Dear Dr. Dutton,

We would like to thank all three referees for their helpful comments that further increased the strength and clarity of the manuscript. We have followed almost all suggestions and revised the paper accordingly. In the following, we provide details how we have addressed the issues raised by the reviewers.

Anonymous referee #1 (AR#1)

"… 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°C (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)."

Yes, most likely annual growth line formation in this species is indeed related to the reproductive cycle. We have expanded the discussion in section 4.2 accordingly.

"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."

This is exactly what we are currently doing in close collaboration with a numerical climate modeler: analyzing SGI chronologies and comparing them to high-resolution climate models. For this purpose, we are using a much larger number of shells than in the present study. According to preliminary data, shell growth fluctuated on time scales of ca. 6 to 8 and 10 to 14 years possibly indicating the presence of some paleo-NAO (also see comment by AR#2). However, we think it would be beyond the scope of this paper to include this aspect here.

We therefore decided to lower down our tone on decadal-scale variability and rather speak of inter-annual differences in seasonality.

Line 15, page 4097: the average $\delta^{18}O_{water}$ 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 $\delta^{18}O_{water}$ value close to 1.5 ‰. How could you explain the difference between this value and the one you calculated from tooth enamel?

As we wrote in section 4.3, based on fossil assemblages, the climate of the Mainz Basin was similar to that of the modern Mediterranean Sea (= warm). This does not imply that all environmental parameters (salinity, $\delta^{18}O_{water}$) were the same. In contrast to the modern Mediterranean and Baltic Seas, the Mainz Basin experienced a strong exchange with the open ocean (here: the Nordic Seas). As a consequence, other than in the modern Baltic Sea, freshwater influx through rivers – despite higher precipitation rates ~30 Ma ago – did not have a strong effect on the isotope signature of the Mainz Basin; likewise, evaporation rates were lower than in the modern Mediterranean. This likely explains why the $\delta^{18}O_{water}$ value of the Mainz Basin (-0.9‰) was only 0.4‰ more negative than that of the open ocean during the Early Oligocene (-0.5‰). It should be added that the fauna was indicative of a fully marine environment with very little seasonal salinity fluctuations (including corals; information was added to the text).

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.

We agree and changed “Central Europe” to “Europe”.

Line 17, page 4088: although I am no specialist of Glycymeris planicostalis, I hardly imagine a worldwide distribution for this species. All actual Glycymeris species are only restricted to relatively "narrow" geographic areas.

Yes, that is true. The manuscript has been modified accordingly (genus *Glycymeris* instead of a particular species).

Page 4089: I don’t see any sound reason for excluding the section "study area" from the Material & Methods section.

The manuscript has been modified accordingly. Section 2.1 = Study area

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.

Done.

Lines 19–22, page 4090: replace "nannoplankton" with "nanoplankton"

The manuscript has been modified accordingly.

Lines 4–5, pages 4091: precise what you mean with "surface waters" (upper first meter? upper 10 m?) and "bottom waters" (what depth?).

In this sentence, we report data from the literature (recalculated with our $\delta^{18}O_{water}$ value). In the original publications, water temperatures were reconstructed from shark teeth and referred to as surface temperatures. As discussed in the text (page 4102, line 13) it is difficult to constrain the water depth in which sharks formed their teeth. However, the shark teeth belonged to a non-bottom dwelling open water species. Therefore, they have most likely recorded temperatures of the upper water column. Hence, we substituted “surface water” with “shallow water”.

The bottom water temperatures came from $\delta^{18}O$ values of foraminifera recovered from basinal sediments of the Mainz Basin (Bodenheim Formation). Water depth estimates suggest a maximum water depth of 150 m (Grimm 1994). According information was added to the text.

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.

The studied shells, originate from the outcrop “Trift” near Weinheim, which is the stratotype of the Alzey Formation, the costal facies of the Mainz Basin. In Figure 1B, we added the boundary between the Mainz Basin and Upper Rhine Graben.

Line 2, page 4092: delete "of" before Glycymeris.

Done.

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.

Samples were taken from the ventral margin. Sampling was performed in the ontogenetically youngest shell portions. Text has been changed accordingly.

Lines 7–8, page 4094: you must provide the reader more information about the method you used to get this 0.3°C accuracy in your temperature reconstruction. Which statistical descriptor did you use?

Error propagation method was applied. We averaged the precision errors of the mass spectrometric analyses of both the bivalve shells and sirenian teeth samples. Furthermore, the standard deviation of the reconstructed average $\delta^{18}O_{water}$ value was also included in the calculation of the error. Altogether, the combined temperature uncertainty is equal to ±1.3°C. The manuscript has been modified accordingly, and this information was added at the end of chapter 2.3.

Line 17, page 4095: remove bracket before Coplen.

OK

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.

The manuscript has been modified accordingly.

- *Line 17, page 4105: salinity must be expressed without unit (PSU, ‰, g/L). It is a dimensionless number. Remove PSU.*

OK

Figure 2: please add information on the different photographs about their orientation.

Figure 2 has been modified accordingly.

Anonymous referee #2 (AR#2)

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 reviewer addresses a number of fundamental issues associated with ultra-high-resolution deep-time climate reconstructions. First of all, such studies are still relatively rare, but will most likely move into the limelight of paleoclimate research, because climate varies significantly on short, i.e. seasonal to multi-decadal time-scales. If we want to understand how the future climate will likely change on time-scales relevant on a human perspective, we need to increase the temporal resolution of proxy data and numerical climate simulations. For an excellent article that illustrates why paleoseasonality data are extremely relevant for paleoclimate research and that such data are recorded in accretionary skeletal carbonates (such as bivalve shells) the interested reader is referred to Ivany (2012).

We strongly agree with AR#2 that it is necessary to extend this dataset in both space and time (and cross-check with information from other archives) in order to better understand the climate patterns of the Oligocene. Indeed, this is what we are ultimately aiming at. However, this is not in the scope of the present paper. We understand that the goals of our paper need to be defined more precisely. In the revised manuscript we explained that we first needed to lay the groundwork for ultra-high resolution paleoclimate reconstructions in the Oligocene, because there are currently no paleoseasonal archives available from that time interval. Furthermore, we emphasized more clearly that *G. planicostalis*. is a suitable proxy archive for such studies. Shells are extremely well preserved, grew during both seasonal extremes and recorded the ambient environment over many years.

As far the reliability of bivalve sclerochronological archives is concerned: undoubtedly, existing paleoclimate archives have collated a tremendous body of knowledge on climate cycles and trends in the past (e.g. Zachos et al., 2001). Yet, there are intrinsic limitations associated with the most frequently used archives. For example, temperature reconstructions based on foraminiferan test mostly rely on bulk analyses of several specimens (e.g. Lear et al., 2000; Billups and Schrag 2002). In the case of fossil foraminifera, it remains difficult to determine during which season of the year the tests were formed, how much time is represented by each shell (days, weeks) and at which water depth each shell was formed. This precludes “comparison on equal footing” with instrumental records. Most certainly, the specimens used in such bulk samples were not alive during the same year. In addition, the chemical composition of a single foraminifera test is extremely heterogeneous (e.g. Eggins et al., 2003). Paleoclimate data reconstructed from foraminifera are thus strongly time-averaged. The biggest advantage of using bivalve shells is the possibility to infer seasonal environmental amplitudes and extremes over a coherent time interval of several years or decades. A resolution of 20 samples per annual increment (= growing season) resulted in a temporal resolution of about two weeks per sample. The resampling technique ensured that similar time slices were compared to each other. In some species, the amount of time represented by each isotope sample can be further constrained by using daily microgrowth patterns. That way, a “comparison on equal footing” with instrumental records is possible.

Concerning the difficulty of interpreting the $\delta^{18}O_{shell}$ data: bivalves are sessile organisms that record environmental conditions at a given depth throughout lifetime (like a buoy). Other than many planktonic microfossils, the water depth can be estimated from the fossil assemblage. The rich benthic assemblage and the occurrence of corals suggest a water depth of 30 to 40 m for strata from which the (autochthonous) shells of *G. planicostalis* were collected (this information was added to the revised manuscript). Furthermore, these faunal elements are indicative of fully marine conditions without significant seasonal variations of salinity (and $\delta^{18}O_{water}$). At 30-40 meter depth, seasonal changes in salinity and $\delta^{18}O_{water}$ are much less pronounced than in the upper water column. Even in restricted environments which are strongly influenced by riverine discharge (e.g. Gulf of Trieste), $\delta^{18}O_{water}$ values remain stable over space and time below ca. 20 m depths (Stenni et al. 1995). Periods of stratification in the Mainz Basin have been recognized by Pross and Schmiedl (2002). However stratification only affected the deeper part of the basin, were the organic-rich pelites of the Bodenheim Formation were deposited, but not the shallow, well-mixed water bodies (Alzey Formation). We admit that our text was misleading and not precise enough.

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.

… 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 reconstruction of past $\delta^{18}O_{water}$ values via the oxygen isotopes composition of sirenian teeth is a well-established method. Many studies using this technique were published in high ranked journals (e.g. Clementz and Sewall, 2009). It is not the scope of the present paper to present a systematic discussion on the efficacy of this method. Like other large mammal teeth (e.g. Kohn, 2004), sirenian teeth are expected to mineralize continuously in a time frame of a year up to multiple years. Thus, they should record annual to multi-annual average $\delta^{18}O_{water}$ values.

We are aware of factors that could bias the annual average $\delta^{18}O_{PO4}$ values such as freshwater or physiology. For these very reasons, we used an average value of specimens from different localities.

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.

Another $\delta^{18}O_{PO4}$-to-$\delta^{18}O_{water}$ relationship for sirenians was published by Lécuyer et al. (1996). However, these authors only plotted the data without giving an equation. Furthermore, they only used four $\delta^{18}O_{PO4}$ values (three from the extant *Dugong dugon* from Djibouti and one from the extinct Arctic steller´s sea cow; using an extinct species for calibration is not ideal) and merely assumed a regional $\delta^{18}O_{water}$ value (with an assumed error range of ±0.5‰). We therefore prefer to use the equation by Tütken presented in his PhD thesis (https://publikationen.uni-tuebingen.de/xmlui/handle/10900/48514?locale-attribute=en, page 132, Fig. 73). This equation ($\delta^{18}O_p = 0,86 \times \delta^{18}O_{H2O} + 20,23$; $r^2 = 0,97$; $n = 10$) is well defined and based on the measurements of ten specimens (wild and kept in captivity) of the two extant species *Dugong dugon* and *Manatus manatus* from 4 different marine and fresh water settings covering a 10‰ range of ambient water values. For the low $\delta^{18}O$ value end member, a manatee from the Tiergarten Nuremberg, the local well water was measured, while for the other specimens ambient water values were taken from published measurements of the according water bodies in which the sea cows lived.

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.

The accompanying fauna of the studied shells clearly indicates fully marine conditions, not brackish. Furthermore, the presence of corals in that environment suggests that stenohaline conditions prevailed throughout all seasons. Even dinocyst assemblages, on which salinity reconstructions are based, clearly indicate fully marine conditions (Pross and Schmiedl, 2002). We have expanded the text in the description of the facies. Despite sirenians lived in much shallower water than the studied bivalves, the oxygen isotope values of their teeth were only 0.4 per mil more negative than the open ocean. During the Early Oligocene, the Mainz Basin/Upper Rhine Graben System was connected to open marine basins to the north and west (paleo-North Sea Basin and Paris Basin). Furthermore, based on fish communities, a connection to the Western Paratethys has been postulated (e.g. Pharisat and Micklich, 1998). A connection to the south (Tethys) is still under debate (e.g. Picot 2002, Grimm, 2006; Spiegel et al 2006). Sedimentological data indicate siliciclastic transport and water exchange between the different basins and the open ocean during the Rupelian (see Sissingh, 2003, for a schematic reconstruction of paleo-currents). All this precludes brackish conditions in the Mainz Basin (Berger et al., 2005a, b).

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 only way to test if our data are reliable or not is to compare them with published data. Temperatures reconstructed from foraminifera tests and shark teeth yield larger temperature ranges than *G. planicostalis* for reasons given in the text. The fact that our reconstructions lay within previously reported ranges further substantiates their reliability.

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).

The actual reconstructed temperature range is about 10°C, whereas 4°C is the average seasonal range of the resampled data. Mathematically resampled data smooth out seasonal extremes and should only be used for inter-annual comparisons. In Sessa et al. (2012), values were not resampled.

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.

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.

We agree that such ultra-high-resolution proxy data can only play off their full potential if combined with appropriate numerical climate models. For the studied time interval and region such models do not exist, but the current study is part of a larger research project that tackles this very question.

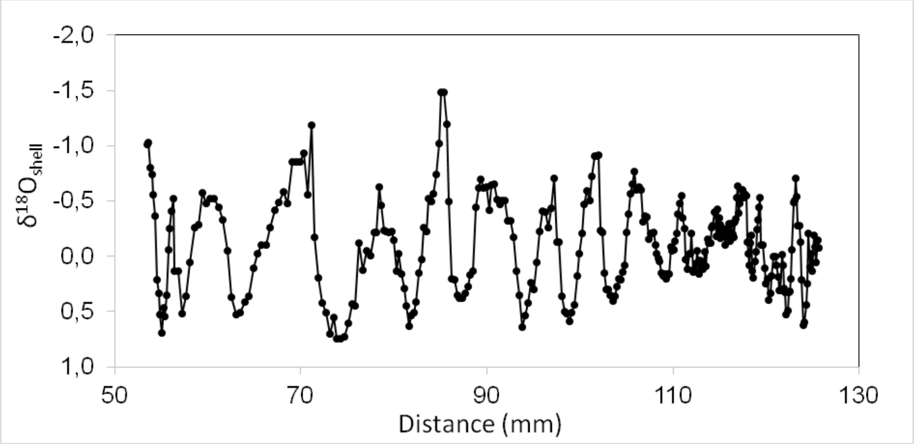
We also understand that the goals of this paper need to be better constrained. This has been done in the revised version. We refocused the manuscript on the evaluation of *G. planicostalis* as $\delta^{18}O_{shell}$-based proxy archive for seasonal temperature oscillations in the Oligocene. Furthermore, we excluded any discussion on decadal climate oscillations from the revised manuscript. In the end, we showed how to $\delta^{18}O_{shell}$-derived temperatures can be used to refine previous climate reconstructions based on other proxy archives, which have a much lower temporal resolution.

As for the suggestion to compute how SGI values and (re-sampled) isotope-derived temperature extremes are correlated, we do not think this will result in meaningful data. For a robust statistical analysis of how growth and temperature are related to each other, our isotope time-series are not long enough. As demonstrated by a recent study by Marali & Schöne (2015), the relationship between shell growth and temperature is often non-stationary. At times, the correlation can be strong and positive, at other times zero or even negative. To evaluate how the correlation evolves through time, longer time-series are essential. Also, the response of shell growth to temperature can change during ontogeny. Furthermore, as demonstrated by modern sclerochronological studies, temperature is not necessarily the main driver of shell growth rate. Food availability and food quality are often much more important.

Despite these considerations, we have done some regression analyses. Results partly meet our expectations: Only specimen #7 (ontogenetic years 6 to 15) shows a statistically significant ($p<0.05$) positive correlation with summer ($R^2=0.63$) and winter temperature ($R^2=0.23$). If only the ontogenetic years 6 to 15 are considered in the regression analysis, specimen 2 also shows a strong ($p<0.05$) positive relationship with summer ($R^2=0.43$) and winter temperature ($R^2=0.52$). The correlation in specimen 4 is not significant and very low.

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.

The aim of Fig. 4 is to show how seasonal oscillation varies from year to year. We decided to plot the data versus sample number because this representation style helps to make the inter-annual comparison easier. However, when the data were plotted versus distance, seasonal cycles would become increasingly narrow and difficult to discern (see below).



Distance plot for specimen EOW-MB-Wht-2.

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.

The shells were sampled in the ventral margin. We clarified this in the revised manuscript. In addition, we added a photograph of the entire shell to Fig. 2.

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

Grossman et al. (1996) has been added.

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

OK, deleted.

pg 4099, line 10 – awkward wording;

Sentence has been rephrased.

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

We removed the reference.

pg 4099, line 28 – maybe more likely to simply dissolve, no?

Dissolution and re-precipitation is only one way to transform polymorphs.

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

The manuscript has been modified accordingly.

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.

The manuscript has been modified to address this issue.

line 21 – not clear where these places are geographically in comparison – include them on the map, and include paleolatitudes.

The Map (Fig. 1) shows the paleogeographical settings of Europe during the Oligocene, not the modern configuration. Adding the position of the two modern localities would make things more difficult to understand.

line 25 - reverse the order of reported temps to make order the same as the Lebanon data

The text has been modified accordingly.

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?

The aim is to demonstrate how temperature information from the shell compares to previous paleoclimate reconstructions. Previous reconstructions stated that the paleoclimate conditions of the Mainz Basin were similar to areas in the southeastern, subtropical Mediterranean Sea. Our results demonstrate that the seawater was cooler than previously assumed/reconstructed. The temperature yielded by the fossil shells show that temperatures were similar to the modern northwestern Mediterranean Sea. It would be beyond the scope of this study to reconstruct the hydrological dynamics of the Mainz Basin.

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

There are several studies indicating that the incorporation of Sr (and other trace elements) into bivalve shells is controlled by a variety of different variables including biological fraction (vital effects), salinity (Wanamaker et al., 2008) etc. As demonstrated for *Arctica islandica* by one of us (BRS), after proper mathematical elimination of inherent age-trends (or growth rate related effects on Sr/Ca levels), a significant correlation exists between Sr/Ca and ambient water temperature (Schöne et al., 2010). Of course, this needs to be confirmed for *Glycymeris* spp. In ongoing tank experiments, we are currently studying this very issue with living specimens. To combine different proxies, specifically proxies from the shells, is certainly useful to further constrain $\delta^{18}O_{water}$ estimates, particularly because this was a major criticism.

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 text has been modified accordingly

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

OK, we refer to genus, not species.

Referee #3 Donna Surge

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 the focus of the paper up front.

We agree and have therefore slightly modified the Abstract and Introduction in order to better specify the goals of this study.

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.

Although this should be considered in numerical climate models, the effect is small on these time-scales. According to computer models (Crowley, 1993), the solar flux was ca. 3 to 5% lower during the early Paleozoic (450Ma) than at present. Projecting this model into the early Oligocene would result in a 0.2 to 0.3% less intense sun than today. Conversely, a 2% increase in solar flux results in a global mean temperature rise that corresponds to a doubling of atmospheric carbon dioxide (Cockell, 2007). In order to keep the Rupelian world as warm as ours would have required only a few tens of ppm higher CO_2 levels than at present. Oligocene values were ca. 400 to 500 ppm (Zachos et al., 2008).

Where on the shell were the oxygen isotope samples collected?

Samples were collected on the ventral portion of the valve (outer shell layer). This information has been added to the manuscript.

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.

We have phrased this more careful in the revised version.

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

The manuscript has been modified accordingly.

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

Here, we disagree. Delta is a value computed from ratios.

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

OK.

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

Done.

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

OK

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

OK

We hope you find our manuscript now acceptable for publication. If there are any questions, please let us know. We look forward to hearing from you.

Additional references

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The bivalve *Glycymeris planicostalis* as a high-resolution paleoclimate archive for the 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 seasonal extremes and the year-to-year variability of seasonality. To better constrain the mode and tempo of the anticipated changes, climatologists require ultra-high-resolution proxy data of time intervals in the past, e.g. the Oligocene, during which boundary conditions were similar to those predicted for the near future. In the present paper, we assess if such information can be obtained from shells of the long-lived bivalve mollusk *Glycymeris planicostalis* from the late Rupelian of the Mainz Basin, Germany. Our results indicate that the studied shells are pristinely preserved and provide an excellent archive to reconstruct changes of sea surface temperature on seasonal to inter-annual time scales. Shells of *G. planicostalis* 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 reconstructed from $\delta^{18}O_{shell}$ values assuming a $\delta^{18}O_{water}$ signature that was extrapolated from coeval sirenian tooth enamel. Reconstructed values range between 12.3°C and 22.0°C and agree well with previous estimates based on planktonic foraminifera and shark teeth. However, temperatures during seasonal extremes vary greatly on inter-annual time scales. Mathematically re-sampled (i.e., corrected for uneven number of

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samples per annual increment) winter and summer temperatures averaged over 40 annual increments of three specimens equal 13.6 ± 0.8°C and 17.3 ± 1.2°C, respectively. Such high-resolution paleoclimate 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.

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1 Introduction

Current CO_2-induced global warming is likely to result in a unipolar glaciated world ultimately followed by one 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 & 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 Europe (Ottersen et al., 2001; Stenseth et al., 2002).

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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). This applies specifically to time scales of human perception, i.e., seasonal extremes and inter-annual variability. 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

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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 inter-annual) climate dynamics during that time. The significance of Oligocene sediments from the Rhenish triple junction system was first stressed by Beyrich (1854), 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 more macrofossils than their open marine counterparts. Moreover, the shallow water depth 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). Modern *Glycymeris* spp. have recently been identified as promising tools for ultra-high-resolution climate reconstructions (Brocas et al., 2013; Royer et al., 2013; Bušelić et al., 2014). This genus occurs worldwide in subtidal settings and lives infaunally in sandy and gravelly sediments (Ansell and Trueman, 1967; Thomas, 1978). Their fossil history dates back to the Aptian (Gillet, 1924; Casey, 1961) and despite some evolutionary innovations acquired during the early Cenozoic, their fundamental *bauplan* has 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 that 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. Some bivalve species live for decades to several centuries and can therefore provide uninterrupted records of seasonality 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 analyzed the ontogenetically young shell portions of three *G. planicostalis* specimens from the upper Rupelian of the Mainz Basin, SW Germany, with

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Gelöscht: 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).

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regard to their oxygen isotopic composition in order to assess their potential as ‘deep-time’ archives of paleoseasonality. Such data are currently not available. In particular, we focused on elucidating (i) whether the shells are sufficiently well preserved to permit reconstruction of water temperatures from shell oxygen isotope data; (ii) what the timing and rate of seasonal shell growth of these specimens were; and (iii) how the seasonal $\delta^{18}O_{shell}$-derived water temperatures compare to existing temperature proxy data from that region. In order to assess the oxygen isotope composition of the local seawater ($\delta^{18}O_{water}$) in the Mainz Basin during the Rupelian we measured the phosphate oxygen isotope composition ($\delta^{18}O_{PO4}$) of the enamel of seven teeth of the sea cow *Halitherium schinzii* from the same formation as the *G. planicostalis* shells. The $\delta^{18}O_{PO4}$ value has been successfully exploited as a $\delta^{18}O_{water}$ proxy by many authors (e.g. Clementz and Koch, 2001, Clementz et al., 2006, Thewissen et al., 2007 and Clementz and Sewall, 2009). Hence, this study lays the groundwork for future ultra-high resolution paleoclimate reconstructions for the Oligocene.

2 Material and methods

2.1 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 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., late Early Oligocene; 34.9 – 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 that 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, 2005b; 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.

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(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 nanoplankton (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 nanoplankton zonation, the Alzey and Bodenheim Formations comprise the upper part of nanoplankton zone NP23 and the lower part of nanoplankton 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; Pross et al., 2000). The Mainz Basin experienced repeated alternations between drier and wetter conditions during the deposition of the Alzey Formation, which caused fluctuations in surface water salinity levels (remaining within the range of normal marine conditions) and the episodic formation of water-mass stratifications (Pross 2001; Pross and Schmiedl, 2002). 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 for shallow-water settings (Tütken, 2003) and 5.9° to 14.9°C for bottom waters (maximum depth: 150 m; Grimm, 1994; Grimm et al., 2011).

2.2 Material

The studied shell material was collected by Prof. Jürgen Boy during the 1970s and 1980s and has 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. Numerical dating with strontium isotope (^{87}Sr/^{86}Sr) stratigraphy of a well-preserved bivalve shell from the

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outcrop yielded an age of 30.1 ± 0.1 Ma (Grimm et al., 2003). The outcrop exhibits a highly diverse and fully marine benthic fauna dominated by bivalves, gastropods and scaphopods that dwelled in shallow subtidal waters. Furthermore, corals were found suggesting limited seasonal salinity changes. 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 sea cow teeth originated from four localities located along the southwestern paleo-coastline of the Mainz Basin (Fig. 1; Table 1), and were stored at the Paleontological collection of the Institute of Geosciences and the collection of the Museum of Natural History Mainz (in german: Landessammlung für Naturkunde Rheinland-Pfalz)

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2.3 Methods

From the *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.

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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 (Grossman et al., 1996; 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 & 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 (Fig. 2A-C). Then, 675 individual carbonate powder samples were micromilled from the outer shell layer (ventral margin) 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 & Co. KG, model no. 835 104 010). Sampling was performed in the ontogenetically youngest part of the shells. 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.

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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:

$$T_{\delta^{18}O}(°C) = 20.60 - 4.34 \cdot (\delta^{18}O_{shell} - (\delta^{18}O_{water} - 0.27)) \qquad (1)$$

where $\delta^{18}O_{shell}$ is measured relative to VPDB and $\delta^{18}O_{water}$ relative to VSMOW. To compute reliable temperatures from $\delta^{18}O_{shell}$ values also requires knowledge of the $\delta^{18}O_{water}$ value during shell formation. This value was reconstructed from $\delta^{18}O_{PO4}$ values of tooth enamel of sea cows, i.e., homoeothermic marine mammals, from the same stratigraphic level. The average $T_{\delta 18O}$ error was calculated by combining the average precision errors of the mass spectrometric analyses of bivalve shells and sirenian teeth (error propagation method). This resulted in an average $T_{\delta 18O}$ error of ±0.4 °C. An additional source of uncertainty is represented by the standard deviation of the reconstructed average $\delta^{18}O_{water}$ values (±0.3‰). The integration of both values results in a combined temperature error of ±1.3°C.

2.4 Sea cow teeth

The oxygen isotope composition of tooth enamel from marine vertebrates can provide information on the $\delta^{18}O_{water}$ value of ambient seawater (e.g. Lécuyer et al., 1996; Clementz and Koch, 2001; Clementz et al., 2006; Clementz and Sewall, 2009). Therefore, we measured the phosphate oxygen isotope composition ($\delta^{18}O_{PO4}$) 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. Five teeth, which were large enough, were sampled twice, one sample at top and another one at the bottom of the crown. 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 pretreated 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 calibrated in-house standards, Tu-1 and Tu-2 (Vennemann et al., 2002) and reported in δ-notation versus VSMOW. Replicate (n=6) analyses of NBS 120c (pretreated as

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the samples) yielded a $\delta^{18}O_{PO4}$ value of 21.6 ± 0.13‰ which agrees well with the value of 21.7‰ reported by Lécuyer et al. (1993) and subsequently confirmed by many other laboratories (summarized in the appendix of Chenery et al., 2010). The $\delta^{18}O_{PO4}$ 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):

$$\delta^{18}O_{water} = \frac{\delta^{18}O_{PO_4} - 20.23}{0.86} \qquad (2)$$

where $\delta^{18}O_{water}$ and $\delta^{18}O_{PO4}$ are given relative to VSMOW. We used the equation of Tütken (2003) instead the one proposed by Lécuyer et al. (1996), because the calibration of Eq. 2 is based on more sea cow specimens and covers a 3-times larger range of measured ambient $\delta^{18}O_{water}$ values. However, $\delta^{18}O_{water}$ values reconstructed using both equations yielded similar values that are statistically invariant (Tütken, 2003: -0.9 ± 0.3‰; Lécuyer et al., 1996: -0.6 ± ca. 0.8‰).

In order to assess the possibility of diagenetic alteration of the enamel oxygen isotope composition, the carbonate ($\delta^{18}O_{CO3}$) and the phosphate ($\delta^{18}O_{PO4}$) group of the enamel were plotted against each other and compared to a compilation of $\delta^{18}O_{CO3}$ vs. $\delta^{18}O_{PO4}$ pairs from extant mammals published by Pellegrini et al. (2011). The $\delta^{18}O_{CO3}$ 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 $\delta^{18}O_{CO3}$ 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):

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

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2.5 Mathematical re-sampling of intra-annual isotope data

Gelöscht: resampling

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. 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.

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3 Results

3.1 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. 2D-F). Alternately, the 1st order lamellae appear dark and bright because the higher order-lamellae are arranged in a

Gelöscht: 2A-C

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. 2G), especially in the juvenile portion of the shells. On rare occasions, these tubuli (ca. 10µm in diameter) are filled with pyrite crystals or iron oxides.

Gelöscht: 2D

Like the bivalves, the studied sirenian teeth are well preserved (Fig. 3). The $\delta^{18}O_{CO3}$ vs. $\delta^{18}O_{PO4}$ 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). Digenetic alteration of tooth enamel would in the first place have affected the carbonate-bound oxygen (Iacumin et al., 1996) and resulted in $\delta^{18}O_{CO3}$ *vs.* $\delta^{18}O_{PO4}$ 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 $\delta^{18}O_{PO4}$ values of the enamel using equation 2. On average, the $\delta^{18}O_{water}$ value of the ambient seawater was -0.9 ± 0.3‰ (1σ).

Gelöscht: pristinely

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3.2 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. 2H). 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.

Gelöscht: 2

Oxygen isotope curves of all three specimens exhibit 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 $\delta^{18}O_{shell}$ values of each cycle (Fig. 4; see Supplements). In other words, the full seasonal amplitudes are preserved in the shells including winter and summer values. The annual growth line formation occurred in late summer/early fall.

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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 $\delta^{18}O_{shell}$´ 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.

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The average annual $\delta^{18}O_{shell}$ values and seasonal $\delta^{18}O_{shell}$ 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 $\delta^{18}O_{water}$ value, this translates into total temperature ($T_{\delta18O}$) ranges of 9.7°C, 7.6°C and 7.8°C in specimens MB-Wht-2, MB-Wht-4 and MB-Wht-7, respectively. Taking the resampled values 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 (summer) values of 17.3 ± 1.2°C (1σ). Noteworthy, the seasonal amplitudes vary through time. In some years, the seasonal $T_{\delta18O}$ range was less than 2°C (Fig. 4).

Gelöscht: average value

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4 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 over a coherent time interval of several years that prevailed in the Mainz Basin ~30 Ma ago. Furthermore, the shells are pristinely preserved and their $\delta^{18}O_{shell}$ values can potentially reflect changes of ambient water temperature.

Gelöscht: 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.

4.1 Preservation

According to diagenetic screening the studied *G. planicostalis* shells are well preserved. The shells consist of pristine aragonite. Furthermore, SEM analysis revealed original delicate shell

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microstructures including the typical skeletal feature of glycymerids, i.e., microtubuli. 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 microtubuli of the studied specimens were typically hollow and only rarely contained pyrite. 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).

Gelöscht: microtubules

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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; Crippa, 2013). Since *Glycymeris* spp. dwell 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 as this is the case with the 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).

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4.2 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. Similar findings on shell growth during seasonal extremes were recently reported 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. On the contrary, 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

Gelöscht: and recorded the full seasonal amplitude of environmental variables. Such data are crucial for paleoclimate studies.

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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 (e.g., Ansell, 1968; Jones & Quitmyer, 1996).

Gelöscht: . It is therefore required to conduct thorough calibration studies prior to using shells for environmental reconstructions.

A number of explanations have been proposed to explain the reason for periodic cessation of shell growth. Temperature stress seems to limit shell growth in many bivalves. Above and below a taxon-specific water temperature range, biomineralization ceases and results in the formation of winter or summer growth lines (Jones and Quitmyer, 1996) or even both (Schöne et al., 2002). For example, *Mercenaria mercenaria* stops shell growth above 31°C and below 9°C (Ansell 1968). Following this explanation, modern *G. glycymeris* from the North Atlantic forms winter lines when temperatures fall below the tolerance limit of this species, as suggested by Royer et al. (2013). In some taxa, annual growth line formation can also be linked to the reproductive cycle. For example, *Phacosoma japonicum* from Japan not only forms winter lines, but also slows down shell growth regularly during June and July, i.e., during the peak spawning phase (Sato, 1995). Instead of biomineralizing shell, the energy is then allocated to the formation of eggs and sperms. Spawning breaks may be limited to species lacking specific tissues for energy (lipids) storage. Modern *G. glycymeris* from the North Atlantic, for example, belongs to this group of bivalves and reportedly spawns once or twice per year between spring and fall (Galap et al. 1997). In the Mediterranean Sea, *G. nummaria* spawns in July and August, followed by a sudden decrease of the condition index in late summer/fall (Crnčević et al., 2013). However, it has remained unresolved whether modern *Glycymeris* spp. can only form shell during periods of sexual inactivity. Existing studies on seasonal shell growth of this genus were based on juvenile specimens or juvenile portions of adult specimens (Peharda et al., 2012; Bušelić et al., 2014; Royer et al., 2013). Therefore, it is difficult to draw conclusions on how the reproductive cycle affects seasonal growth in (modern) *Glycymeris* spp. It is not possible to determine whether growth line formation of *G. planicostalis* was governed by reproduction or other environmental factors. At least the annual growth lines in the studied specimens from the Oligocene are unrelated to seasonal temperature extremes because the lines do not fall together with the most negative and positive oxygen isotope-derived water temperatures (Fig. 4).

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 fall and winter. This finding has implications for geochemical

Gelöscht: Early

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.

4.3 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; Pross et al., 2000). These estimates compare well with those obtained from fossil floras of other contemporaneous localities in Central Europe (Mosbrugger et al., 2005; Erdei et al., 2012).

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Knowledge on water temperatures of the Mainz Basin comes from oxygen isotope compositions of biogenic skeletons. Tütken (2003) reported $\delta^{18}O_{PO4}$ values of shark teeth that correspond to absolute temperatures between 6.9° and 23.3°C (temperatures recalculated assuming a $\delta^{18}O_{water}$ 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 that can be converted into absolute temperatures using the paleothermometry equation by Anderson and Arthur (1983) and a $\delta^{18}O_{water}$ 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°C and 22.0°C), although the lowest temperatures are ~5°C higher than those obtained from shark teeth (Fig. 6). 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:

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(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. On the opposite, each sample taken from the bivalve shells represents, on average, about two weeks to one month worth of growth. Foraminifera samples analyzed so far may not necessarily have grown when the most extreme seasonal temperatures occurred. Accordingly, actual winter temperatures may have been slightly colder and summers slightly warmer than suggested by the $\delta^{18}O$ values of foraminifera.

(ii) Seasonal temperature extremes given by sharks may not represent the actual temperatures where the bivalves lived. Being highly mobile, nektonic organisms, the sharks may have foraged temporarily 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 teeth that provided temperature estimates of 22°C may actually have been formed while the animals lived in warmer waters farther south or near the coast.

(iii) Actual sea surface temperatures during both winter and summer may have been underestimated by the planktonic foraminifera (and sharks while they resided in shallowest, coastal waters), because the assumed average $\delta^{18}O_{water}$ 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 $\delta^{18}O_{water}$ value. Increased evaporation 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. Indications for a seasonally varying $\delta^{18}O_{water}$ value come, to some extent, from sirenian teeth. Like their extant relatives, sea cows lived in the upper ten meters of the ocean and near the coast (Louise Chilvers et al., 2004). Thus, they have recorded the isotope signature of the near-coastal surface water in which the planktonic foraminifera (*Globigerina* sp.) lived. Reconstructed $\delta^{18}O_{water}$ values fluctuated between -0.2‰

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Gelöscht: 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

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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°C and 27°C.

(iv) Bivalve shell-based temperature estimates cannot be compared directly 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. At 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 benthic faunal associations of the Mainz Basin have been interpreted as reflecting paleoclimate conditions similar to those of the modern southeastern Mediterranean Sea (Grimm et al., 2003, 2011). However, temperature estimates derived from *G. planicostalis* shells suggest lower water temperatures. According to hydrographical studies from coastal regions in the northwestern Mediterranean (France) and southeastern Mediterranean (Lebanon), the temperature in 30 to 40 m water depth is still influenced by surface conditions (Abboud-Abi Saab et al., 2004). At 35 m water depth, the temperatures off Lebanon ranged between 16.9° and 29.1°C with an annual average of 22.5° ± 4.1°C (1σ), whereas the coastal waters off France ranged between 12.3° and 21.8°C with an annual average of 15.2° ± 2.2°C (1σ). Temperatures recorded by *G. planicostalis* lay well within these ranges which would suggest that water temperatures were more similar to regions in the northwestern Mediterranean than those from subtropical areas. However, the mean annual precipitation in the area of Marseille (Mediterranean coast of southern France) equals 751 ± 172 mm (Harris et al., 2014), which is considerably lower than 1000-1250 mm/a reconstructed precipitation rates for the hinterland of 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).

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4.4 Advantages of using shells of *Glycymeris planicostalis* for reconstruction of Oligocene climate conditions

The studied specimens of *G. planicostalis* offer a number of advantages over existing marine paleoclimate archives. As sessile organisms, bivalves record 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. 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 variability of winter and summer temperatures over the course of several years. Future studies should generate $\delta^{18}O_{shell}$ time-series of *G. planicostalis* that are long enough to permit spectral analyses. These data should then be combined with numerical climate models for that time. Furthermore, $\delta^{18}O_{shell}$ chronologies should also be compared to increment widths in order to identify potential influences of temperature on shell growth rates.

The $\delta^{18}O_{water}$ value 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 significant 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 (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

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Gelöscht: Otoliths are calcareous ossicles (usually aragonite) that grow in the inner ear of fish.

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Gelöscht: $\delta^{18}O_{shell}$ 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).

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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 composition 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 $\delta^{18}O_{PO4}$ value of the sirenian teeth serves as a reasonable estimate of the Rupelian $\delta^{18}O_{water}$ value (-0.9‰) of the Mainz Basin. A similar value (-1‰) was also assumed by Grimm (1994). For comparison, the $\delta^{18}O_{water}$ of the open ocean was -0.5‰ at that time (Lear et al., 2000). 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 (Eagle et al., 2013).

5 Summary and conclusions

Shells of *Glycymeris planicostalis* serve as excellent recorders of sea surface temperatures in the Mainz Basin during the Rupelian stage. Since the shells were preserved as pristine aragonite, the $\delta^{18}O_{shell}$ values can be used to reconstruct ambient water temperature. The $\delta^{18}O_{water}$ value for the temperature calculation was reconstructed using tooth enamel $\delta^{18}O_{PO4}$ values of the sea cow *Halitherium schinzii* from the same strata. 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, in which *G. planicostalis* lived, 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, even up to decades. As shown in the present study, summer and winter temperatures varied greatly from year to year. As yet, such data are hardly available from any other paleoclimate archive of the Oligocene. Such information can be highly relevant for numerical climate studies aiming to predict possible future climates in a unipolar glaciated or polar ice-free world.

Acknowledgements

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Gelöscht: seen in foraminiferan tests. Our data also revealed decadal-scale oscillations

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Figure Captions

Figure 1. Map showing the paleogeography during the Rupelian stage 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. (2007). (B) Sample locality of the shells (outcrop ‘Trift’ near Weinheim; white dot) and sea cow teeth (red dots). The presence of a western gateway (dashed area) connecting the Mainz Basin to the Paris Basin is unclear. Dashed line denotes the tectonic boundary between the MB and URG. Modified after Grimm et al. (2011). (C) Photograph of the outcrop “Trift” near Weinheim, type locality of the Alzey Formation from which the bivalves were collected.

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Figure 2. Macroscopic and microscopic views of the studied shell material (*Glycymeris planicostalis*) from the early Oligocene of the Mainz Basin. (A) Left valve. Dotted lines = cutting axis. (B) Outer and inner portions of the outer shell layer (oOSL, iOSL) as well as the inner shell layer (ISL) are clearly visible in the umbo-ventral margin cross-section (dotted line in A) of specimen EOW-MB-Wht-7. (C) Carbonate powder was collected from the outer shell layer after removing the outer chalky shell portions. Arrows point to annual growth lines. (D-G) SEM images show the extraordinary preservation state of the studied shell material. Primary microstructures are still present. (D) Outer crossed-lamellar layer, (E) inner complex crossed-lamellar layer and (F) transition zone between outer and inner shell layer (dotted lines). Arrows point to tubule openings. (G) Detailed view of a tubule. The lack of diagenetic fillings inside the cavity further supports the absence of any significant diagenetic overprint. (H) Distinct growth lines (yellow dotted lines) are visible in the hinge plate of Mutvei-stained cross-sections. DOG=direction of growth.

Gelöscht: SEM images showing the extraordinary preservation state of the

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Figure 3. Cross-plot of mammal tooth enamel $\delta^{18}O_{PO4}$ and $\delta^{18}O_{CO3}$ 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 composition of the phosphate group.

Figure 4. Raw (grey) and re-sampled (black) $\delta^{18}O_{shell}$ values for each of the three *Glycymeris planicostalis* shells analyzed 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 $\delta^{18}O_{PO4}$ values 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 temperature ranges. (A) Comparison between raw (circles) and mathematically re-sampled (squares) summer (red) and winter (blue) temperature data based

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Gelöscht: 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.

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 $\delta^{18}O_{shell}$ 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) and palynological associations (Pross et al., 2000). (C) Seawater temperatures off Lebanon and southern France at 35 m depth (Abboud-Abi Saab et al., 2004) and air temperatures in southern France (GHCN Monthly Dataset; Lawrimore et al., 2011).

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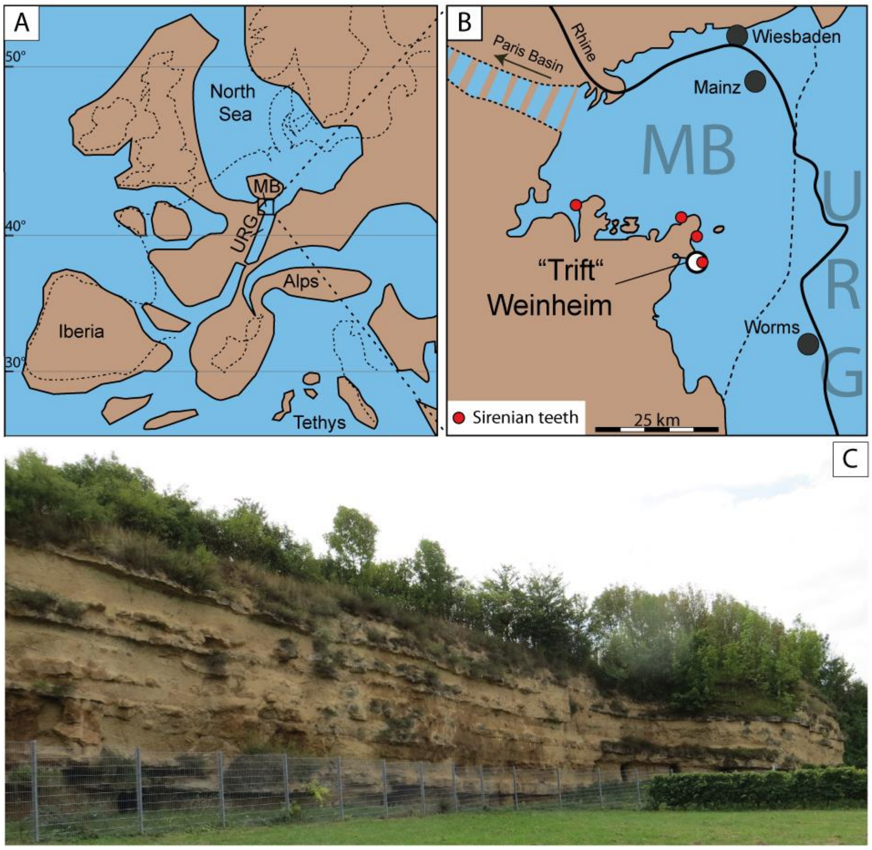

Figure 1

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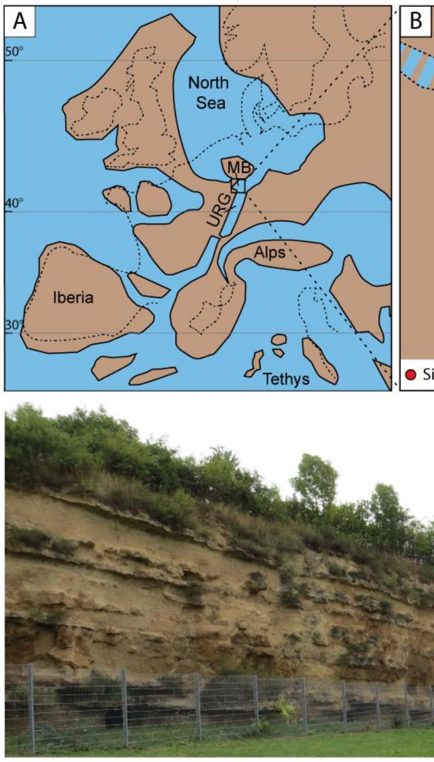

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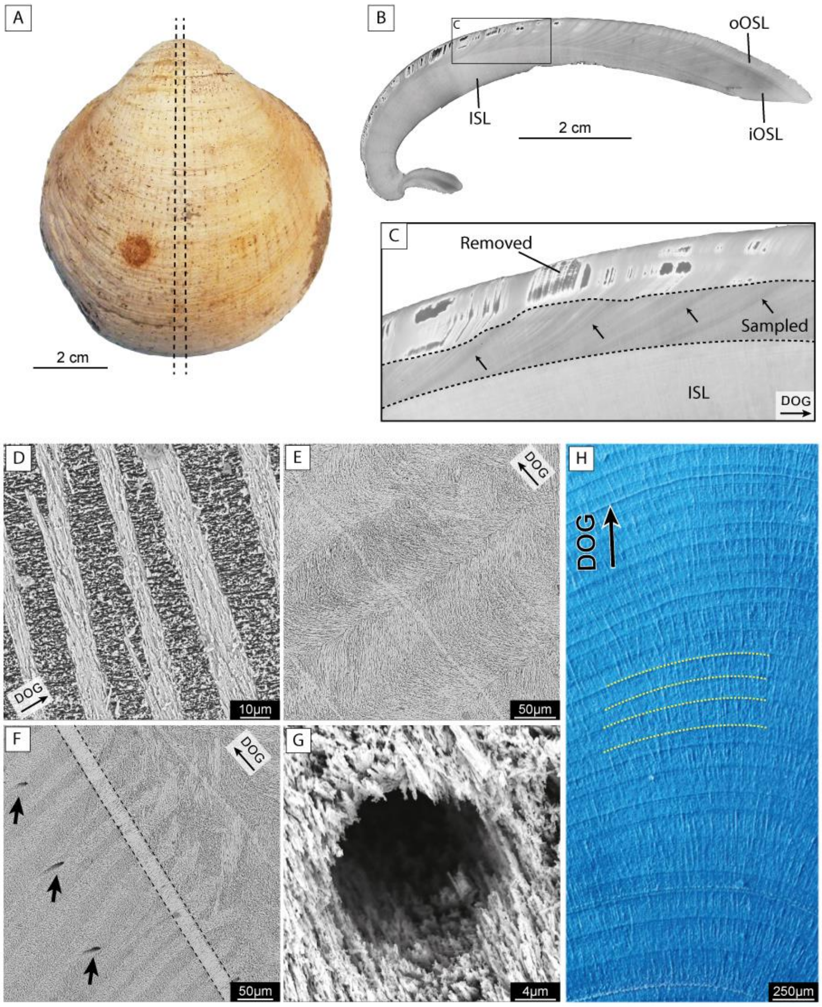
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Figure 2

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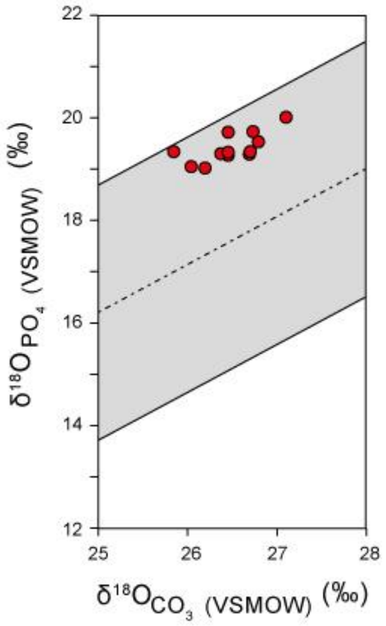
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$\delta^{18}O_{PO_4}$ (VSMOW) (‰)
$\delta^{18}O_{CO_3}$ (VSMOW) (‰)

Figure 3

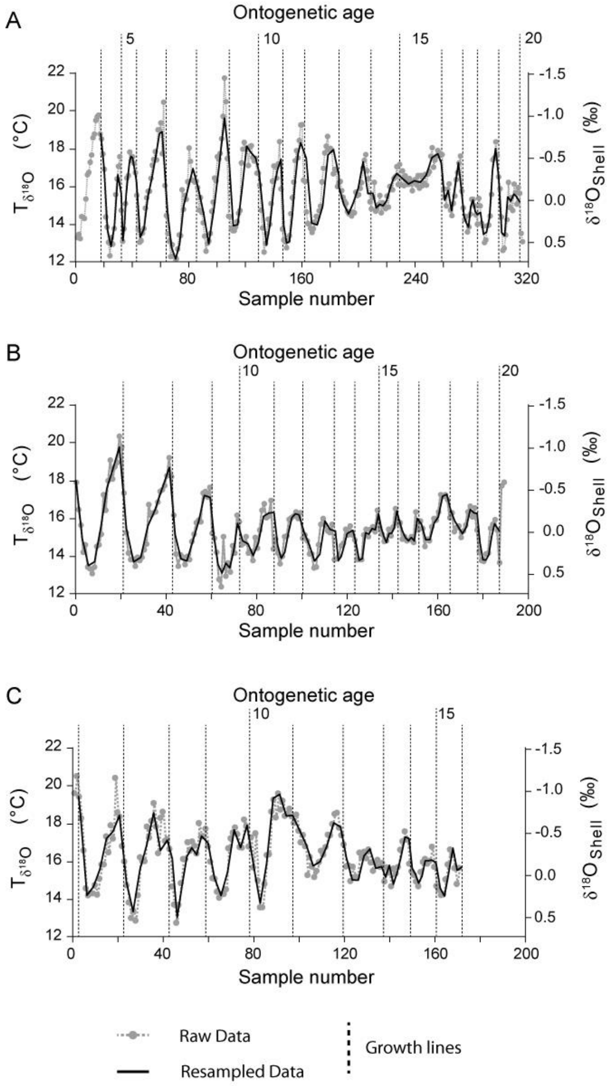
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Figure 4

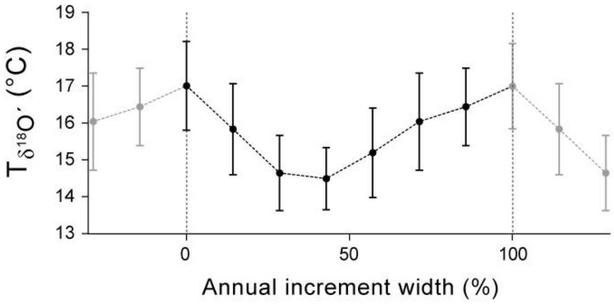
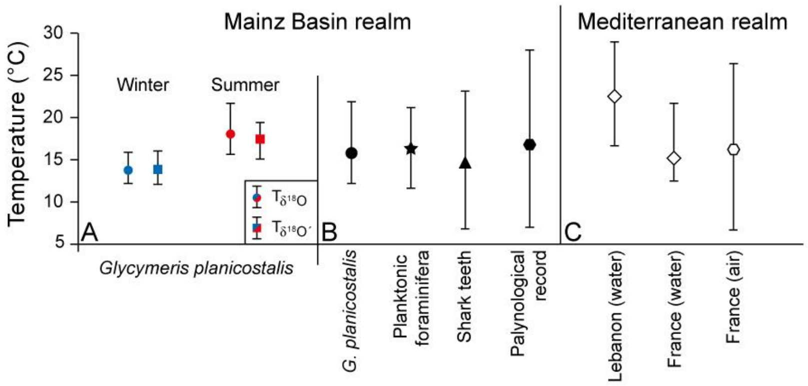


Figure 5


Mainz Basin realm
Mediterranean realm
Temperature (°C)
30
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10
5
Winter
Summer
$T_{\delta^{18}O}$
$T_{\delta^{18}O'}$
A
B
C
Glycymeris planicostalis
G. planicostalis
Planktonic foraminifera
Shark teeth
Palynological record
Lebanon (water)
France (water)
France (air)

Figure 6

Table Captions

Table 1. Enamel $\delta^{18}O_{PO4}$ and $\delta^{18}O_{CO3}$ values (VSMOW) of the sea cow teeth from the Alzey Formation deposits of the Mainz Basin and $\delta^{18}O_{water}$ values calculated from the sea cow enamel $\delta^{18}O_{PO4}$ values. See text for details.

Sample ID	Sample Locality	$\delta^{18}O_{PO4}$ [‰]	$\delta^{18}O_{CO3}$ [‰]	$\delta^{18}O_{water}$ [‰]
Trai 01-1	Traisen	19.36	25.79	-1.01
Trai 01-2	Traisen	19.04	26.14	-1.38
Eck 01-1	Eckelsheim	19.29	26.40	-1.09
Eck 01-2	Eckelsheim	19.74	26.40	-0.57
Wein 01-1	Weinheim	19.31	26.63	-1.07
Wein 01-2	Weinheim	19.36	26.64	-1.01
PW 2008/5017-LS-2-1	Alzey-Weinheim	19.32	26.31	-1.06
PW 2008/5017-LS-2-2	Alzey-Weinheim	19.55	26.74	-0.79
PW 2008/5017-LS-1B	Alzey-Weinheim	20.03	27.05	-0.23
PW 2008/5017-LS-1A	Alzey-Weinheim	19.35	26.40	-1.02
STS-BE 62-1	Eckelsheim	19.07	25.98	-1.35
PW 2005/5042-LS-1	Wendelsheim	19.75	26.67	-0.56
Average ± 1σ		19.43 ± 0.29	26.43 ± 0.35	-0.9 ± 0.3
Min		19.04	25.79	-1.38
Max		20.03	27.05	-0.23

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Gelöscht: 64
Gelöscht: 01
Gelöscht: PW 2008/
Gelöscht: -1
Gelöscht: 32
Gelöscht: 31
Gelöscht: 06
Gelöscht: 2
Gelöscht: 55
Gelöscht: 74
Gelöscht: 0.79
Gelöscht: -1B
Gelöscht: 27.05
Gelöscht: 23
Gelöscht: 20.03
Gelöscht: STS-BE 62-1
Gelöscht: 19.07
Gelöscht: 25.98
Gelöscht: -1.35
Gelöscht: PW 2005/5042-LS
Gelöscht: 75
Gelöscht: 26.67
Gelöscht: 0.56
Gelöscht: Eck 01-2
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Gelöscht: 40
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Table 2. Oxygen isotope values ($\delta^{18}O$ vs. 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

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Table 3. Dentine and enamel $\delta^{18}O_{PO4}$ values (VSMOW) of shark teeth recovered from the early Oligocene deposits of the Mainz Basin (Tütken, 2003). Values have been converted to temperature ($T\delta^{18}O_{PO4}$) using the paleothermometry equation by Longinelli and Nutti (1973) assuming $\delta^{18}O_{water}$ = -0.9‰.

Sample ID	Genus	$\delta^{18}O_{PO4}$ [‰]	$T\delta^{18}O_{PO4}$ [°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

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Table 4. Oxygen isotope values ($\delta^{18}O$ vs. 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

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