at least partially attributed to the stratigraphic incompleteness of many Oligocene successions. In particular, shallow-water sequences of Oligocene age are often compromised by unconformities resulting from strong, glacially induced eustatic sea-level fluctuations (e.g. Miller et al., 2005; Pälike et al., 2006).

The epicontinental sedimentary archives from the Oligocene of Central Europe, notably the Rhenish triple junction system (e.g. Sissingh, 2003), can play a prime role in elucidating the short-term (i.e., seasonal to decadal) climate dynamics during that time. The significance of Oligocene sediments from the Rhenish triple junction system was first stressed by Beyrich (1954), whose work on strata from the Mainz and Kassel Basins ultimately led to the coinage of the term "Oligocene". These shallow marine successions exhibit much higher sedimentation rates and generally contain considerably more macrofossils than their open-marine counterparts. Moreover, their extremely proximal position with regard to the paleo-coastline and the low water-mass inertia as compared to the open ocean make them particularly sensitive to short-term paleoclimatic and paleoceanographic change. Furthermore, these strata contain well-preserved shells of long-lived bivalves (*Glycymeris planicostalis*, Lamarck 1819) whose modern representatives have recently been identified as highly promising tools for ultra-high-resolution climate reconstructions (Brocas et al., 2013; Royer et al., 2013; Bušelić et al., 2014). This species occurs worldwide in subtidal settings and lives infaunally in sandy and gravelly sediments (Ansell and Trueman, 1967; Thomas, 1978; Squires, 2010). Their fossil history dates back to the Aptian (Gillet, 1924; Casey, 1961) and besides some evolutionary innovations acquired during the Early Cenozoic, their fundamental bauplan remained largely unvaried until today (Thomas, 1975).

Bivalve shells serve as reliable recorders of ambient environmental conditions (e.g. Wanamaker et al., 2011). The production of shell material occurs on a periodic basis resulting in the formation of distinct growth lines which separate the growth pattern into time slices of equal duration, so-called growth increments. These growth patterns serve as a calendar which can be used to place each shell portion and each geochemical data point in a precise temporal context. Furthermore, the relative rate at which the shells grow is controlled by environmental variables. For example, warmer temperature and better food supply typically result in broader increments. In combination with geochemical analyses of the shell, increment width data can thus provide useful information on past environmental variables (e.g. Ivany and Runnegar, 2010; Mettam et al., 2014). Some bivalve species live for several centuries and can therefore provide uninterrupted environmental records covering hundreds of years such as the genera *Glycymeris* (Ramsay et al., 2000; Brocas et al., 2013), *Arctica* (e.g. Ropes, 1985; Butler et al., 2013) and *Panopea* (e.g. Strom et al., 2004; Black et al., 2008).

In the present study, we have sclerochronologically analyzed specimens of *G. planicostalis* from the upper Rupelian of the Mainz Basin, SW Germany, in order to assess their potential as "deep-time" paleoclimate archives. In particular, we focused on elucidating (i) whether the shells are sufficiently well preserved to permit reconstruction of water temperatures from oxygen-isotope data; (ii) what the timing and rate of seasonal shell growth of these specimens were; and (iii) how the seasonal $\delta^{18}O_{\text{shell}}$-derived water temperatures compare to existing temperature proxy data from that region. In order to assess a realistic oxygen isotope signature of the water ($\delta^{18}O_{\text{water}}$) during the Rupelian we measured the phosphate oxygen isotope ($\delta^{18}O_{PO_4}$) value of the tooth enamel of seven seacows (*Halitherium schinzii*) from the same formation as the *G. planicostalis* shells. The $\delta^{18}O_{PO_4}$ signature has been successfully exploited as a $\delta^{18}O_{\text{water}}$ proxy by many authors, e.g. Clementz and Koch (2001), Clementz et al. (2006), Thewissen et al. (2007) and Clementz and Sewall (2009). Our results demonstrate that – similar to their modern relatives – fossil *G. planicostalis* can be successfully employed for reconstructions of seasonal and decadal-scale environmental oscillations that prevailed during the Rupelian in Central Europe, i.e., data that as yet no other fossil archive could provide.

2 Study area

The Mainz Basin is located near the northwestern margin of the Upper Rhine Graben. Its formation dates back to the Middle Eocene and is related to the taphrogenesis of the European Cenozoic rift system (Dèzes et al., 2004; Ritzkowski, 2005; Grimm et al.,

2011) (Fig. 1). Its sedimentary succession, which was mainly deposited in shallow marine and brackish water settings, covers a time interval of ca. 20 Ma, from the Lutetian (∼ 49.5 Ma) to the early Burdigalian (∼ 18.5 Ma). During the late Rupelian (i.e. Early Oligocene; 33.9–28.4 Ma; Gradstein et al., 2004), central Europe experienced a period of extended marine transgressions due to local tectonic subsidence and eustatic sea level rise. As a consequence, the Mainz Basin became part of a marine strait, which extended from the paleo-North Sea Basin to the southernmost Upper Rhine Graben (Picot, 2002; Sissingh, 2003; Berger et al., 2005a). A possible southern connection with the western Molasse Basin has been controversially debated (Martini, 1982; Picot, 2002; Berger et al., 2005a, b; Grimm, 2006).

According to Berger et al. (2005b), marine conditions in the Mainz Basin lasted for about 2.5 Ma from the sea-level high stand Ru2/Ru3 (∼ 32 Ma;) to Ru3/Ru4 (∼ 29.5 Ma) of Haq et al. (1988). Nearshore deposits representing that time comprise coarse-grained (sand to gravel) siliciclastics of the Alzey Formation (from which the studied fossil material was collected – see below) and the overlaying Stadecken Formation. Contemporaneously deposited basinal sediments (pelites) belong to the Bodenheim Formation (Grimm et al., 2000; Sissingh, 2003; Berger et al., 2005b). Age control for the marine strata of the Mainz Basin is mainly based on calcareous nannoplankton (Martini and Müller, 1971; Martini, 1982), dinoflagellate cysts (e.g. Pross, 1997), and, to a lesser extent, benthic foraminifera (Grimm, 1998, 2002). With regard to the nannoplankton zonation, the Alzey and Bodenheim Formations comprise the upper part of nannoplankton zone NP23 and the lower part of nannoplankton zone NP24 (Grimm, 1994; Pross and Schmiedl, 2002; Berger et al., 2005b).

Paleoenvironmental reconstructions of the Alzey Formation are based on palynological and faunal data indicating an overall warm climate comparable to modern subtropical climate zones of the Mediterranean (Grimm et al., 2011). Reconstructed mean annual air temperature in the hinterland fluctuated between ∼ 16 and ∼ 17 °C, and mean annual precipitation was between 1000 and 1250 mm per year (Pross et al., 1998, 2000). The fully marine setting of the Mainz Basin was characterized by alternating dry and wet phases, which led to strong fluctuations of salinity levels (Pross and Schmiedl, 2002), and the episodic formation of water-mass stratification (Pross, 2001). Temperature estimates of the seawater have been derived from the δ^{18}O values of shark teeth and foraminiferan tests. These estimates yielded values of 6.9 to 23.3 °C (Tütken, 2003) for surface waters and 5.9 to 14.9 °C for bottom waters (Grimm, 1994).

3 Material and methods

3.1 Material

The studied shell material was collected by Jürgen Boy during the 70s and 80s of the last century, and has then been stored at the Paleontological collection of the Institute of Geosciences in Mainz. Samples originate from the outcrop "Trift" near Weinheim, the stratotype of the Alzey Formation (Grimm et al., 2000) (Fig. 1). Additional information about the precise stratigraphic position of the sampled layer is not available. The outcrop is ∼ 8 m thick and ∼ 40 m wide; it consists of fossiliferous middle to coarse sands and fine gravels. ^{87}Sr/^{86}Sr dating of a well-preserved *Glycymeris* sp. shell from the outcrop yielded an age of 30.1 ± 0.1 Ma (Grimm et al., 2003). The outcrop exhibits a highly diverse benthic fauna dominated by bivalves, gastropods and scaphopods that dwelled in shallow subtidal waters. Water-depth estimates, which are based on sedimentological features (Grimm et al., 2003) and ichnofossils (Schindler et al., 2005), range from ∼ 30 to ∼ 40 m. The teeth material originated from four localities located along the southwestern paleo-coastline of the Mainz Basin (Fig. 1; Table 1), and was also stored at the Paleontological collection. The samples were embedded in the siliciclastic deposits of the Alzey Formation. A more precise determination of their stratigraphic position was not possible in the field.

3.2 Methods

From the of *Glycymeris planicostalis* specimens collected at the outcrop "Trift", three large valves (~ 8 cm in height) that visually appeared well-preserved were selected for further investigations. These valves were labeled (MB-Wht-2, MB-Wht-4 and MB-Wht-7), mounted on Plexiglas cubes with GlueTec Multipower plastic welder and coated with WIKO metal epoxy resin to avoid fracture during cross-sectioning. From each valve, two ca. 3 mm-thick slabs were cut perpendicular to the growth lines and along the axis of maximum growth from the umbo to the commissure using a low-speed precision saw (Buehler Isomet 1000; at 200 rpm) equipped with a wafering-thin (0.4 mm), diamond coated blade. Both shell slabs were glued to glass slides with the mirroring sides facing up, ground on glass plates (320, 800, 1200 grit SiC powder) and polished with 1 µm Al_2O_3 powder. After each preparation step, the samples were ultrasonically rinsed in deionized water.

One polished slab of each specimen was firstly used for diagenetic screening. For this purpose, a set of different methods was employed including cathodoluminescence petrography, Raman spectroscopy and immersion of the shell slabs in Feigl solution. The presence of Mn^{2+} (> 10–20 ppm) in calcium carbonates produces an orange cathodoluminescence (Machel et al., 1991) and is typically regarded as an indicator of diagenetic neomorphism (Flügel, 2004) because biogenic aragonite is non-cathodoluminescent (Major, 1991). Like modern *Glycymeris* spp., shells of fossil representatives of this genus consisted of aragonite which is prone to change to calcite during diagenesis. Raman spectroscopy can yield detailed and spatially highly resolved information on the type of polymorphs of $CaCO_3$. Likewise, the Feigl test can distinguish between aragonite and calcite (Feigl, 1958). Feigl solution stains aragonite black and calcite pale grey. After diagenesis screening, the shell slabs were ground and polished again, and prepared for sclerochronological studies and subsequent scanning electron microscopic (SEM) analyses. For this purpose, polished cross-sections were immersed in Mutvei's solution for 40 min under constant stirring at 37–40 °C (Schöne et al., 2005a). After the staining process, the samples were gently rinsed in deionized water, air-dried and then photographed with a digital camera (Canon EOS 600D) mounted to a binocular microscope (Wild Heerbrugg M8). Growth increments were counted and their width measured with the image processing software Panopea (© Peinl and Schöne). Subsequently, samples were sputter-coated with a 2 nm thick gold layer and viewed under a scanning electron microscope (LOT Quantum Design Phenom Pro, 2nd generation) in order to describe the prevailing microstructures and identify possible neomorphic minerals that may have formed during diagenesis (Fig. 2).

The other polished slab of each specimen was used for the analysis of oxygen isotope values ($\delta^{18}O_{shell}$). Prior to the analysis, the outer ca. 0.5 to 1 mm thick chalky rim of the shell surfaces was physically removed. Then, 675 individual carbonate powder samples were micromilled from the outer shell layer of the three specimens (316, 193 and 166 samples from specimens MB-Wht-2, MB-Wht-4 and MB-Wht-7, respectively) using a Rexim Minimo dental drill mounted to a stereomicroscope and equipped with a cylindrical, diamond-coated bit (1 mm diameter; Komet/Gebr. Brasseler GmbH and Co. KG, model no. 835104010). Individual milling steps contoured the shell growth patterns and measured between 100 and 200 µm in width. Carbonate powder samples weighing between 50 and 120 µg were reacted with 100 % phosphoric acid in He-flushed borosilicate exetainers at 72 °C. The resulting CO_2 was measured with a GasBench II-coupled Thermo Finnigan MAT 253 gas source isotope ratio mass spectrometer in continuous flow mode at the Institute of Geosciences of the University of Mainz. Oxygen isotope values are reported in δ-notation and given as parts per mil (‰). Data were calibrated against a NBS-19 calibrated IVA Carrara marble ($\delta^{18}O = -1.91$ ‰). On average, replicated internal precision (1σ) and accuracy (1σ) were better than 0.05 ‰, respectively.

If the bivalves formed their shell in oxygen isotopic equilibrium with the ambient water, the $\delta^{18}O_{shell}$ values can provide information on water temperature during growth (Epstein et al., 1953). For aragonitic shells, the paleothermometry equation of Grossman and Ku (1986) with a scale correction of −0.27 ‰ (see Dettman et al.,

1999) is typically employed:

$$T_{\delta^{18}\text{O}}(^\circ\text{C}) = 20.60 - 4.34 \cdot (\delta^{18}\text{O}_{\text{shell}} - (\delta^{18}\text{O}_{\text{water}} - 0.27)), \quad (1)$$

where $\delta^{18}\text{O}_{\text{shell}}$ is measured relative to VPDB and $\delta^{18}\text{O}_{\text{water}}$ relative to VSMOW. To compute reliable temperatures from $\delta^{18}\text{O}_{\text{shell}}$ values also requires knowledge of the $\delta^{18}\text{O}_{\text{water}}$ signature during shell formation. These data were estimated from the tooth enamel of sea cows, i.e., homoeothermic marine animals, from the same stratigraphic level. The precision errors of the mass spectrometric analyses of bivalve shells and sirenian teeth resulted in a combined average $T_{\delta 18O}$ error of ± 0.3 °C (1σ).

3.3 Sea cow teeth

The oxygen isotope composition of tooth enamel from marine vertebrates can provide information on the $\delta^{18}\text{O}_{\text{water}}$ value of ambient seawater (e.g. Lécuyer et al., 1996a; Clementz and Koch, 2001; Clementz et al., 2006; Clementz and Sewall, 2009). Therefore, we measured the phosphate oxygen isotope composition ($\delta^{18}\text{O}_{\text{PO}_4}$) of the enamel from seven sirenian teeth of *Halitherium schinzii* recovered from the deposits of the Alzey Formation.

The surface of the teeth was physically cleaned and then sampled with a hand-held dental drill. A fraction of each enamel powder sample was then treated with 2 % NaOCl and 0.18 mL of 0.1 molar acetic acid to remove organics and potential diagenetic carbonates, respectively. Subsequently, ca. 4 mg of each sample were converted into silver phosphate (Ag_3PO_4) following the method of O'Neil et al. (1994) with modifications of Dettman et al. (2001) and Tütken et al. (2006). Triplicates of 500 µg of each Ag_3PO_4 sample were analyzed with a Thermo Fisher Delta Plus XL mass spectrometer coupled to a TC-EA, at the University of Tübingen, Germany. Measured values were normalized to in-house standards, Tu-1 and Tu-2 (Vennemann et al., 2002) and reported in δ-notation vs. VSMOW. Replicate ($n = 6$) analyses of NBS 120c resulted in an average $\delta^{18}\text{O}_{\text{PO}_4}$ value of 21.6 ± 0.13 ‰ which is well in the range of the average value (21.7 ‰) given by Lécuyer et al. (1993, 1996a) and O'Neil et al. (1994). The $\delta^{18}O_{PO_4}$ values of the *H. schinzii* teeth of the Mainz Basin were converted into $\delta^{18}O_{water}$ values using the equation determined for modern sirenians by Tütken (2003):

$$\delta^{18}O_{water} = \frac{\delta^{18}O_{PO_4} - 20.23}{0.86}, \tag{2}$$

where $\delta^{18}O_{water}$ and $\delta^{18}O_{PO_4}$ are given relative to VSMOW.

In order to assess the possibility of diagenetic alteration of the enamel oxygen isotope composition, the carbonate ($\delta^{18}O_{CO_3}$) and the phosphate ($\delta^{18}O_{PO_4}$) group of the enamel were plotted against each other and compared to a compilation of $\delta^{18}O_{CO_3}$ vs. $\delta^{18}O_{PO_4}$ pairs from extant mammals published by Pellegrini et al. (2011). The $\delta^{18}O_{CO_3}$ values were determined in the remaining fraction of the pretreated *H. schinzii* enamel powders. About 800 µg of each enamel powder sample were analyzed with a Thermo Finnigan MAT 253 gas source isotope ratio mass spectrometer in continuous flow mode equipped with a GasBench II at the University of Mainz. The $\delta^{18}O_{CO_3}$ values were measured against VPDB and normalized to a NBS-18 and NBS-19 calibrated Laaser marble (−5.21 ‰; replicated precision, 1σ, better than 0.1 ‰). Afterward, the results were converted to the SMOW scale using the equation of (Coplen et al., 1983):

$$\delta^{18}O_{SMOW} = 1.03091 \cdot \delta^{18}O_{PDB} + 30.91. \tag{3}$$

3.4 Mathematical resampling of intra-annual isotope data

In bivalves, shell growth rate declines during ontogeny resulting in increasingly narrow annual growth increments with increasing lifespan (Jones and Quitmyer, 1996). Since the isotope samples were taken at approximately equidistant intervals (100 to 200 µm), the number of samples per year decreases through lifetime and the time represented by each carbonate sample (= time-averaging) increases in ontogenetically older shell portions. To compensate for that bias and make the isotope samples from different ontogenetic years comparable to each other, the number of $\delta^{18}O_{shell}$ values per year was mathematically equalized by a re-sampling technique similar to that described in Schöne et al. (2004) and Hallmann et al. (2011). Following previous work (e.g. Schöne and Fiebig, 2008; Wanamaker et al., 2011), we fitted the isotope data of each annual increment with a 7-point cubic spline using the software Analyseries 1.1 (Paillard et al., 1996) and re-sampled each intra-annual curve so that the same number of isotope values were available for each annual increment, i.e., seven $\delta^{18}O_{shell}'$ values. Noteworthy, this re-sampling method slightly deviated from previous approaches (Schöne et al., 2004; Hallmann et al., 2011), because it was impossible to determine seasonal growth curves from microgrowth patterns. Hence, the $\delta^{18}O_{shell}'$ values within a given year most likely represented different amounts of time, but the first, second, third etc. $\delta^{18}O_{shell}'$ values of different years represented same amounts of time.

4 Results

4.1 Preservation of material

According to a set of different diagenesis screening tests outlined above, the studied shells of *Glycymeris planicostalis* from the Rupelian of the Mainz Basin consist of aragonite and were remarkably well preserved. This even applies to the chalky rims of the shells, i.e., the shell portions that were only pale blue stained by Mutvei's solution and lost almost all organics during taphonomy. Orange cathodoluminescence was only emitted from very few isolated spots, i.e., cracks containing neomorphic mineral phases. Most other portions of the shells were dark blue to non-luminescent. Moreover, both reflected light microscope and electron microscope analyses revealed the same shell microstructures that occur in modern representatives of this genus, i.e., crossed-lamellar structures (Fig. 2a–c). Alternately, the 1st order lamellae appear dark and bright because the higher order-lamellae are arranged in a fence-like manner and stand perpendicular to each other (compare Füllenbach et al., 2014). Furthermore, both shell layers are perforated by numerous hollow microtubuli (Fig. 2d), especially in the juvenile portion of the shells. On rare occasions, these tubuli (ca. 10 µm in diameter) are filled with pyrite crystals or iron oxides.

Like the bivalves, the studied sirenian teeth are pristinely preserved (Fig. 3). The $\delta^{18}O_{CO_3}$ vs. $\delta^{18}O_{PO_4}$ pairs of the seven specimens plot well within the 95 % prediction intervals of modern and other well-preserved fossil mammal enamel data compiled by Pellegrini et al. (2011) (Table 1; Fig. 3). Diagenetically altered tooth enamel would in the first place have affected the carbonate-bound oxygen (Iacumin et al., 1996) and resulted in $\delta^{18}O_{CO_3}$ vs. $\delta^{18}O_{PO_4}$ pairs plotting farther away from the regression line depicted in Pellegrini et al. (2011). Given the excellent preservation, $\delta^{18}O_{water}$ values were computed from $\delta^{18}O_{PO_4}$ values of the enamel using Eq. (2). On average, the $\delta^{18}O_{water}$ value of the water was -0.9 ± 0.3‰ (1σ).

4.2 Bivalve sclerochronology: $\delta^{18}O_{shell}$ and reconstructed water temperatures

The studied fossil *G. planicostalis* specimens show distinct growth lines in the ventral margin and the hinge plate of Mutvei-stained cross-sections (Fig. 2). These lines were previously identified as periodic annual features (Berthou et al., 1986; Royer et al., 2013; Bušelić et al., 2014) separating the growth pattern in annual time slices, i.e., annual growth increments. The annual growth lines are more distinctly developed and hence easier to discern in the hinge plate than in the ventral margin. Based on annual increment counts, it was possible to determine the ontogenetic ages of the specimens. Specimens MB-Wht-2, MB-Wht-4 and MB-Wht-7 reached life spans of 77, 84 and 67 years, respectively.

Oxygen isotope curves of all three specimens exhibits distinct seasonal oscillations (16, 14 and 10 cycles in specimens MB-Wht-2, -4, and -7, respectively) with the annual growth lines occurring shortly after the most negative $\delta^{18}\mathrm{O}_{\mathrm{shell}}$ values of each cycle (Fig. 4; see the Supplement). In other words, the full seasonal amplitudes are preserved in the shells including winter and summer values. The annual growth line formation occurred in later summer/early fall.

The shells grew faster during the first half of the year than after summer. This is well reflected in the seasonal temperature curve based on the averaged $\delta^{18}\mathrm{O}'_{\mathrm{shell}}$ values of all 40 measured annual increments (Fig. 5). There are more data points in shell portions formed during spring than in shell portions formed during fall (Fig. 5). Accordingly, the reconstructed temperature curve is right-skewed.

The average annual $\delta^{18}\mathrm{O}_{\mathrm{shell}}$ values and seasonal $\delta^{18}\mathrm{O}_{\mathrm{shell}}$ ranges are fairly similar among the three studied specimens (Table 2). Seasonal extremes fluctuate between −1.48 ‰ (summer value) and 0.75 ‰ (winter value) in specimen MB-Wht-2, between −1.16 and 0.67 ‰ in specimen MB-Wht-4, and between −1.19 and 0.60 ‰ in specimen MB-Wht-7. Using the reconstructed $\delta^{18}\mathrm{O}_{\mathrm{water}}$ value, this translates into total temperature ($T_{\delta^{18}\mathrm{O}}$) ranges of 9.7, 7.6, and 7.8 °C in specimens MB-Wht-2, MB-Wht-4 and MB-Wht-7, respectively. Taking the average value of the 40 seasonal cycles of all three specimens, the average annual temperature is 15.4 ± 0.7 °C (1σ), and the seasonal temperature range equals 3.7 °C with average minimum (winter) values of 13.6 ± 0.8 °C (1σ) and average maximum (maximum) values of 17.3 ± 1.2 °C (1σ).

Noteworthy, the seasonal amplitudes vary through time. In some years, the seasonal $T_{\delta^{18}\mathrm{O}}$ range was less than 2 °C (Fig. 6). Although the isotope time-series are too short to reliably identify lower-frequency oscillations, the seasonal ranges seem to vary on a quasi-decadal time-scale.

5 Discussion

As demonstrated by this study, shells of *Glycymeris planicostalis* provide an excellent archive to reconstruct climate dynamics – in particular changes of sea surface temperature – during the Oligocene on subseasonal to inter-annual time-scales. Shells of the studied species grew during both the coldest and warmest periods of the year and therefore contain information on the full seasonal temperature amplitude that prevailed in the Mainz Basin 30 Ma ago. Like modern *Glycymeris glycymeris* (e.g. Ramsay et al., 2000), the Oligocene representatives of this genus lived for several decades which make them excellent recorders of decadal-scale climate variability. Furthermore, the shells are pristinely preserved and their $\delta^{18}O_{shell}$ values reflect changes of ambient water temperature.

5.1 Preservation

The excellent preservation of the studied *G. planicostalis* shells is remarkable. Not only consisted the shells of aragonite, SEM analysis also revealed original delicate microstructures including the typical skeletal feature of glycymerids, i.e., microtubules. These cylindrical cavities perforate the inner and outer shell layers and are filled with organics during the lifetime of the animal (e.g. Waller, 1980; Crippa, 2013). The diagenetic loss of organic material leaves behind hollow cavities that potentially can be filled with neomorphic mineral phases. However, the microtubules of the studied specimens were typically hollow and only rarely contained pyrite. Noteworthy, pyrite crystals can even occur in shells of living bivalves and are possibly related to the bacterial degradation of organic matter (Clark and Lutz, 1980).

In fact, the recovery of pristinely preserved fossil glycymerids has been reported from many other localities and geological time intervals (e.g. Tsuboi and Hirata, 1935; Dorman and Gill, 1959; Crippa, 2013). Since *Glycymeris* spp. dwells in sandy to fine gravelly habitats, shells of this genus are usually embedded in coarse grained and highly porous sediments. In such type of host rock and stratigraphic age, one would not expect aragonitic shell preservation, particularly if the burial depth is shallow (few tens of meters) and the sediment is still unconsolidated such as weakly cemented sandstones of the Alzey Formation. Under surface conditions, aragonite is metastable and slowly turns into the more stable polymorph of $CaCO_3$, i.e., calcite (Boettcher and

Wyllie, 1967). This conversion into calcite can be expedited when a fluid is present (Putnis and Putnis, 2007) and when temperature is increased (Dasgupta, 1963). The resistance of glycymerid shells against diagenetic alteration likely resulted from low organic content and the dense crossed-lamellar microstructure (Taylor and Layman, 1972).

5.2 Timing and rate of shell growth

Pristine preservation is a major prerequisite for the reconstruction of environmental variables from geochemical properties of the shells including ambient water temperature from $\delta^{18}O_{shell}$ values. According to shell oxygen isotope data the studied shells grew during winter and summer and recorded the full seasonal amplitude of environmental variables. Such data are crucial for paleoclimate studies. Similar findings on shell growth during seasonal extremes were recently reported by for modern *Glycymeris bimaculata* from Croatia (Bušelić et al., 2014). The only difference is that the Oligocene shells formed annual growth lines in late summer/early fall, whereas the period of extremely slow or no shell growth in specimens from Croatia occurs during spring. Noteworthy, modern *G. glycymeris* from the North Atlantic form annual growth breaks in winter (Berthou et al., 1986; Royer et al., 2013). These findings suggest that the timing and rate of shell growth can vary greatly among different species of the same genus and most likely even among specimens of the same species alive at different localities. It is therefore required to conduct thorough calibration studies prior to using shells for environmental reconstructions.

Shell growth rates of the studied bivalves from the Early Oligocene of the Mainz Basin also varied during the main growing season. For example, shell production was faster during spring and summer than during winter. This finding has implications for geochemical sampling strategies. In order to obtain reliable information on the actual seasonal temperature spread, a higher sampling resolution has to be applied in slow-growing shell portions.

5.3 Temperatures of the Mainz Basin during the Rupelian

Only few temperature estimates of the Mainz Basin and adjacent regions during the Rupelian are currently available. For example, sediments of the Alzey Formation contain a diverse warm-water fauna including marine fish, mammals and crocodiles as well as terrestrial turtles. Based on this fossil assemblage, subtropical climate conditions – similar to the modern southeastern Mediterranean – were inferred for the Mainz Basin (Grimm et al., 2003, 2011). Furthermore, macroflora and palynological data from the Bodenheim Formation yielded winter and summer air temperatures of 7.1–10.2 °C and 25.7–28.1 °C, respectively (Pross et al., 1998, 2000). These estimates compare well with that at other contemporaneous localities in Central Europe (Mosbrugger et al., 2005; Erdei et al., 2012).

Knowledge on water temperatures of the Mainz Basin comes from oxygen isotope values of biogenic skeletons. Tütken (2003) reported the δ^{18}O values of shark teeth apatite that correspond to absolute temperatures between 6.9 and 23.3 °C (temperatures recalculated assuming a $\delta^{18}\text{O}_{\text{water}}$ value of -0.9 ‰; Table 3), using the thermometry equation of Longinelli and Nuti (1973). Grimm (1994) reported oxygen isotope data of planktonic and benthic foraminifera which can be converted into absolute temperatures using the paleothermometry equation by Anderson and Arthur (1983) and a $\delta^{18}\text{O}_{\text{water}}$ value of -0.9 ‰. Based on this calculation, sea surface temperatures of the Mainz Basin fluctuated between 11.7 and 21.3 °C (Table 4), whereas bottom water (up to 150 m depth; Grimm et al., 2011) temperatures were as cold as 5.9 to 14.9 °C during the Rupelian. Similar surface water temperatures were reconstructed from bivalve shells in the present study (12.3 and 22.0 °C), albeit the lowest temperatures were ~ 5 °C higher than those obtained from the shark teeth (Fig. 7). Leaving aside the fact that it is rather unlikely that the studied bivalves, sharks and foraminifera lived during the exact same time interval, a direct comparison of temperature extremes derived from the different marine archives seems problematic for a variety of reasons:

(i) The temporal resolution provided by foraminifera is much higher than that of bivalves. Foraminiferan tests can grow within a few weeks (Bé et al., 1981). Thus, each specimen recorded environmental conditions during a very short time interval of the year. However, each sample taken from the bivalve shells represents, on average, about one month worth of growth. With a higher sampling resolution it would likely be possible to better capture the actual seasonal temperature extremes. This applies particularly to winter temperatures, because the shells grew slower during the cold season of the year than during summer (Fig. 5). Notably, the precise timing of the year when the foraminifera formed their skeletons remains unknown. Samples analyzed so far may not necessarily have grown when the most extreme seasonal temperatures occurred. Accordingly, actual winter temperatures may have been even colder and summers warmer than suggested by the foraminifera δ^{18}O values.

(ii) Seasonal temperature extremes given by sharks may not represent the actual temperatures where the bivalves lived. Sharks are highly mobile, nektonic organisms. Temporarily, they may have scavenged in the shallowest waters near the coast and at other times dived to the very bottom of the sea. In addition to vertical movements, they may have travelled large distances such as modern sharks (e.g. Domeier and Nasby-Lucas, 2008). Lowest temperatures recorded by sharks may thus represent conditions below the thermocline or settings much further north instead of winter temperatures in the Mainz Basin. In turn, those portions of the teeth that provided temperature estimates of 22 °C may actually have been formed while the animal lived in warmer waters much farther south or very near the coast.

(iii) Actual sea surface temperatures during winter and summer may have been underestimated by the planktonic foraminifera (and sharks while they resided in shallowest, coastal waters), because the assumed average δ^{18}O$_{\text{water}}$ value did not reflect the actual isotope signature of the water. Planktonic foraminifera lived in the upper few meters of the water column in a narrow, shallow epicontinental sea. In such a habitat, seasonally varying riverine freshwater influx, precipitation and evaporation rates likely resulted in seasonal changes of the δ^{18}O$_{\text{water}}$ value. Increased evaporation

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during summer may have shifted the $\delta^{18}O_{water}$ value toward more positive values resulting in lower than actual reconstructed water temperatures near sea surface. In contrast, higher precipitation rates during winter may have shifted the $\delta^{18}O_{water}$ value toward more negative values so that the oxygen isotope-derived temperatures appeared colder than they actually were. Implications for a seasonally varying $\delta^{18}O_{water}$ value come from sirenian teeth. Like their extant relatives, sea cows lived the upper ten meters of the ocean and near the coast (Louise Chilvers et al., 2004) and have thus recorded the isotope signature of the water in which the foraminifera lived. Reconstructed $\delta^{18}O_{water}$ values fluctuated between −0.2 and −1.4 ‰. If the latter value reflected conditions during winter and the former during summer, actual seasonal temperatures in the upper few meters of the Mainz Basin reconstructed from foraminifera ranged between ca. 11 and 27 °C.

(iv) Bivalve shell-based temperature estimates cannot be directly compared to those of planktonic foraminifera even if the fluctuating $\delta^{18}O_{water}$ values in the upper few meters of the ocean were precisely known. In ca. 30–40 m water depth, bivalves likely experienced a smaller seasonal temperature range than organisms in the upper few meters of the sea.

The robustness of temperature estimates derived from *G. planicostalis* shells is further supported by data on thermal regimes of the water column in modern semi-enclosed seas. According to hydrographical studies of the coastal regions in the northwestern Mediterranean (France) and southeastern Mediterranean (Lebanon), the water in 30–40 m water depth is still strongly influenced by surface conditions (Abboud-Abi Saab et al., 2004). At 35 m water depth the water temperatures in Lebanon ranged between 16.9 and 29.1 °C with an annual average of 22.5 ± 4.1 °C (1σ), whereas the coastal waters in France ranged between 21.8 and 12.3 °C with an annual average of 15.2 ± 2.2 °C (1σ). Temperatures recorded by *G. planicostalis* lay well in these thermal regimes suggesting paleoclimate conditions were more similar to regions in the northwestern Mediterranean than subtropical. However, the mean annual precipitation in the area of Marseille equals 751 ± 172 mm (Harris et al., 2014), which is considerably lower than 1000–1250 mm a^{-1} reconstructed precipitation rates in the Mainz Basin (Pross et al., 1998, 2000). A possible explanation for the high precipitation rates in Central Europe during the Oligocene has been provided by Pross and Schmiedl (2002). The deposition of the Alzey formation and its basinal counterparts, the Bodenheim formation, took place during sea-level highstands, which could have increased the moisture concentration in the atmosphere, and so, intensified rainfalls. Such linkage between sea level rise and precipitation has recently been postulated for the Early Holocene intensification of the Australian–Indonesian monsoon rainfall (Griffiths et al., 2009).

5.4 Advantages of using shells of *Glycymeris planicostalis* for reconstruction of the climate conditions during the Rupelian

The studied specimens of *G. planicostalis* offer a number of advantages over existing marine paleoclimate archives. As sessile organisms, bivalves faithfully recorded the water properties at a specific locality and depth throughout their lifetimes. Since their shells grew almost year-round, each isotope sample can be assigned to a particular season. If preservation permits, daily microgrowth increments can be employed to temporally contextualize the seasonal shell growth to the nearest week or so (e.g. Schöne et al., 2005b) Such an internal calendar is missing in foraminifera.

The studied *G. planicostalis* specimens lived for several decades and recorded seasonal temperature changes over the course of many consecutive years. This is a clear advantage over other climate archives that only provide very short temporal snapshots of unknown timing within the year such as foraminifera or shark teeth, or few consecutive years, such as fish otoliths. Otoliths are calcareous ossicles (usually aragonite) that grow in the inner ear of fish. Analogously to bivalve shells, they form growth lines, and their oxygen isotope composition can be used for seasonal paleotemperature reconstructions, for example, at the Eocene/Oligocene boundary (Ivany et al., 2000). Although fish otoliths are very common components of marine nektonic microfossil assemblages, their reduced size makes them difficult to sample, and analyses of their chemical composition usually cover only short time intervals.

Long proxy records offer the possibility to track decadal-scale variability of winter and summer temperatures. Although the $\delta^{18}O_{shell}$ chronologies of *G. planicostalis* are too short to conduct statistically reliable time-series analyses, the seasonal extremes, specifically winter temperatures, seem to have changed periodically through time. Such decadal climate dynamics are well known from modern settings in the Northeast Atlantic sector (Hurrell and Van Loon, 1997) and can be attributed, for example, to the North Atlantic Oscillation (Hurrell and Deser, 2009). Future studies should conduct isotope measurements of longer-lived specimens of *G. planicostalis* and generate time-series that are long enough to permit spectral analyses. Furthermore, these data should then be combined with numerical climate models for that time.

The $\delta^{18}O_{water}$ signature at 30–40 m water depth was most probably much less variable than near the sea surface. Seasonal changes in freshwater influx into the Mainz Basin likely did not have any effect on the isotope signature of the water in which the bivalves lived. In fact, modern *G. glycymeris* from the North Atlantic is most prolific in water with stable salinity of 34–35 PSU (Rombouts et al., 2012). If the same preference is true for the Oligocene relatives of this genus, water temperatures can be reconstructed with smaller error bars from oxygen isotope values of the bivalve shells than from skeletal hard parts of nektonic and planktonic organisms. Evidently, absolute temperature estimates from $\delta^{18}O$ values require knowledge of the oxygen isotope signature of the ambient water, which is rarely available for fossil environments. In the present study, the $\delta^{18}O_{water}$ value was reconstructed from the tooth enamel of sea cows from the same stratigraphic level. Although the bivalves and the sea cows did most certainly not live during the exact same time and the sphere of action of the sea cows was the upper ten meters of the ocean, the average $\delta^{18}O_{PO_4}$ value of the sirenian teeth serves as a reasonable estimate of the $\delta^{18}O_{water}$ signature (−0.9 ‰) of the Mainz Basin during the Rupelian. A similar value (−1 ‰) was also assumed by Grimm (1994). To test the temperature estimates obtained from $\delta^{18}O_{shell}$ values and circumvent uncertainties related to the precise $\delta^{18}O_{water}$ signature during shell formation, future studies should explore other potential temperature proxies such as Sr/Ca and Δ_{47} values.

6 Summary and conclusions

Shells of *Glycymeris planicostalis* provide faithful recorders of sea surface temperatures in the Mainz Basin during the Rupelian. Since the shells were preserved as pristine aragonite, the $\delta^{18}O_{shell}$ values can be used to reconstruct ambient water temperature. Although the exact oxygen isotope signature of the water is not known, it is highly likely to assume that the $\delta^{18}O_{water}$ value in 30–40 m water depth remained largely invariant through time. Attributed to its notable longevity, shells of this species can be used to study seasonal temperature changes over several consecutive years. As shown in the present study, summer and winter temperatures varied greatly on inter-annual time-scales. Unless many samples are analyzed, this variability is hardly seen in foraminiferan tests. Our data also revealed decadal-scale oscillations of seasonal extremes which have – in the absence of appropriate climate archives – never been identified before for the Oligocene. This information can be highly relevant for numerical climate studies aiming to predict possible future climates in a unipolar glaciated or polar ice-free world.

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Table 1. Enamel δ^{18} values (VSMOW) of the sea cows teeth from the Alzey Formation deposits of the Mainz Basin and $\delta^{18}O_{water}$ values calculated from the sea cow enamel $\delta^{18}O_{PO_4}$ values. See text for details..

Sample ID	$\delta^{18}O_{PO_4}$ [‰]	$\delta^{18}O_{CO_3}$ [‰]	$\delta^{18}O_{water}$ [‰]
Trai 01-1	19.36	25.79	−1.01
Trai 01-2	19.04	26.14	−1.38
Eck 01-1	19.29	26.40	−1.09
Wein 01-1	19.31	26.63	−1.07
Wein 01-2	19.36	26.64	−1.01
PW 2008/2-1	19.32	26.31	−1.06
PW 2008/2-2	19.55	26.74	−0.79
PW 2008-1B	20.03	27.05	−0.23
STS-BE 62-1	19.07	25.98	−1.35
PW 2008-1A	19.35	26.40	−1.02
PW 2005/5042-LS-1	19.75	26.67	−0.56
Eck 01-2	19.74	26.40	−0.57
Average ±1σ	19.43 ±0.29	26.43 ±0.35	−0.9 ±0.1
Min	19.04	25.79	−1.38
Max	20.03	27.05	−0.23

Table 2. Stable oxygen isotope values (VPDB) of the three *Glycymeris planicostalis* shells analyzed in this study. The table lists seasonal extremes ($\delta^{18}O_{min}$ and $\delta^{18}O_{max}$) as well as average summer ($\delta^{18}O'_{summer}$; re-sampled values; explanation see text) and winter extremes values ($\delta^{18}O'_{winter}$).

Sample ID	$\delta^{18}O_{min}$ [‰]	$\delta^{18}O'_{summer} \pm 1\sigma$ [‰]	$\delta^{18}O_{max}$ [‰]	$\delta^{18}O'_{winter} \pm 1\sigma$ [‰]	$\delta^{18}O_{mean} \pm 1\sigma$ [‰]
MB-Wht-2	−1.48	−0.66 ±0.21	0.75	0.38 ±0.23	−0.12 ±0.13
MB-Wht-4	−1.16	−0.40 ±0.31	0.67	0.28 ±0.14	−0.03 ±0.13
MB-Wht-7	−1.19	−0.61 ±0.23	0.60	0.24 ±0.19	−0.20 ±0.16

Table 3. Dentine and enamel $\delta^{18}O_{PO_4}$ values (VSMOW) of shark teeth recovered from the Lower Oligocene deposits of the Mainz Basin (Tütken, 2003). Values have been converted to temperature ($T\delta^{18}O_{PO_4}$) using the paleothermometry equation by Longinelli and Nuti (1973) assuming $\delta^{18}O_{water} = -0.9$‰.

Sample ID	Genus	$\delta^{18}O_{PO_4}$ [‰]	$T\delta^{18}O_{PO_4}$ [°C]
FD HAI MB 2	*Carcharias* sp.	22.9	9.1
FZ HAI MB 2	*Carcharias* sp.	22.8	9.5
FZ HAI MB 3	*Carcharias* sp.	19.6	23.3
FD HAI MB 4	*Carcharias* sp.	21.0	17.2
FZ HAI MB 4	*Carcharias* sp.	21.5	15.1
FZ HAI MB 8	*Carcharias* sp.	20.1	21.1
FZ HAI MB 9	*Carcharias* sp.	21.0	17.2
FZ HAI MB 10	*Carcharias* sp.	23.4	6.9
Average ± 1σ		21.5 ± 1.3	14.9 ± 5.9
Min		19.6	6.9
Max		23.4	23.3

Table 4. Stable oxygen isotope values (VPDB) of foraminiferan tests from the Bodenheim Formation (wells Kriegsfeld 5 and Bodenheim 65) reported by Grimm (1994). $\delta^{18}O_{Glob}$ = *Globigerina* sp. (planktonic foraminifera); $\delta^{18}O_{Bol}$ = *Bolivina* sp. (benthonic foraminifera). Values have been converted to temperature ($T\delta^{18}O_{Glob}$, $T\delta^{18}O_{Bol}$) using the equation by Anderson and Arthur (1983) assuming $\delta^{18}O_w = -0.9$‰.

Kriegsfeld 5 Depth [m]	$\delta^{18}O_{Glob}$ [‰]	$T\delta^{18}O_{Glob}$ [°C]	Bodenheim 65 Depth [m]	$\delta^{18}O_{Bol}$ [‰]	$T\delta^{18}O_{Bol}$ [°C]
15	−1.8	18.7	21.5	1.5	5.9
23	−2.4	21.3	70	−0.9	14.9
25	−0.1	11.7	80	1.0	7.6
28	−1.3	16.5	85	1.1	7.3
30	−2.0	19.5	90	0.7	8.7
32	−0.7	14.1	95	−0.03	11.4
34	−0.8	14.5	99	0.7	8.7
Average ±1σ	2.75 ±0.81	16.6 ±3.4	Average	0.6 ±0.8	9.5 ±2.9
Min	−2.4	11.7	Min	−0.9	5.9
Max	−0.1	21.3	Max	1.5	14.9

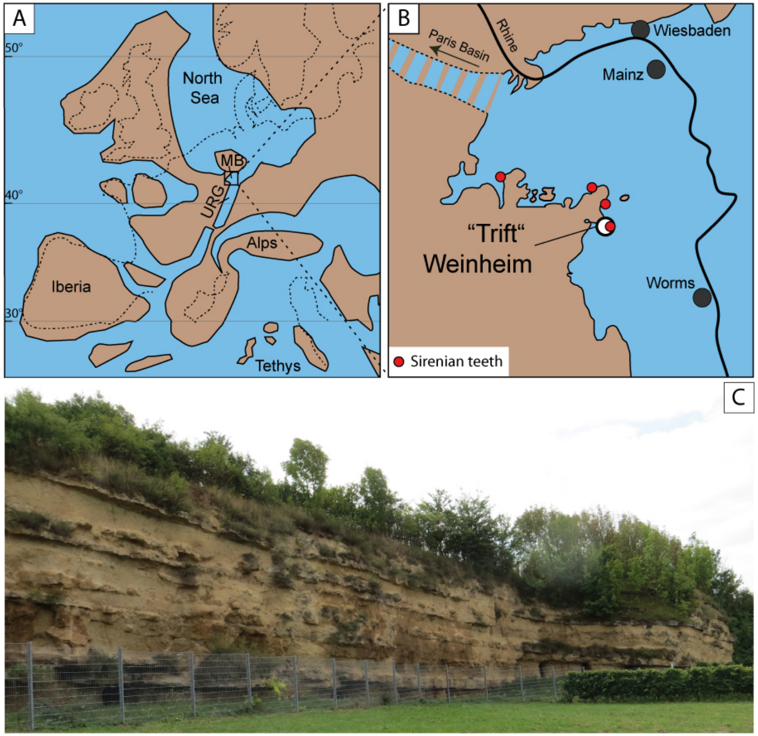

Figure 1. Map showing the paleogeography during the Rupelian and the sample locality in the Mainz Basin. **(a)** Position of the Mainz Basin (MB) in Central Europe. URG = Upper Rhine Graben. Emerged land areas are shown in brown and marine environments in blue. Modified from Spiegel et al. (2006). **(b)** Sample locality of the shells (outcrop "Trift" near Weinheim; open circle) and sea cow teeth (red dots). The presence of a western gateway (dashed area) connecting the Mainz Basin to the Paris Basin is unclear. Modified after Grimm et al. (2011). **(c)** Photograph of the outcrop "Trift" near Weinheim.

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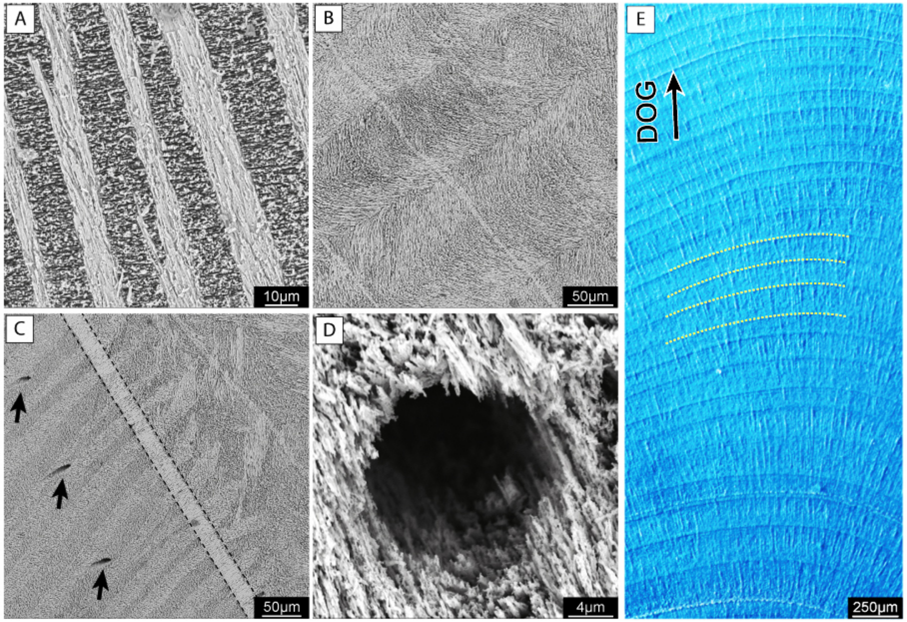

Figure 2. SEM images showing the extraordinary preservation state of the *Glycymeris planicostalis* shells from the Early Oligocene of the Mainz Basin. Primary microstructures are still present. **(a)** Outer crossed-lamellar layer, **(b)** inner complex crossed-lamellar layer and **(c)** transition zone between outer and inner shell layer (dotted lines). Arrows point to tubule openings. **(d)** Detailed view of a tubule. The lack of diagenetic fillings inside the cavity further supports the absence of any significant diagenetic overprint. **(e)** Distinct growth lines (yellow dotted lines) are visible in the hinge plate of Mutvei-stained cross-sections. DOG = direction of growth.

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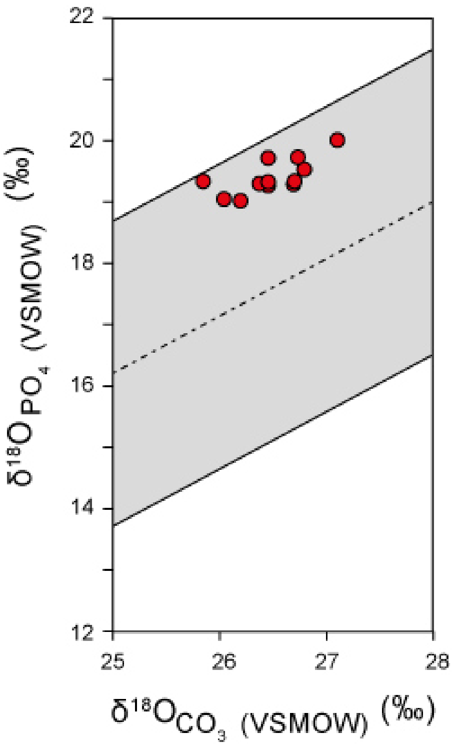

Figure 3. Cross-plot of mammal tooth enamel $\delta^{18}O_{PO_4}$ and $\delta^{18}O_{CO_3}$ pairs (dashed line = average; grey area = 95 % prediction intervals) compiled by Pellegrini et al. (2011) with respective data from the seven Oligocene sirenian teeth of the present study (red filled circles). Sea cow isotope data plot within the 95 % prediction intervals suggesting that diagenesis has not affected the isotope signature of the phosphate group.

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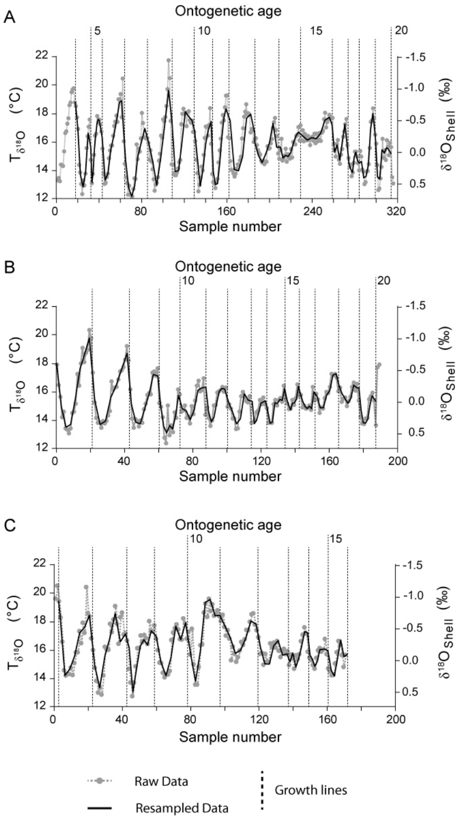

Figure 4. Raw (grey) and re-sampled (black) $\delta^{18}O_{shell}$ values for each of the three *Glycymeris planicostalis* shells used in this study (**a** = MB-Wht-2; **b** = MB-Wht-4; **c** = MB-Wht-7). Vertical dotted bars represent annual growth lines. Temperatures were calculated using Eq. (2) with a $\delta^{18}O_{water}$ value reconstructed from $\delta^{18}O_{PO_4}$ of sea cow tooth enamel (see text for description).

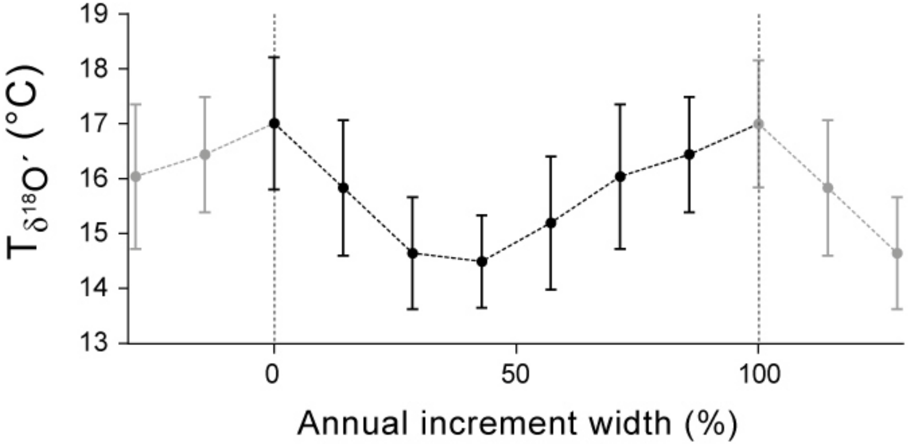

Figure 5. Average seasonal temperature changes (black dots, ±1σ) based on mathematically re-sampled shell oxygen isotope values ($\delta^{18}O'_{shell}$ values; see text for explanation) of 40 annual increments measured in three specimens of *Glycymeris planicostalis*. Note that the resultant temperature curve is not symmetric as one would expect, but right-skewed indicating slower shell growth occurred during fall and winter than during the remainder of the year. In other words, more shell material has been deposited during spring and summer than during fall and winter.

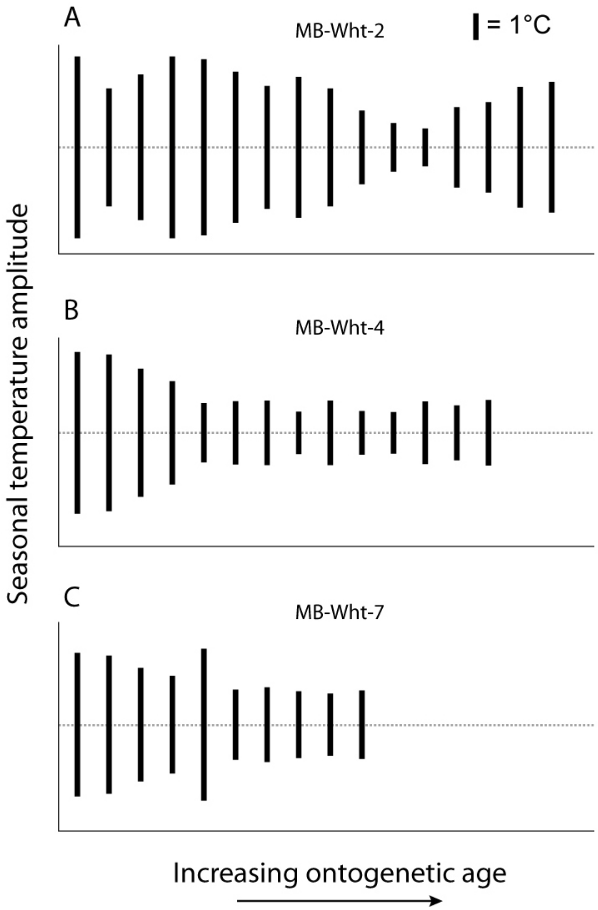

Figure 6. Seasonal shell oxygen isotope-derived temperature amplitudes (black bars) of *Glycymeris planicostalis* (**a** = MB-Wht-2; **b** = MB-Wht-4; **c** = MB-Wht-7) vary on quasi-decadal time-scales.

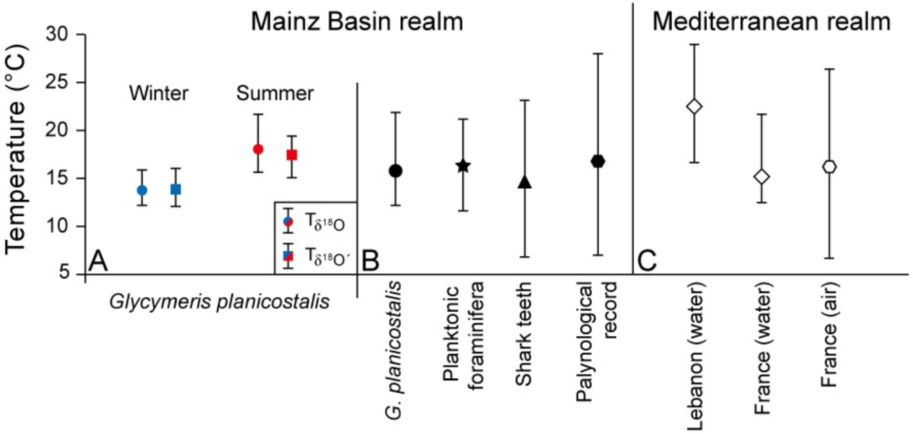

Figure 7. Seasonal temperature ranges. **(a)** Comparison between raw (circles) and mathematically re-sampled (squares) summer (red) and winter (blue) temperature data based on shell oxygen isotope data of three fossil *Glycymeris planicostalis* shells. Whereas mathematical re-sampling did not greatly affect average values and winter ranges, the summer temperature range of re-sampled data is truncated. **(b)** Comparison of the reconstructed temperature data based on $\delta^{18}O_{\text{shell}}$ values of the three studied bivalve shells (filled black circle) and previously published temperature data based on planktonic foraminifera (Grimm, 1994), shark teeth (Tütken, 2003), palynological associations (Pross et al., 1998, 2000). **(c)** Seawater temperatures in Lebanon and southern France at 35 m depth (Abboud-Abi Saab et al., 2004) and air temperatures in southern France (GHCN Montly Dataset; Lawrimore et al., 2011).

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Interactive comment on "The bivalve *Glycymeris planicostalis* as a high-resolution paleoclimate archive for Rupelian (Early Oligocene) of Central Europe" *by* E. O. Walliser et al.

Anonymous Referee #1

Received and published: 12 November 2014

The sclerochronology paper by Eric Otto Walliser and his co-authors deals with the use of fossil shells of *Glycymeris planicostalis*, a bivalve mollusk species that lived during the Oligocene, as archives of past seawater temperature in the Mainz Basin (Germany). They analysed several specimens collected in an outcrop formed 30 Ma ago for their age and stable isotope composition. They counted the number of growth increments in the hinge plate section of the shell in order to age all specimens, based on the (reasonable) assumption that these increments were formed annually (as on modern *Glycymeris* species). The three shells they worked on were 67 to 84 years old. After checking that shells were not diagenetically altered, they drilled carbonate samples in order to analyse their oxygen isotope composition. After conversion of this value into paleo-temperatures (using a $\delta^{18}O_{water}$ value reconstructed from Oligocene sirenian tooth enamel collected in the same area as shells), they concluded that these shells lived in a marine setting with seawater temperature between 12.3 and 22.0 ℃, a range typical of current conditions prevailing in modern environments such as the northwestern Mediterranean.

This manuscript is well written and definitely suitable for the readership of an international journal such as *Climate of the Past*. It presents new data for an epoch (Early Oligocene) that has been under-investigated from a climatic prospect, although climate conditions during this period were roughly similar to predictions for the coming millenia. The abstract clearly reflects and summarises the content of the paper. The state-of-the-art methods used to achieve the main goals of the paper are well described and appropriate for this kind of studies. The discussion is of appropriate size given the amount of results presented in the manuscript. Subsection 5.3 within the discussion is particularly interesting and I appreciated that the authors tried to explain the discrepancies between their $\delta^{18}O_{bivalve}$ temperature reconstruction and the paleo-temperature data provided by other archives such as teeth, forams, etc.

Nevertheless, the discussion would have benefited from some hypotheses about what drives the fall growth stop. Given the annual temperature range reconstructed from $\delta^{18}O_{bivalve}$, i.e. temperature between 13.6 (winter average) and 17.3 ℃ (summer average), it is quite unlikely that thermal stress (extreme temperatures) could explain this growth stop. I'd rather suggest that this growth stop could be formed during the main gametogenesis period of the year as this represents a high metabolic demand (energy can therefore not anymore be allocated to shell growth).

I am also wondering why the authors did not use the structural information archived in the shell in the form of growth increment width. Measurement of growth increment width in *G. planicostalis*, followed with ontogenetic detrending, would have been useful to confirm the hypothesis of a quasi-decadal oscillation in extreme temperatures. I understand that it is difficult to sample carbonate all along the outer shell cross-section, from umbo to ventral margin, and that temperature cannot be reconstructed for the whole lifespan of the animal. But extreme temperatures can also lead to changes in growth increment width. The construction of SGI (standardized growth increments) chronologies, spanning the 67–84 years of growth of each specimen, could reveal oscillations related to quasi-decadal climatic oscillation. I think this is important information, easily available, that could definitely strengthen the hypothesis of quasi-decadal climatic oscillation in the late Rupelian.

The study by Walliser *et al.* is definitely an important contribution towards a better understanding of climate conditions prevailing during the Early Oligocene. The manuscript is worthy of publication, although some issues (listed below) require further consideration. I also strongly suggest the authors to add data about growth increment width (see my comment above). To conclude, I recommend publication of this work after minor-to-moderate revisions.

- Line 15, page 4097: the average δ^{18}O$_{water}$ value calculated from sirenian tooth enamel is -0.9 ‰. A comparison with modern value would suggest that such water was typical of subpolar settings or the current Baltic Sea. But you state page 4090 (lines 24–29) that the Mainz Basin had an overall warm climate comparable to modern subtropical climate zones of the Mediterranean during the Oligocene. Today, these environments have a δ^{18}O$_{water}$ value close to 1.5 ‰. How could you explain the difference between this value and the one you calculated from tooth enamel?
- Lines 12–13, page 4087: apart from the coasts of the Baltic Sea, I cannot see any other "densely populated coastal areas and ecosystems in Central Europe". I think the coasts of Western Europe must also be mentioned are they are much longer than the Baltic shoreline of Central Europe.
- Line 17, page 4088: although I am no specialist of *Glycymeris planicostalis*, I

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hardly imagine a worldwide distribution for this species. All actual *Glycymeris* species are only restricted to relatively "narrow" geographic areas.

- Page 4089: I don't see any sound reason for excluding the section "study area" from the Material & Methods section.
- Lines 19–23, page 4089: It is relatively weird to me to read the main conclusion of the paper at the very end of the introduction. This should be deleted.
- Lines 19–22, page 4090: replace "nannoplankton" with "nanoplankton"
- Lines 4–5, pages 4091: precise what you mean with "surface waters" (upper first meter? upper 10 m?) and "bottom waters" (what depth?).
- Lines 19–20, page 4091: According to Figure 1, it actually seems that your fossils come from the paleo-coastline of the Upper Rhine Graben, and not from the southwestern shore of the Mainz Basin.
- Line 2, page 4092: delete "of" before *Glycymeris*.
- Lines 11–16, page 4093: where were the carbonate samples drilled in the shell? You sampled the equivalent of 10 to 16 years of growth whereas the specimens lived up to 84 years old. I guess you didn't sample the shell for oxygen isotope analyses close to the ventral margin, i.e. you didn't sample the last 10–16 years of shell growth. I would rather think that you sampled the ontogenetically youngest years of shell growth, i.e. the shell portions close to the umbo region. Please mention it.
- Lines 7–8, page 4094: you must provide the reader more information about the method you used to get this 0.3℃ accuracy in your temperature reconstruction. Which statistical descriptor did you use?
- Line 17, page 4095: remove bracket before Coplen.

- Lines 20–23, page 4098: you should remove these sentences as your time-series is definitely too short to identify any decadal oscillation in your records. I think all discussion about this periodicity is purely speculative.
- Line 17, page 4105: salinity must be expressed without unit (PSU, ‰, g/L). It is a dimensionless number. Remove PSU.
- Figure 2: please add information on the different photographs about their orientation.

Clim. Past Discuss., 10, C1932–C1938, 2014
www.clim-past-discuss.net/10/C1932/2014/

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Interactive comment on "The bivalve *Glycymeris planicostalis* as a high-resolution paleoclimate archive for Rupelian (Early Oligocene) of Central Europe" *by* E. O. Walliser et al.

Anonymous Referee #2

Received and published: 16 November 2014

Walliser and colleagues present 40 years of high-resolution intra-annual stable oxygen isotope data from fossil bivalves to help constrain paleoenvironmental conditions during the early Oligocene, an interval that the authors effectively argue to be an excellent analog for the near future (southern hemisphere ice only, somewhat higher CO2). Fossil shells are well preserved, beautifully prepared, and copiously sampled, yielding impressive records of seasonal isotopic variation reflecting temperatures experienced by the organisms during their ontogenies. Water composition, so as to allow for temperature calculation, is estimated from the composition of marine mammalian phosphate in the same unit. The data are compared to those from other roughly coeval taxa from the same region, and with modern semi-restricted marine settings.

While I continue to be captivated by these sorts of datasets, I am nonetheless skeptical of the degree to which you can interpret the data meaningfully in a broad paleoclimate context. The problem is that these data come from only one time slice and one place (and one taxon as well), and it is very unclear how to compare such results with data from other places, times, and taxa – for many of the reasons acknowledged in the manuscript. There are so many potential ways to make comparisons spurious, be it water depth, stratification, salinity, sampling resolution, season of shell accretion… all of these will affect seasonal extremes in isotope values, and none of them are what you want to actually study. Difficulty of comparison on equal footing is particularly true when fossil proxy data are compared to modern instrument records for SSTs. There is no way to know whether you are comparing apples to apples. This is the frustration of studies that generate data like these which are isolated in time. I find it much more useful to have the same type of data arrayed in space or time so that spatial or temporal patterns can become evident within an internally consistent dataset. Trends in the same kind of data from the same kind of environment are more robust than comparisons of snapshots of one kind with snapshots of another kind. E.g., does central Europe get less (or more) seasonal during the course of the Oligocene? Is seasonal range higher in the north than the south? By how much? Gradients are easier to compare directly with modern data, even if the mean values are not immediately comparable.

The paleotemperature estimates presented here hang upon several assumptions, not the least of which is the longstanding frustration of all oxygen isotope paleothermometry, that of the unknown composition of water. The authors argue that they can recover a reasonable estimate of water composition and that it does not vary throughout the year. There is a substantial degree of uncertainty here, which they acknowledge, but the final analysis just moves forward and doesn't really encompass or deal with that uncertainty in a systematic way. Estimating dw from the composition of sirenian phosphate is a creative solution to the water problem, but I was unable to access any of the references cited – the cited Tutken equation was only published in a thesis, in German.

Sirenians were not likely to be living/precipitating in the same water as the bivalves (nor were they collected from the same locations), as the former are in shallower water (they are benthic feeders) while the bivalves are benthic with estimated paleodepths around 30-40m, and so likely farther offshore. Sirenians would have experienced any freshwater lens in a more pronounced way than the bivalves. I also do not know the timeframe over which sirenian teeth mineralize, and so don't know how much that value could be biased from an annual average (though the reported values are fairly consistent, so encouraging). The dw estimated from sirenian teeth is -0.9 per mil, implying that the water was somewhat brackish (as global Oligocene average values are closer to -0.5). Given the 'extremely proximal' paleoenvironment and estimated dw, runoff likely contributed to the salinity of the water and salinity was likely variable throughout the year as well, as acknowledged on pg. 4088. This degree of uncertainty could shift mean temperatures by several degrees and seasonal extremes by more. Agreement with other published estimates is not enough to alleviate concerns, particularly when the published range is so great (top p. 4091); the authors argue the same later, beginning at the bottom of pg. 4101. However, Fig 7b does show good general agreement in the mean values, moreso than is apparent from the text – this should be emphasized a bit more. Is there reason to believe that similarity is more than coincidental, given the assumptions the other authors had to make as well? The seasonal range of under 4 deg C though is quite low for a mid-latitude Oligocene site, given similar published ranges from the early Eocene at lower latitudes (e.g., Sessa et al 2012).

I found myself still somewhat unclear about the main purpose of the paper after reading through it. Is the main goal to present Glycymeris as another potential skeletal archive of paleoclimate information, or to present a rigorous analysis of Oligocene climate? This should be clarified up front, and the text adjusted as appropriate to reinforce that goal. The first is certainly within range of the current manuscript, though perhaps not quite as interesting or broadly relevant as the second. The second, however, is a much more difficult proposition, and I am not convinced of the conclusions in this regard, for reasons outlined above.

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Regarding claims about interannual variation - based on the abstract, I was expecting to see a numerical analysis of interannual data to show decadal scale oscillations. But nothing was provided in the text other than the statement that seasonal ranges ‘seem to have changed periodically’. If this is all there is to it, and pattern cannot be substantiated statistically or otherwise, then it doesn’t merit appearing in the abstract. I agree it is interesting, and I have seen similarly suggestive patterns in other bivalve datasets, but that’s about all you can do with it unless there are more years in the data. I don’t think the authors should make so much of that observation. Fig 6 is perhaps not warranted.

One option to increase the power of that apparent pattern might be to at least demonstrate that the variation in seasonal range is non-random – that there are long runs of decreasing or increasing something (be it summer, winter, range, etc) that cannot be explained simply by randomly variable years. In other words, the climate system has memory. Perhaps there is some useful comparison to be made with modern shelf water temperatures in this regard. How variable are coastal temperatures from year to year in, e.g., the North Sea today, and is the pattern of variation similar in terms of amount of memory?

Another perhaps more satisfying but time intensive possibility - might there be a correlation between detrended annual increment widths and isotope values (seasonal ranges or extremes or annual temperature means) that could allow the authors to increase the number of consecutive years in their study? If width can be correlated to some climate variable in the 40 years for which there are isotope data, then there would be the potential for a longer time series if additional increments and potentially additional shells are measured. Shell records could be strung together to produce a single long composite record as well. The potential for periodic climate variation could then be statistically assessed. I’m not sure what the anticipated period driver might be – some proto NAO perhaps – but at least there would be a concrete test to compare modern pattern with the Oligocene pattern. Whether it is there or not should provide some insight, either way, about the Oligocene condition that would be directly comparable to today.

In the end, I am unclear what exactly we learn from this study as it stands about how the Oligocene compares to today. These are beautiful data, but I am unsure how to interpret them, given that I do not know to what I can meaningfully compare them, nor do I have confidence in the value and constancy of the assumed water composition, and hence temperatures. I recommend revisions to clarify the main point of the paper, tone down claims about interannual periodicity, and more fully address uncertainty associated with assumptions about water composition. If this is to be primarily a paper about Oligocene conditions, a broader context in which to discuss the results would be useful.

Some line-by-line comments are provided below:

I'd advocate plotting isotope data versus distance rather than sample number, unless the samples are equally spaced throughout. The stated 100-200 microns could be a fairly big range depending on how wide the growth increments are. It will make it easier to interpret changes in calcification rate through the year.

Were these shells sampled in the hinge or on the main valve? Not clear – can affect temporal sampling resolution.

A picture of the shell and a growth curve, might be helpful. The references to the taxon are in hard to access publications or in theses, and so the species can't be easily assessed.

p. 4092 – there are lots of references regarding Mn and other techniques for assessing preservation – cite a few of them (e.g., Grossman)

p. 4097 line 26 – 'exhibits' has extra 's'

pg 4099, line 10 – awkward wording; line 22 - Dorman and Gill 1959 is not cited in the references; line 28 – maybe more likely to simply dissolve, no?

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p. 4100, line 19 – see papers by Jones, Arthur etc on Mercenaria for a well-documented example of this

p. 4103, line 18 – this is an odd transition - the previous paragraphs are good, and clearly outline why comparisons among taxa are difficult to make - why then are the bivalve temps more robust than the rest, or the aggregate? needs a transition - maybe all estimates are robust for those taxa and individuals, but not for the goal of estimating actual SST (or benthic T) in one place all year round line 21 – not clear where these places are geographically in comparison – include them on the map, and include paleolatitudes line 25 - reverse the order of reported temps to make order the same as the Lebanon data line 26-27 - awkward wording - what is 'these thermal regimes'? Lebanon is considered subtropical here, yes? clarify

p. 4104 – I'm not entirely sure what the point of this paragraph is – it's all a pretty good stretch if precipitation is that high, because it's likely then that salinity was variable. The rationale is difficult to follow - are we comparing Olig data to places with similar basin configuration/stratification, similar latitude, or similar precip regime? All will introduce variation. A more expanded discussion of each type of comparison and what you might learn from it would be easier to follow. Similar basin types tell you that bottom water temps reflect air temp (yes?). Germany temps are more similar to France temps than to Lebanon, but both are quite a bit lower in latitude - be explicit about this and what you learn from it. Is there even a reason to mention Lebanon temps if they don't compare favorably? Then say how Oligocene Germany is thought to differ from France - it is wetter. What does this do to you expectations?

p.4106 line 3 – Sr/Ca is likely growth rate dependent – see work by Rosenthal; the end of this section is a weak way to end your discussion

The word 'noteworthy' is overused, and occasionally misapplied; 'faithfully' is also occasionally used in an odd way, e.g., 'temperatures were faithfully reconstructed' – this is difficult to determine!

The genus and species names are not used correctly – the genus has a worldwide distribution, not the species

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Interactive comment on Clim. Past Discuss., 10, 4085, 2014.

Clim. Past Discuss., 10, C2011–C2012, 2014
www.clim-past-discuss.net/10/C2011/2014/

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Interactive comment on “The bivalve *Glycymeris planicostalis* as a high-resolution paleoclimate archive for Rupelian (Early Oligocene) of Central Europe” *by* E. O. Walliser et al.

D. Surge (Referee)

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Received and published: 1 December 2014

This is a very interesting and well-written manuscript that is worthy of publication in Climates of the Past. The methods employed are well grounded, and the diagenetic assessment is thorough and convincing. I only have a few comments that I recommend be addressed before publication.

When I began reading this manuscript, I was expecting a paleoclimate reconstruction for the Early Oligocene, but when I got towards the end of the manuscript it more seemed like an evaluation of whether Glycymeris planicostalis shells are useful to reconstruct climate conditions during this time. The authors should more clearly direct

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the focus of the paper up front.

What was insolation like at this time? How similar or different was it from today? This is potentially important when suggesting that the early Oligocene climate is similar to conditions predicted for the near future.

Where on the shell were the oxygen isotope samples collected?

The authors should be careful about making statements about quasi-decadal oscillations in their data series because the intervals sampled are too short to make such an assessment.

Other minor comments:

First line on page 4092 is missing a word: From the of Glycymeris. . .

Page 4093, lines 10 and 22: Should be “oxygen isotope ratios” or “oxygen isotope composition” not “oxygen isotope values”. Fix throughout.

Page 4098, line 19: Should be . . .average maximum (summer) values. . .

Page 4099, lines 10-11: Reword the beginning of the second sentence: Not only do the shells consist of aragonite. . .

Page 4103, line 25: Reverse the order of the temperature range so that the lower value is first.

Page 4103, line 26: Should be: . . .lay well within these. . ..

Interactive comment on Clim. Past Discuss., 10, 4085, 2014.

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