Quantifying the effect of seasonal and vertical habitat tracking on planktonic foraminifera proxies

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Key points:

- PF depth and seasonal habitat change with temperature
- PF proxy signals therefore underestimate gradients in space and time
- Depth and seasonal habitat variability can be predicted and thus accounted for

Abstract

The composition of planktonic foraminiferal (PF) calcite is routinely used to reconstruct climate variability. However, PF ecology leaves a large imprint on the proxy signal: seasonal and vertical habitats of PF species vary spatially, causing variable offsets from annual mean surface conditions recorded by sedimentary assemblages. PF seasonality changes with temperature in a way that minimises the environmental change that individual species experience and it is not unlikely that changes in depth habitat are also result from such habitat tracking. While this behaviour could lead to an underestimation of spatial or temporal trends and variability in proxy records, most paleoceanographic studies are (implicitly) based on the assumption of a constant habitat. Up to now, the effect of habitat tracking on foraminifera proxy records has not yet been formally quantified on a global scale. Here we attempt to characterise the effect on the amplitude of environmental change recorded in sedimentary PF using core top $\delta^{18}O$ data from six species. We find that the offset from mean annual near-surface $\delta^{18}O$ values varies with temperature, with PF $\delta^{18}O$ indicating warmer than mean conditions in colder waters (on average by -0.1‰ (equivalent to 0.4°C) per °C), thus providing a first-order quantification of the degree of underestimation due to habitat tracking. We subsequently use an empirical model to estimate the contribution of seasonality to the observed difference between PF and annual mean $\delta^{18}O$ and use the residual $\Delta\delta^{18}O$ to assess trends in calcification depth. Our analysis indicates that given an observation-based model parametrisation calcification depth increases with temperature in all species and sensitivity analysis suggests that a temperature related seasonal habitat adjustment is essential to explain the observed isotope signal. Habitat tracking can thus lead to a significant reduction in the amplitude of recorded environmental change. Yet the predictable nature of this behaviour allows to take it into account, enabling more meaningful reconstructions and improved data-model comparison.

1. Introduction

The chemical composition of planktonic foraminifera shells reflects the environmental conditions in which they precipitate and fossil shells serve as the prime source of information about the past state of the oceans. Planktonic foraminifera species are non-uniformly distributed across the world ocean, indicating they inhabit distinct ecological niches (Bé and Tolderlund, 1971). Indeed, such habitat preferences are routinely used for paleoenvironmental reconstruction based on fossil foraminifera assemblages. However, habitat preferences also affect reconstructions based on single species. Since, planktonic foraminifera inhabit a wide vertical range of the water column and often show distinct variability in their seasonal abundance (e.g. Field, 2004; Tolderlund and Bé, 1971; Fairbanks et al., 1980; Jonkers et al., 2010; Jonkers et al., 2013; Deuser et al., 1981), it is well-known that, rather than reflecting annual mean surface conditions, the average proxy signal in sedimentary planktonic foraminifera is weighted towards conditions at the depth and season of calcification (Mix, 1987). While species-specific seasonality and calcification depth are often taken into account, it is often implicitly assumed that both remain constant in time and space. This assumption is at odds with observations from the present-day ocean and, which likely has important implications for reconstructions of climate change and proxy calibrations based on core top data.

Plankton tow and sediment trap studies have shown large variability in the phenology within individual planktonic foraminifera species (e.g. Tolderlund and Bé, 1971; Zaric et al., 2005). A recent review demonstrated that this variability is widespread and follows a predictable pattern consistent with the concept that foraminifera (passively) track their optimum habitat (Jonkers and Kučera, 2015). Two broad ecological groups with different seasonality patterns were found; outside the tropics, warm-water species narrow their occurrence into the season of maximum temperatures. The seasonality in cold-water species also shows a clear relationship with near surface temperature as their flux peak generally occurs earlier in the year in warmer waters (Jonkers and Kučera, 2015). While the latter trend appears to be driven by the timing of food availability rather than by temperature, both patterns have the same effect on the fossil record since they reduce the amplitude of (temperature) change that bulk samples of their fossil shells will reflect.

The depth habitat of planktonic foraminifera species also shows clear variability in space and time (Field, 2004; Fairbanks and Wiebe, 1980; Schiebel et al., 2001; Peeters and Brummer, 2002; Rebotim et al., 2017). Food and light availability, (thermal) stratification and temperature have all been suggested to be potential drivers of the vertical distribution of planktonic foraminifera (Schiebel et al., 2001; Fairbanks and Wiebe, 1980; Ortiz et al., 1995; Salmon et al., 2015; Fairbanks et al., 1982). In contrast to seasonality a global overview is lacking and the exact controls on depth habitat variability within species remain poorly constrained. The issue of changing depth habitat is further complicated by the tendency that many foraminifera likely migrate in the water column during their life and add proportionally more calcite at later stages in their life, potentially resulting in a mismatch between depth habitat and calcification depth (e.g. Duplessy et al., 1981). Whereas depth habitat can be directly observed, calcification depth is generally estimated from Mg/Ca or stable oxygen isotope data and hence more uncertain. Nevertheless, depth habitat and calcification depth are related, as deeper dwelling species will also have a greater calcification depth.

Here we hypothesise that, similar to seasonality, the depth habitat and therefore calcification depth is related to temperature and that changes in temperature will lead to adjustments in depth habitat such that the environmental changes planktonic foraminifera experiences during their life cycle are minimised. The combined effect of seasonal and depth habitat tracking would be that temporal and spatial gradients in planktonic foraminiferal proxy records are reduced compared to the gradients in the mean annual value of the reconstructed parameter. For instance, in the case of temperature, it would lead to positive offsets from annual mean near-surface temperatures at times of cooling as planktonic foraminifera shift their seasonal and depth habitats to the warmer season and/or to shallower depths. The partitioning of this effect into seasonality and depth habitat likely varies by region, depending on the ratio of seasonal over vertical temperature variability in the upper water column (Fig. 1). This implies that for tropical species constraining the depth habitat will be more important than seasonality, whereas the opposite is true for species living in mid- and high latitudes.

Variability in seasonal and vertical habitat within individual species is well known and the dependency of foraminifera habitat on climate has been implicated before (Ganssen and Kroon, 2000; Mix, 1987; Mulitza et al., 1998; Jonkers and Kučera, 2015; Skinner and Elderfield, 2005). In addition, several modelling studies have investigated the potential dampening effect of seasonality (Fraile et al., 2009a; Fraile et al., 2009b; Kretschmer et al., 2016). However, surprisingly for an effect that may strongly affect proxy records, studies attempting to demonstrate the effect of habitat tracking, or the non-passive recording by foraminifera (and how to deal with the problem) are scarce. Moreover, while habitat tracking behaviour can be expected, a systematic quantification of the effect on planktonic foraminifera proxies based on observational evidence, as well as an assessment of the respective roles of seasonality and depth habitat, is lacking. Essentially, the existence of a habitat tracking effect on proxy signals in planktonic foraminifera has either been treated by attempting to derive a "correction factor" which was applied more or less uniformly (e.g. Barker et al., 2005), or by trying to detect the effect by multi-species analyses (Skinner and Elderfield, 2005). In both approaches, the most difficult aspect was to deal with the possibility of the effect of habitat tracking being variable. Here we aim to bring the issue (back) to the attention of the community, stimulate discussion and suggest some ways forward. We use core top stable isotope data to first demonstrate that foraminifera proxies are indeed affected by habitat tracking. We then show that this effect can be parametrised and assess the relative importance of variable seasonality and depth habitat. Our findings have important implications for the interpretation of paleoceanographic records and could help to bridge the gap between paleoceanographic data and model simulations.

2. Data and approach

If shifts in depth and seasonal habitat would act to minimise the change in the ambient environment of the planktonic foraminifera, then the proxy signal preserved in their shells should show an offset from mean annual values that varies with temperature. To test this conjecture we compare core top stable oxygen isotope ($\delta^{18}O$) values from different species with seasonally and vertically resolved estimates of equilibrium $\delta^{18}O$. We use quality controlled data with strict age control (chronozone 1-4) from the MARGO core top dataset (Waelbroeck et al., 2005). This dataset contains data for six morpho-species of planktonic foraminifera: *Trilobatus sacculifer* (n = 38), *Globigerinoides ruber* (white (n = 131) and pink (n = 20) varieties), *Globigerina bulloides* (n = 131), *Neogloboquadrina incompta* (n = 46) and *Neogloboquadrina pachyderma* (n = 253); the existence of different genotypes within these species was not taken into account. We exclude samples from the Mediterranean from our analysis because of difficulties of estimating seawater $\delta^{18}O$ in this evaporative basin, and removed *T. sacculifer* data from Pacific Ocean sites deeper than 3 km as these are thought to be affected by dissolution (Wu and Berger, 1989). We use the median standard deviation of replicate measurements within the dataset (0.12 ‰) as an estimate of the observational uncertainty. This value reflects analytical uncertainty as well as uncertainty associated with different integration time of each sample and selective sampling due to low and variable numbers of shells used for analysis.

We compare the planktonic foraminifera $\delta^{18}O$ ($\delta^{18}O_{foram}$) to predicted $\delta^{18}O$ ($\delta^{18}O_{eq}$) calculated using $\delta^{18}O$-temperature equation by Kim and O'Neil (1997). Calibration uncertainty is estimated from measurements on planktonic foraminifera shells from sediment traps from a period of complete mixing of the upper water column (Jonkers et al., 2013). This value (0.2 ‰) is larger than the calibration error based on laboratory cultures (Bemis et al., 1998). Following the approach of LeGrande and Schmidt (2006) we estimate seawater $\delta^{18}O$ using regionally defined salinity-$\delta^{18}O_{sw}$ relationships for the upper 200 m using the Global Seawater Oxygen-18 Database (Schmidt et al., 1999). Standard errors of prediction vary regionally and reach a maximum of 0.91 ‰ in the Arctic. Conversion from the SMOW to PDB scale was done by subtracting 0.27 ‰ (Hut, 1987). Temperature and salinity data were taken from the World Ocean Atlas 2001 (Boyer et al., 2002; Stephens et al., 2002) and area weighted averages were obtained from the four 1 degree areas surrounding each core top position.

We start with comparing the observed $\delta^{18}O_{foram}$ to annual mean $\delta^{18}O_{eq}$ for the upper 50 m as this is the depth interval where these species are most likely to calcify. To estimate the uncertainty on the relationships between predicted and observed values we use a Monte Carlo approach. Assuming a normal distribution of the uncertainty, we perform regressions on 10,000 representations of the data sampled modified within the combined range of uncertainty based on the square root of the sum of the squared errors mentioned above.

3. Results and discussion

3.1 Habitat tracking in planktonic foraminifera

The observed $\delta^{18}O$ of all species show deviations from expected mean annual $\delta^{18}O_{eq}$ by up to 3 ‰ (Sup Fig. 1). If our hypothesis of habitat tracking holds, the $\Delta\delta^{18}O$ ($\delta^{18}O_{foram}$ - $\delta^{18}O_{eq}$) should show a positive relationship with temperature. Indeed, the $\Delta\delta^{18}O_{annual.mean}$ values of the three tropical species (*G. ruber* (white and pink) and *T. sacculifer*) show a significant positive relationship with mean annual temperature (MAT; Fig. 2). The slopes vary between 0.04 and 0.14 ‰ $°C^{-1}$. In general, $\Delta\delta^{18}O_{annual.mean}$ values are close to 0 at high mean annual temperatures and negative $\Delta\delta^{18}O_{annual.mean}$ values, indicating calcification temperatures higher than annual mean, occur in colder waters. Among the cold-water species, *N. incompta* also displays a consistent positive relationship between temperatures and $\Delta\delta^{18}O_{annual.mean}$ above ~5 °C, whereas below this temperature the relationship has the opposite sign (Fig. 2). These observations at low temperature stem from samples in the Nordic Seas outside the direct path of the North Atlantic Drift. We suspect that these (partly) reflect right-coiling variants of *N. pachyderma* (Bauch et al., 2003) and we have therefore excluded them from further analysis. $\Delta\delta^{18}O_{annual.mean}$ values of *N. pachyderma* are generally positive and show an increased spread towards higher values in warmer waters (Fig. 2). *G. bulloides* is the only species that does not show any trend in $\Delta\delta^{18}O_{annual.mean}$; modal values are close to 0, but the distribution is skewed towards positive offsets (Fig. 2). This species was therefore excluded from further analyses. In summary, five of the six species analysed display a pattern in their $\Delta\delta^{18}O_{annual.mean}$ that is consistent with the hypothesis of habitat tracking acting to minimise the temperature change they experience. In all cases, the relationships are associated with substantial noise, but they are statistically significant and have similar slopes with the same sign. Such coincidence is unlikely to have arisen by chance and we conclude that the data demonstrate the existence of a variable habitat bias in foraminifera proxies, a part of which is predictable as a function of temperature.

3.2 Seasonality

Next, using simple empirical models for seasonality we assess how much of the trend in $\Delta\delta^{18}O_{annual.mean}$ could be due to changes in seasonality alone. To this end we calculate a flux-weighted $\delta^{18}O_{eq}$ ($\delta^{18}O_{season}$) for the upper 50 m of the water column using a simple seasonality model and compute $\Delta\delta^{18}O_{season}$. Based on previous work (Jonkers and Kučera, 2015) we describe the $\log_{10}$-transformed flux pattern as a sine wave of which we change the amplitude and phasing as a function of mean annual temperature. For tropical species we fix the peak in the flux in September (March in the southern hemisphere), which is generally the warmest month, and increase the amplitude linearly with decreasing temperature with a species-specific slope derived from sediment trap data (Fig. 3; Table 1). While this model does not account for the random peak flux timing at high temperatures (Jonkers and Kučera, 2015), the seasonal amplitude of the shell flux and of $\delta^{18}O_{eq}$ are very small in warm waters, and the model serves as a reasonable approximation of the seasonality pattern that characterises this species group. For cold-water species we fix the amplitude at the average value for this group (0.66) and vary the timing of the peak flux as a function of temperature (Fig. 3). Below a critical low temperature we set the peak timing to September and above a critical high temperature to March (reversed for Southern hemisphere); between these temperatures, the modelled flux pattern has two peaks a year that linearly shift towards earlier in the year in colder waters (table 2). While simple, this model represents a realistic scenario that is derived from observations and can thus be applied to the studied species. We gauge the effect of the flux weighting by determining i) the (change in the) spread of the $\Delta\delta^{18}O$ values and ii) the slope of the $\Delta\delta^{18}O$-temperature relationship. The uncertainty of the $\Delta\delta^{18}O_{season}$ values derived when using this model are initially estimated using the same Monte Carlo approach with the same error estimates as outlined above. We later test the sensitivity of the result to the parametrisation by repeating the analyses with formulations assuming stronger/weaker flux seasonality.

Accounting for seasonality using this model reduces the root means square error (RMSE) in the $\Delta\delta^{18}O$ values of *G. ruber* (pink) by 21% and the slope by 37% (Fig. 4). For *G. ruber* (white) the values are 12 and 77 % respectively (Fig. 4). Due to large positive $\Delta\delta^{18}O$ values for *T. sacculifer* at high temperatures, flux-weighting has a negligible effect on the spread in the values (1 %), but it reduces the slope by 22 % (Fig. 4). The values for *N. incompta* are 47 and 57 % and for *N. pachyderma* 16 and 51 % (Fig. 4). For none of the species this adjustment for seasonality leads to an increase in the spread of the $\Delta\delta^{18}O$ values, on the contrary, in most cases the predicted $\delta^{18}O_{eq}$ are closer to the $\delta^{18}O_{foram}$. This indicates that even by using a simple empirical model for seasonality, predictions of the fossil signal can be improved, as long as the mean annual temperature is constrained from independent data.

3.3 Calcification depth

In none of the species investigated here, the adjustment for seasonality completely removes the relationship between $\Delta\delta^{18}O_{season}$ and temperature, although in the case of *G. ruber* seasonality adjustment could remove the $\Delta\delta^{18}O$-MAT slope when the full range of uncertainties is considered (confidence intervals on slopes as shown in Figure 3 contain zero). Therefore, one may assume that at least a part of the relationship could reflect an adjustment of calcification depth. To investigate if the trends in the $\Delta\delta^{18}O_{season}$ reflect an increase of calcification depth towards the tropics, we determine the depth at which $\Delta\delta^{18}O_{season}$ is smallest and assess if there is a relationship between this apparent calcification depth and mean annual temperature. This reveals that of the tropical species *G. ruber* (pink) shows the shallowest (apparent) calcification depth, followed by *G. ruber* (white) and *T. sacculifer* (Fig. 5). All species show an increase in calcification depth with temperature (even though the scatter is large). This rules out that the relationships between $\Delta\delta^{18}O$ and temperature (Fig. 2 and 4) reflect calcification at a constant, but greater depth than in the near surface layer. Rather, this correlation is consistent with the hypothesis that planktonic foraminifera (passively) track an optimum vertical habitat. *N. incompta* has variable calcification depths that show a steep slope with temperature (Fig. 5). The positive $\Delta\delta^{18}O_{season}$ values of *N. pachyderma* indicate a calcification depth consistently below 50 m (Fig. 5).

Next we use the linear relationships between apparent calcification depth and temperature (Fig. 5) to explain the fossil signal. We thus adjust the $\delta^{18}O_{season}$ to a depth-specific signal, using the depth-temperature relationship identified earlier (Fig. 5) to calculate $\Delta\delta^{18}O_{season.depth}$. In *G. ruber* (pink) this leads to a further 50 % reduction in the RMSE and a $\Delta\delta^{18}O_{season.depth}$-temperature slope that is close to

0 (Fig. 6). In *G. ruber* (white) the reduction in the spread in the data is more modest (12 %) and so is the reduction in slope (Fig. 6). For *T. sacculifer* also only modest additional reductions are achieved: 8 and 11 % for RMSE and slope, respectively (Fig. 6). Among the cold-water species *N. incompta* shows the clearest relationship between $\Delta\delta^{18}O_{season.depth}$ and temperature and adjustment for calcification depth yields a reduction of the RMSE of 8 and of the slope of 46 %, which is now within the uncertainty range of 0 (Fig. 6). In *N. pachyderma* no further reduction in the slope is achieved and the RMSE decreases by 22 %.

3.4 Seasonality vs. depth habitat

Our analysis allows assessing the relative contribution of seasonality and calcification depth change in explaining the variable $\Delta\delta^{18}O_{annual.mean}$ for species where temperature seems important for determining their habitat. In general, the improvement of the prediction of the $\delta^{18}O_{foram}$ is larger for the slope of the $\Delta\delta^{18}O$-temperature relationship than for the spread in the $\Delta\delta^{18}O$ values (Fig. 7). This may point to some degree of inherent noise in the observations (e.g. related to different size fractions used for the measurements (Friedrich et al., 2012)), or it could also be due to uncertainty in the $\delta^{18}O_{eq}$ values, which are based on climatology and salinity-based estimates of $\delta^{18}O_{sw}$. Moreover, the noise may also reflect the simplicity of the seasonality model we have used. Nevertheless, *G. ruber* (pink) and *N. incompta* show coherent behaviour with respect to both parameters (Fig. 7). For *N. incompta* seasonality explains most of the trend in $\Delta\delta^{18}O_{annual.mean}$, whereas for *G. ruber* (pink) depth habitat appears more important. This is consistent with their distribution: *N. incompta* predominantly inhabits high and mid latitudes where seasonal temperature change is larger than vertical temperature gradients and *G. ruber* (pink) is restricted to the tropics where the opposite situation prevails (Fig. 1). This pattern provides support for our approach and suggests that both seasonality and depth habitat variability are important for interpretation of the proxy signal preserved in the sediment. The picture is less clear for *G. ruber* (white) and *T. sacculifer*. For the latter species the improvement in the prediction of their $\delta^{18}O$ is generally smaller, which may be due to a remnant dissolution signal at the high temperature end of the species distribution in the Pacific. For *G. ruber* (white), the signal/noise ratio in the data appears lower than in the other species, which may reflect a disproportionate effect of secondary variables, such as changing proportionality and inconsistent recognition of the ecologically distinct morphotypes (Steinke et al., 2005) that are now assigned to different taxa (Aurahs et al., 2011).

An important caveat in the attribution of the improvement in the prediction of the fossil proxy signal to either seasonality or calcification depth is the form and parametrisation of the seasonality model used. We have explored the sensitivity of our model to changes in the slope and intercept of the flux amplitude-temperature relationship (Sfig. 2). This suggests that the formulation of seasonality in our model is conservative: weaker seasonality parametrisation leaves much larger residuals and a slope that cannot be accounted for by depth habitat adjustment. However, we note that in the case of *G. ruber* pink there exists a parametrisation of flux seasonality that leads to a greater improvement in the prediction of $\delta^{18}O_{foram}$ and implies a constant habitat depth adjustment. However, we feel that the parametrisation based on actual data (Jonkers and Kučera, 2015), even if conservative, is the most realistic. It is also important to realise that the sine wave as a template for the seasonal flux pattern is only an approximation and seasonal flux pulses are often narrower and more focussed, leading to flux-weighting to a shorter period within the year. This too implies that the model used here, is a conservative estimate of the importance of seasonality.

Furthermore, implicit in our approach is the assumption that planktonic foraminifera form their skeleton accordance with inorganic calcite precipitation and that their $\delta^{18}O$ can be described using the equation by Kim and O'Neil (1997). While this appears to be the case for some species (Jonkers et al., 2010; Jonkers et al., 2013; Loncaric et al., 2006), there are also indications that, in particular for tropical species, different equations are more appropriate (Mulitza et al., 2003; Spero et al., 2003). Species-specific paleotemperature equations proposed by the latter authors have a non-quadratic form, but almost identical slopes as the Kim and O'Neil (1997) equation yet are offset by 0.3-0.6 ‰, with the offset slightly increasing with temperature. For instance, using the Mulitza et al. (2003) equation for *T. sacculifer* would lead to more positive $\Delta\delta^{18}O_{annual.mean}$ values and slightly steeper $\Delta\delta^{18}O$-temperature relationships (Fig. 8). This suggests a generally greater calcification depth and would change the attribution of depth habitat and seasonality influence, rendering depth habitat more important (Fig. 7). However, it would not affect our main conclusion that the proxy signal of planktonic foraminifera is affected by habitat tracking.

3.5 Additional factors affecting foraminifera proxies

Five out of six species analysed show a temperature dependency of the offset between $\delta^{18}O$ of the foraminiferal shells and the annual mean $\delta^{18}O$ of the upper water column (Fig. 2). In addition, these species show a positive relation between apparent calcification depth and temperature (Fig. 5). Together, these observations provide a strong indication that temperature, either directly or by acting on other temperature-related variables, causes changes in the habitat of foraminifera. Such an important role for temperature in predicting the vertical and seasonal habitat is not unexpected given that temperature appears to be strongly correlated to the spatial distribution of species (Morey et al., 2005; Bé and Hutson, 1977), their flux (Zaric et al., 2005) and seasonality (Jonkers and Kučera, 2015) and appears important for test growth (Lombard et al., 2009).

Several studies have shown that formation of secondary calcite layers (e.g. gametogenic calcite or a crust) at the end of the life of a specimen. Such encrustation could in principle affect our interpretation, since encrustation presumably occurs deep in the water column and could be responsible for higher $\delta^{18}O$ of sedimentary foraminifera compared to those collected in the upper water column (Duplessy et al., 1981; Bé, 1980). To the best of our knowledge there is no evidence that such secondary calcite is formed with a different isotopic (dis)equilibrium than the lamellar calcite. We therefore assume that our inferences are not affected by differences in calcification during ontogeny. Nevertheless, the addition of such a crust in deeper (colder) waters could in principle lead to the observed increase in apparent calcification depth with temperature because of steeper vertical temperature gradients in the tropics. However, foraminifera shell mass increases exponentially during growth and the last chambers that make up most of the test mass are formed in the last few days of their life, presumably close to the time of the secondary calcite formation (Bé, 1980). The compositional contrast between the bulk of the lamellar calcite and the crust calcite is thus likely to be smaller than estimated from the comparison of surface tows and sediment (cf. Jonkers et al., 2016). Consequently, the apparent calcification depth we infer here likely incorporates this effect and the increase in apparent calcification depth that we observe most likely reflects habitat adjustment.

Besides temperature and $\delta^{18}O_{seawater}$ the $\delta^{18}O$ of foraminiferal calcite is to a lesser degree also influenced by the CO_3^{2-} concentration in seawater (Spero et al., 1997). Because of the generally positive correlation between temperature and $[CO_3^{2-}]$ in seawater, the trends we observe in $\Delta\delta^{18}O_{annual.mean}$ (Fig. 2) could be dampened by a CO_3^{2-} influence. However, the CO_3^{2-} effect is only modest (0.002 ‰ μmol^{-1} kg^{-1}) and to fully account for the on average 1‰ difference we observe over the temperature range in our dataset, unrealistically large gradients in $[CO_3^{2-}]$ would be required. The observed $\Delta\delta^{18}O$-MAT trends thus most likely dominantly reflect real changes in the habitat of planktonic foraminifera.

While the majority of the species investigated here show clear indications of temperature-dependent depth and seasonal habitat variability, the picture for *N. pachyderma* is less clear. In the species most of the trend in $\Delta\delta^{18}O_{annual.mean}$ values appears driven by an increased spread in $\Delta\delta^{18}O$ at higher temperatures (Fig. 2). Some of these values are unrealistically large and stem from observations in the northern North Atlantic south of 50° N, thus outside the general distribution range of the species. This suggests that these observations may reflect expatriated specimens that calcified in colder regions or may point to inaccuracies in the chronological control and reflect (partly) shells of glacial age. Alternatively, these samples could be affected by admixture of sinistrally coiled *N. incompta* (Darling et al., 2006). It is puzzling though that the effect of seasonality is not larger since the species shows a clear latitudinal shift in the timing of the peak flux (Jonkers et al., 2010; Jonkers et al., 2013; Jensen, 1998; Wolfteich, 1994; Kohfeld et al., 1996). However, the species is also known to inhabit a broad, but generally deeper, zone of the upper water column (Carstens et al., 1997; Pados and Spielhagen, 2014) where seasonal temperature is smaller than in the near surface layer, possibly rendering a seasonality effect difficult to detect.

Even though the absence of a $\Delta\delta^{18}O_{annual.mean}$-temperature trend in *G. bulloides* may suggest that this species holds the best promise of providing reconstructions of mean annual near surface conditions

(Fig. 2), its $\Delta\delta^{18}O_{annual.mean}$ is noisy, suggesting that caution is required to interpret the species proxy signal. Similar to *N. pachyderma* this species also shows clear latitudinal changes in seasonality (Jonkers and Kučera, 2015; Tolderlund and Bé, 1971). However, *G. bulloides* is characterised by considerable cryptic diversity (Darling and Wade, 2008). Possible genotypic ecological differences could therefore obscure ecological patterns at the morphospecies level. Alternatively, being an opportunistic species, depth and seasonal habitat variability of *G. bulloides* may be driven by other parameters than temperature. Indeed, previous studies have shown that the distribution of this species is driven by food availability (Schiebel et al., 1997; Jonkers and Kučera, 2015). Whether or not the species shows habitat tracking and how this would affect its fossil record remains unclear, but we caution that the result of our study cannot be taken to indicate that proxy records from this species record the actual magnitude of environmental change.

3.6 Implications and outlook

Habitat tracking behaviour of planktonic foraminifera has important implications for paleoceanographic reconstructions. For example, it implies that the temperature niche of planktonic foraminifera inferred from their abundance in the sediment (e.g. Kucera, 2007) may be overestimated since their occurrence is not related to mean annual sea surface temperature, but rather by whether their temperature niche is realised at any depth or season. It should thus be possible to define planktonic foraminifera temperature ranges (sensitivity) more precisely, which may help to improve transfer functions and is important for understanding of their ecology.

Another consequence of habitat tracking is that spatial and temporal differences reflected in the sedimentary foraminifera represent an underestimation of the actual gradients in the mean conditions, because temperature change forces the foraminifera to live in a seasonal or vertical ‘window’ where conditions are closest to optimal (cf. Jonkers and Kučera, 2015). We observe considerable variability in the slope of the $\Delta\delta^{18}O_{annual.mean}$-temperature relationships, but the average for the four species that show the clearest signal (*G. ruber* (pink and white), *T. sacculifer* and *N. incompta*) is 0.1 ‰ $°C^{-1}$ (Fig. 2). This is equivalent to a 40 % (0.4 $°C\ °C^{-1}$) underestimation of reconstructed temperature change.

It is important to note that habitat tracking would not only affect stable isotope records and Mg/Ca-based temperature estimates, but any geochemical proxy based on planktonic foraminifera. However, the size of the effect will depend on the magnitude of the seasonal and vertical gradients in the parameters that are inferred. Recognising habitat tracking and deconvolving the effects of seasonality and calcification depth in data from the fossil record is however not straightforward. For instance, minor changes in mean temperature may be accommodated by changes in the habitat of foraminifera and remain invisible. Nevertheless, the existence of habitat tracking related underestimation can be observed through comparison of time series of different temperature proxies. Previous studies have shown that Holocene temperature trends and temperature variability inferred from foraminiferal Mg/Ca ratios are generally of lower magnitude than those derived from alkenone unsaturation indices (Gill et al., 2016; Leduc et al., 2010). While it is not a priori clear that the alkenone signal is unaffected by seasonal habitat variability of coccolithophores (Rosell-Melé and Prahl, 2013), this comparatively low variability inferred from planktonic foraminifera proxies provides support that habitat tracking minimises amplitude of the recorded environmental change. Comparison of Mg/Ca-derived and transfer function based temperature evolution across the deglaciation provides further indications that habitat tracking dampens the foraminifera proxy signal (Fig. 9). While both proxies indicate a clear warming step during the deglaciation, the amplitude of the Mg/Ca-based estimate is significantly lower. In addition, the single species Mg/Ca-temperature estimate lacks the smaller cooling and warming trends seen in the transfer function-based estimate during the glacial and Holocene respectively. Using the linear $\Delta\delta^{18}O_{annual.mean}$-temperature relationships (Fig. 2) we also predicted the *G. ruber* (pink) temperature signal assuming that the assemblage-based temperatures represent an accurate estimate of mean annual temperature and using a conversion from $\delta^{18}O$-temperature sensitivity of 0.25 ‰ $°C^{-1}$ (Fig. 9). The high degree of agreement between the predicted and observed temperature evolution provides quantitative support for the idea that habitat tracking reduces the amplitude of the foraminifera proxy signal.

Accounting for the dampening effect due to habitat tracking would likely increase the magnitude of reconstructed climate change as well as estimates of climate variability on longer time scales. This could have profound implications for inferred climate dynamics; it may mean, for instance, that estimates of climate sensitivity (e.g. Snyder, 2016) may be too low (or at least that the uncertainty of the estimate can be reduced). In addition, model-data comparison indicates that climate models systematically underestimate temperature variability (Laepple and Huybers, 2014), which has implications for both attribution of ongoing climate change as well as for climate predictions. Since habitat tracking dampens variability in the foraminifera proxy record, the mismatch between modelled and reconstructed climate variability may be even larger.

Several approaches are possible to account for underestimation due to habitat tracking. Ideally, several approaches should be combined – and their consistency checked - to arrive at the most accurate reconstruction of past climate associated with the most meaningful estimate of the uncertainty. The approaches range from very simple and widely applicable to more sophisticated, but harder to apply as they require more input parameters to model the foraminifera habitat.

The simplest would be to use the observed slopes of $\Delta\delta^{18}O_{annual.mean}$-MAT relationships (Fig. 2) to correct the dampening effect. This approach can be applied to any single-species planktonic foraminifera proxy time series without the need for additional data. However, it is a 'black box' method that relies on parametrisation derived from core top observations, and it may not work under oceanographic conditions, which are not represented today. Nevertheless, the similarity between the Mg/Ca signal of *G. ruber* (pink) and the prediction based on the annual mean reconstructed temperature in the example in (Fig. 9) suggest that this method provides a useful first-order approximation of the actual amplitude of temperature change.

Alternatively, multi-proxy and/or multi-species approaches can be applied to observe offsets between species and proxies and use this information to directly constrain the variable habitat bias (e.g. Skinner and Elderfield, 2005). To use this method to correct for the variable bias, better constraints than currently available on the calibration of the individual proxies are needed. This is because most proxies are affected by multiple parameters, rendering a multi-proxy (or multi-species) dataset underdetermined. In this context, a potential shortcut could be to build on the central premise of assemblage transfer functions, i.e. that a species becomes rarer further away from its optimum habitat, and investigate whether relative abundance can be used to correct for habitat tracking. This approach integrates all the environmental forcings contained in fossil assemblages and it would provide estimates of habitat tracking independent of the reconstructed parameter.

Finally, habitat tracking could be accounted for using direct proxy modelling. This approach requires a priori knowledge of the habitat predictor(s) and their change through time, rendering it particularly suitable for comparison of climate model simulations with proxy data. However, if the predictor can be reconstructed independently, the approach could, in theory, also be used in purely proxy-based studies. An early example of this approach is the conceptual model of Mix (1987). In this study, we build on an empirical parametrisation of flux seasonality using temperature as the single predictor and derive a likely habitat depth parametrisation. This is a simplification that could be outcompeted by more complex ecological models that take multiple factors affecting foraminifera habitat into account (Lombard et al., 2011; Fraile et al., 2008).

4. Conclusions

Through comparison of observed and predicted $\delta^{18}O$ data of six common planktonic foraminifera we have demonstrated that the average geochemical signal preserved in a population of fossil shells shows a temperature-dependent offset from mean annual sea surface conditions. This most likely reflects shifts in the seasonal and depth habitat in response to temperature, or temperature-related environmental, changes (Fig. 9). As a consequence of this behaviour, the fossil record of these species, and likely also of others, does not reflect the full range of climate variability. Our analysis indicates that spatial and temporal gradients in temperature may be underestimated by as much as 40 %, highlighting the need to account for climate-dependent habitat variability in the interpretation of paleoceanographic records based on planktonic foraminifera. Using a simple empirical model we attempted to assess the relative influence of seasonality and depth habitat variability. While improvements to this empirical approach are possible, we observe species-specific partitioning of depth habitat versus seasonality that appears consistent with oceanographic conditions within their areal distribution. In the tropical species *G. ruber* (pink) we find that habitat tracking is primarily due to adjustments in the calcification depth. This is in agreement with the larger vertical than seasonal temperature gradients in the tropics. The offsets from annual mean surface conditions in *N. incompta*, on the other hand, appear dominantly driven by changes in the seasonality, consistent with the dominance of seasonal over vertical temperature variability in the regions where it occurs. Our analysis emphasises that an observed change in planktonic foraminifera proxies reflects a change in the climate state as well as a change in the species habitat. Finally, the recognition of predictable habitat tracking will help to improve the accuracy of paleoceanographic reconstructions and aid model-data comparison.

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Tables

Table 1: temperature-amplitude relationships for the modelled flux pattern of tropical species based on Jonkers and Kucera (2015).

Species	intercept	slope
G. ruber (pink)	2.16	-0.07
G. ruber (white)	0.99	-0.02
T. sacculifer	0.85	-0.02

Table 2: critical temperatures (°C) that determine the phasing of the shell flux of cold-water species. Between these two temperatures the flux pattern is characterised by two peaks a year that shift as a function of temperature to earlier in the year in warmer water (Jonkers and Kučera, 2015).

Species	T.crit.lo	T.crit.hi
N. incompta	9	15
N. pachyderma	-5	7

Figure captions

Fig. 1: Distribution of core top $\delta^{18}O$ data used in this study. Background colours represent the $\log_{10}$-ratio of the temperature range at the surface to the temperature range in the annual mean values between 0 and 200 m depth. Blue colours thus indicate areas where seasonal temperature gradients are larger than vertical gradients and red colours indicate the opposite. The thin black contour line shows the zero level of this ratio.

Fig. 2: Temperature dependent offsets between predicted annual mean near surface and observed $\delta^{18}O$ ($\Delta\delta^{18}O_{annual.mean}$), suggesting habitat tracking. All species except *G. bulloides* show a trend in $\Delta\delta^{18}O_{annual.mean}$ values with mean annual temperature in the upper 50 m ($MAT_{0\text{-}50m}$) of the water column suggesting that planktonic foraminifera adjust their habitat to minimise temperature change in their environment. Histograms show the spread in the $\Delta\delta^{18}O_{annual.mean}$ values. The root mean square error (RMSE) and the linear slope (m ± 90 % confidence interval) of the $\Delta\delta^{18}O$-temperature relationship are indicated in the upper left corner of each panel. The uncertainty envelopes depict the 5 to 95 percentile of the uncertainty on the MAT- $\Delta\delta^{18}O_{annual.mean}$ relationships, which are indicated by the solid black line. The grey dots in the panel for *N. incompta* show the data that are excluded from further analyses as they most likely stem from right-coiling morphotypes of *N. pachyderma*.

Fig. 3: Schematic representation of the seasonality model. Upper panels show the annual flux patterns; colours indicate temperature, where blue is cold and red is warm. Lower panels show the timing of the peak in the year. For a more detailed explanation of the model see section 3.2 and tables 1 and 2.

Fig. 4: Offset between flux-weighted predicted using the seasonality model depicted in Fig. 3 and observed $\delta^{18}O$ ($\Delta\delta^{18}O_{season}$). Grey symbols represent $\Delta\delta^{18}O_{annual.mean}$. Note the general reduction in the spread of the data (RMSE) and slopes of the $\Delta\delta^{18}O_{season}$-temperature relationship (m) approaching 0,

compared to $\Delta\delta^{18}O_{annual.mean}$ (Fig. 2), suggesting that seasonal habitat tracking partly explains the trends shown in Fig.2. Error envelope as in Fig. 2.

Fig. 5: Relationship between apparent calcification depth (ACD) and temperature. Data are summarised in 2-degree bins and error bars represent standard deviations within each bin. The data points at the cold temperature end of *G. ruber* (white) are excluded since these are more likely to reflect outliers or advected specimens.

Fig. 6: Offset between seasonality and depth adjusted $\delta^{18}O_{eq}$ and $\delta^{18}O_{foram}$. In most cases both the RMSEs and the $\Delta\delta^{18}O$-temperature slopes are reduced indicating further improvement in the prediction of foraminifera $\delta^{18}O$ and suggesting that the simple empirical parametrisation of habitat variability can be used to correct for habitat tracking. Grey symbols represent $\Delta\delta^{18}O_{season}$; error envelopes as in Fig. 2.

Fig. 7: Partitioning of the improvement in the prediction of the fossil $\delta^{18}O$ signal into seasonality and depth habitat for both RMSE of $\Delta\delta^{18}O$ and the slope between $\Delta\delta^{18}O$ and $MAT_{0\text{-}50m}$. Colours denote species and the size of each dot is proportional to the total improvement achieved. The open circles illustrate the partitioning for *T. sacculifer* using the paleotemperature equation of Mulitza et al. (2003).

Fig. 8: Assessing the effect of the use of a different paleotemperature equation. The panels show the same as Fig. 2, 4, 5 and 6 respectively, but for *T. sacculifer* and using the equation of Mulitza et al. (2003). Note that the basic patterns indicative of habitat tracking remain, but that the general calcification depth appears greater, also at lower temperatures.

Fig. 9: Effect of habitat tracking: reduced magnitude of deglacial temperature change estimated from Mg/Ca of *G. ruber* (pink) (Elderfield and Ganssen, 2000) compared to faunal assemblage based seasonal temperature estimates (Chapman et al., 1996) in the subtropical North Atlantic. The predicted *G. ruber* (pink) temperature, which is similar to the Mg/Ca temperature, is based on the

relationship identified in Figure 2 and the assemblage-derived temperatures. Values are anomalies with respect to the 0-10,000 years BP average.

Fig. 10: Conceptual model of calcification habitat change for warm and cold-water species. The coloured plane indicates the average calcification season and depth as a function of latitude. Dashed lines on top highlight the change in the seasonality.

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Fig. 1

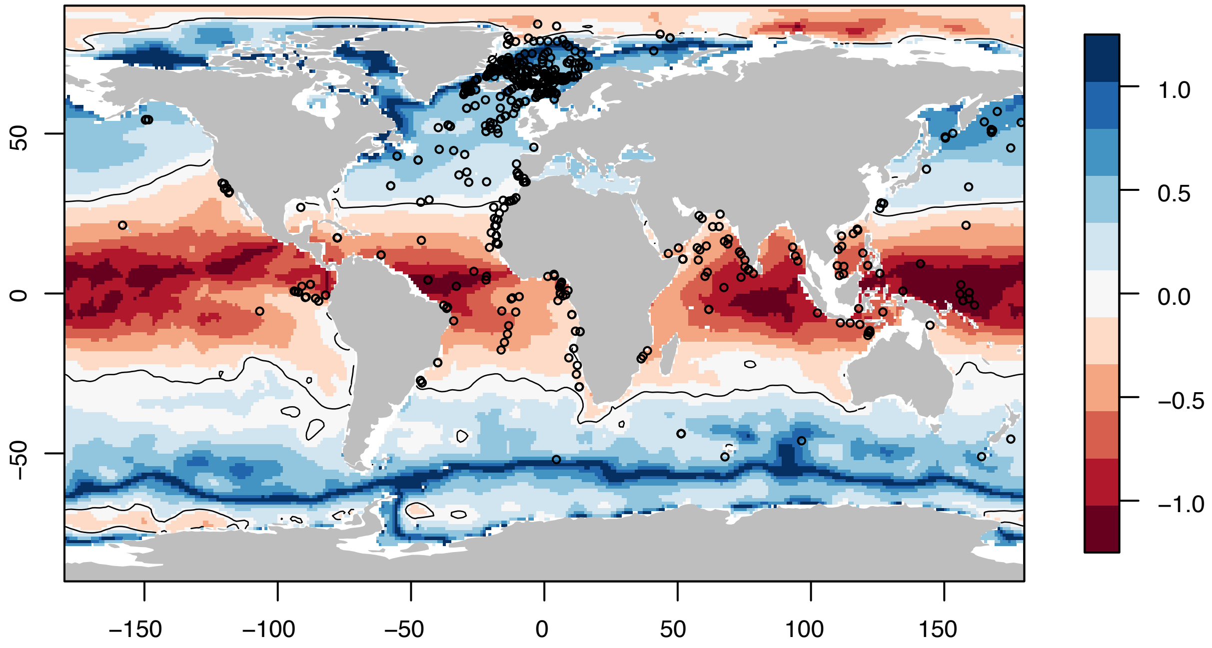


Fig. 2

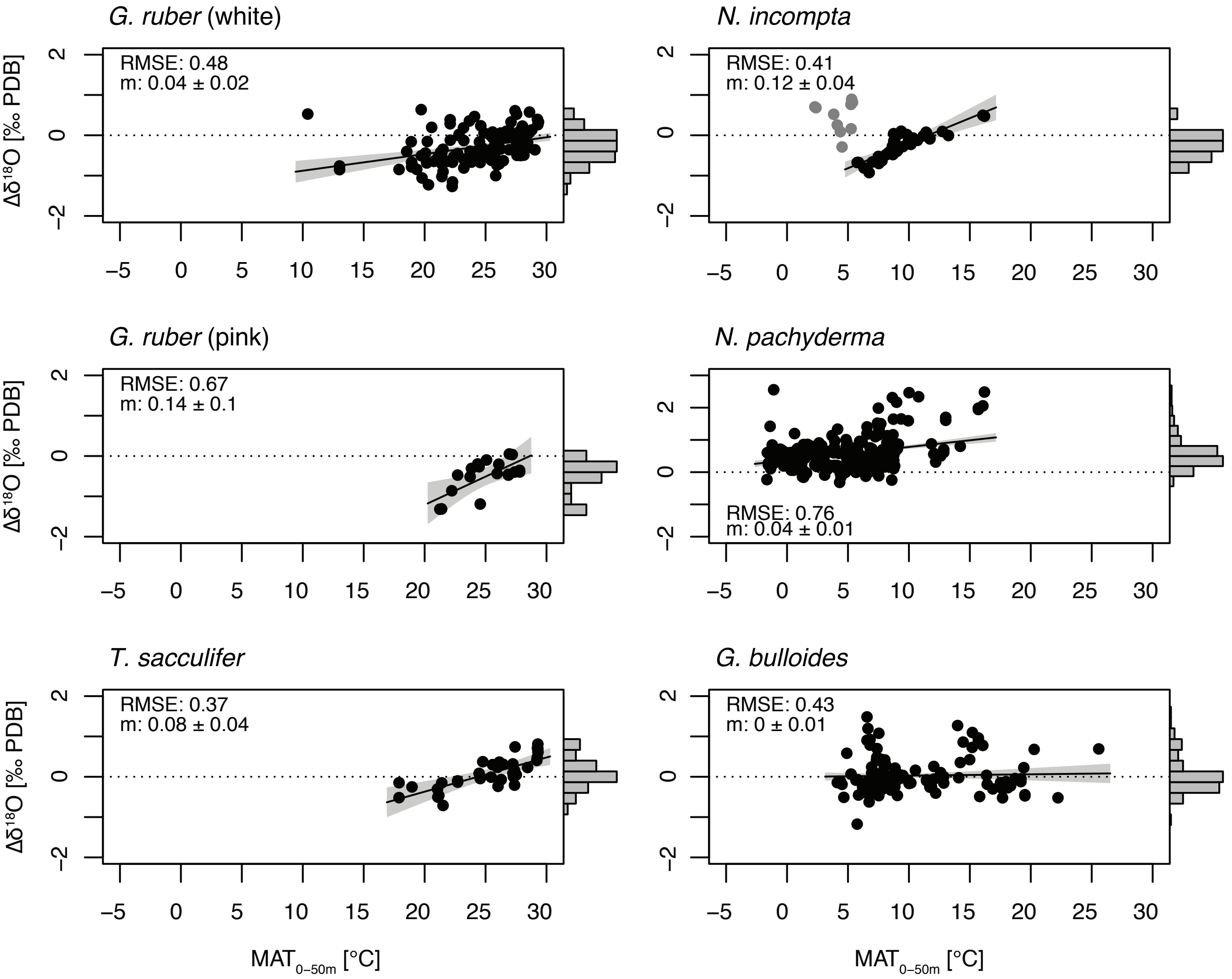

G. ruber (white)
RMSE: 0.48
m: 0.04 ± 0.02
N. incompta
RMSE: 0.41
m: 0.12 ± 0.04
G. ruber (pink)
RMSE: 0.67
m: 0.14 ± 0.1
N. pachyderma
RMSE: 0.76
m: 0.04 ± 0.01
T. sacculifer
RMSE: 0.37
m: 0.08 ± 0.04
G. bulloides
RMSE: 0.43
m: 0 ± 0.01
Δδ18O [‰ PDB]
2
0
−2
−5
0
5
10
15
20
25
30
MAT0–50m [°C]

Fig. 3

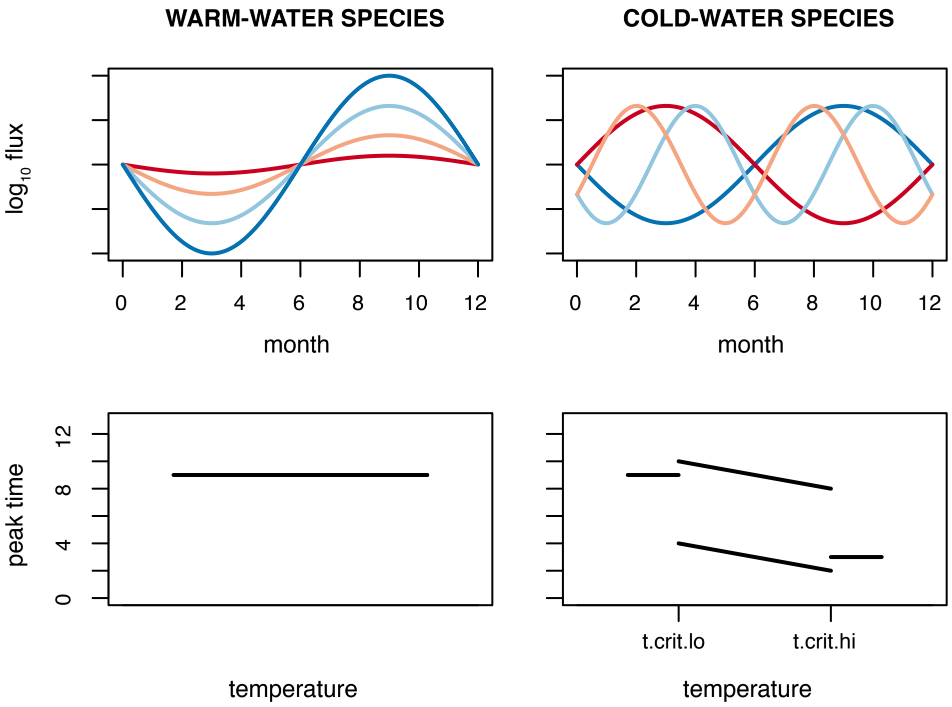

WARM-WATER SPECIES
COLD-WATER SPECIES
$\log_{10}$ flux
0
2
4
6
8
10
12
month
peak time
0
4
8
12
temperature
t.crit.lo
t.crit.hi

Fig. 4

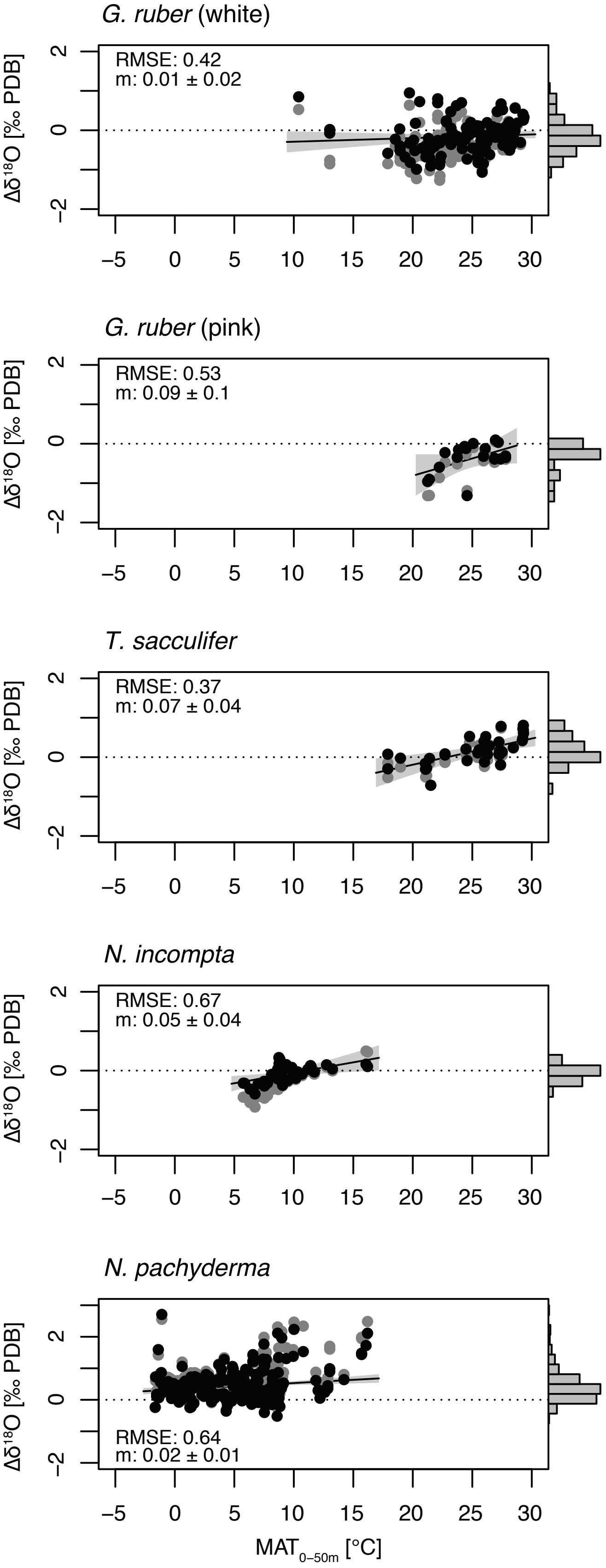

G. ruber (white)
RMSE: 0.42
m: 0.01 ± 0.02
G. ruber (pink)
RMSE: 0.53
m: 0.09 ± 0.1
T. sacculifer
RMSE: 0.37
m: 0.07 ± 0.04
N. incompta
RMSE: 0.67
m: 0.05 ± 0.04
N. pachyderma
RMSE: 0.64
m: 0.02 ± 0.01
Δδ18O [‰ PDB]
−2
0
2
−5
0
5
10
15
20
25
30
MAT0–50m [°C]

Fig. 5

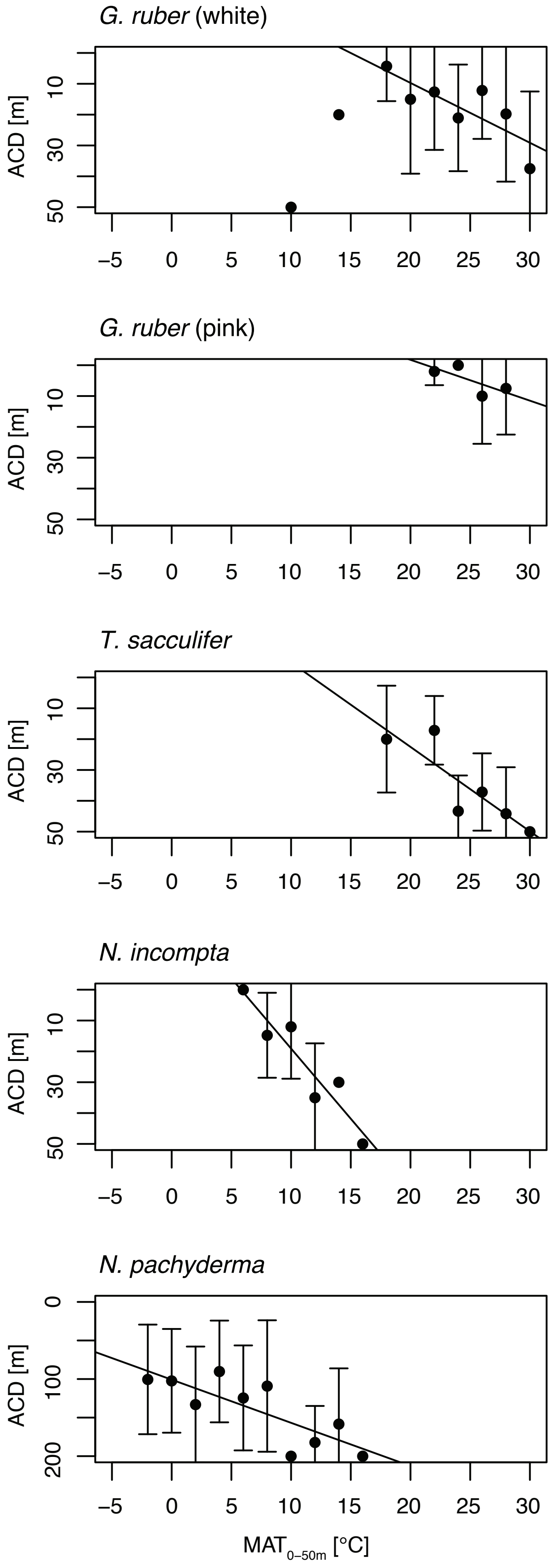
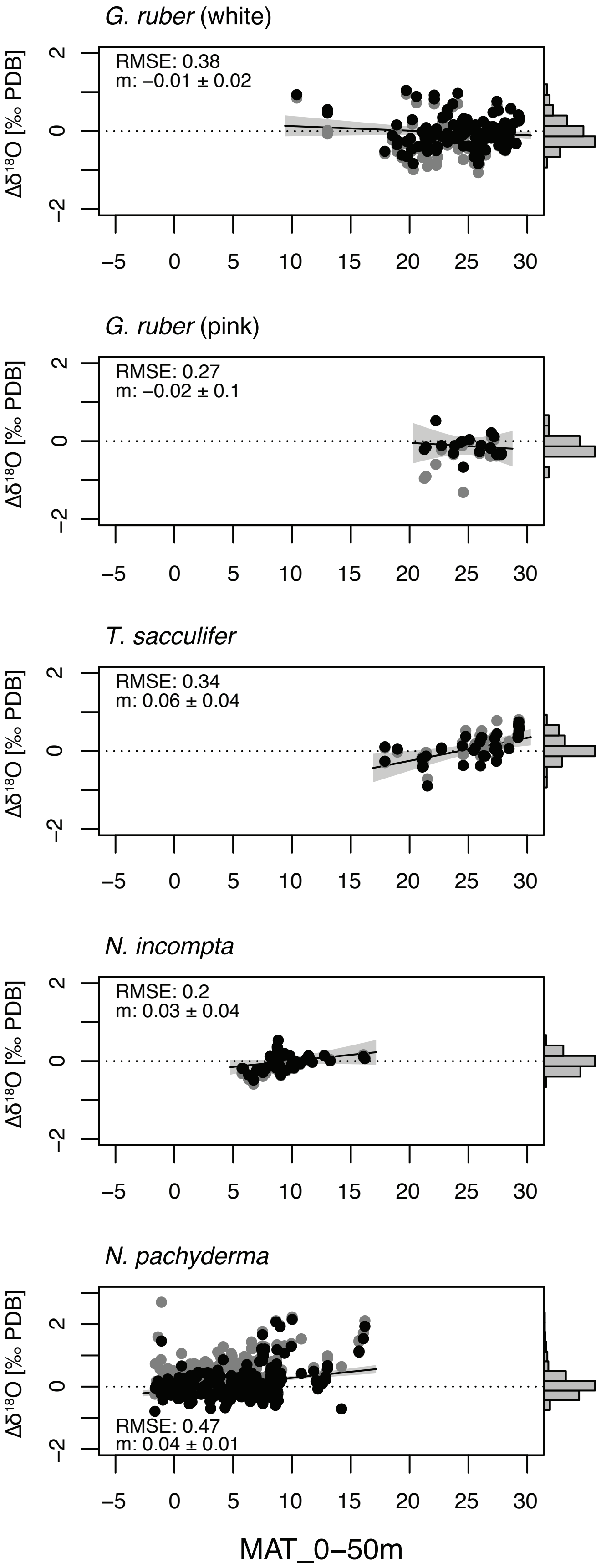

G. ruber (white)
G. ruber (pink)
T. sacculifer
N. incompta
N. pachyderma
ACD [m]
10
30
50
0
100
200
–5
0
5
10
15
20
25
30
MAT$_{0–50m}$ [°C]

Fig. 6



G. ruber (white)
RMSE: 0.38
m: −0.01 ± 0.02
G. ruber (pink)
RMSE: 0.27
m: −0.02 ± 0.1
T. sacculifer
RMSE: 0.34
m: 0.06 ± 0.04
N. incompta
RMSE: 0.2
m: 0.03 ± 0.04
N. pachyderma
RMSE: 0.47
m: 0.04 ± 0.01
Δδ¹⁸O [‰ PDB]
2
0
−2
−5
0
5
10
15
20
25
30
MAT_0−50m

Fig. 7

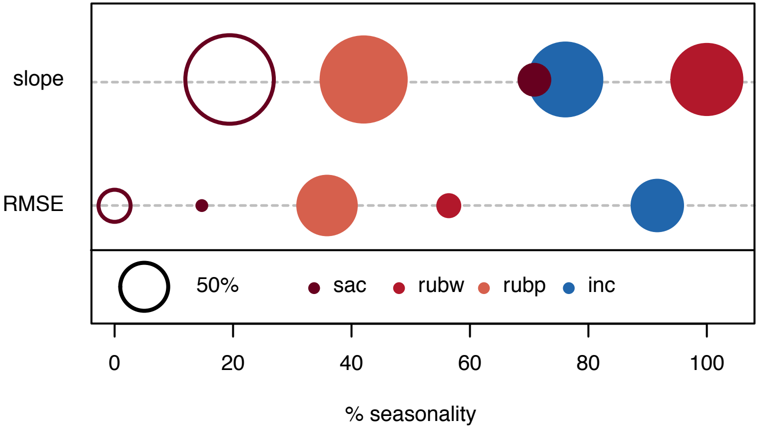


Fig. 8

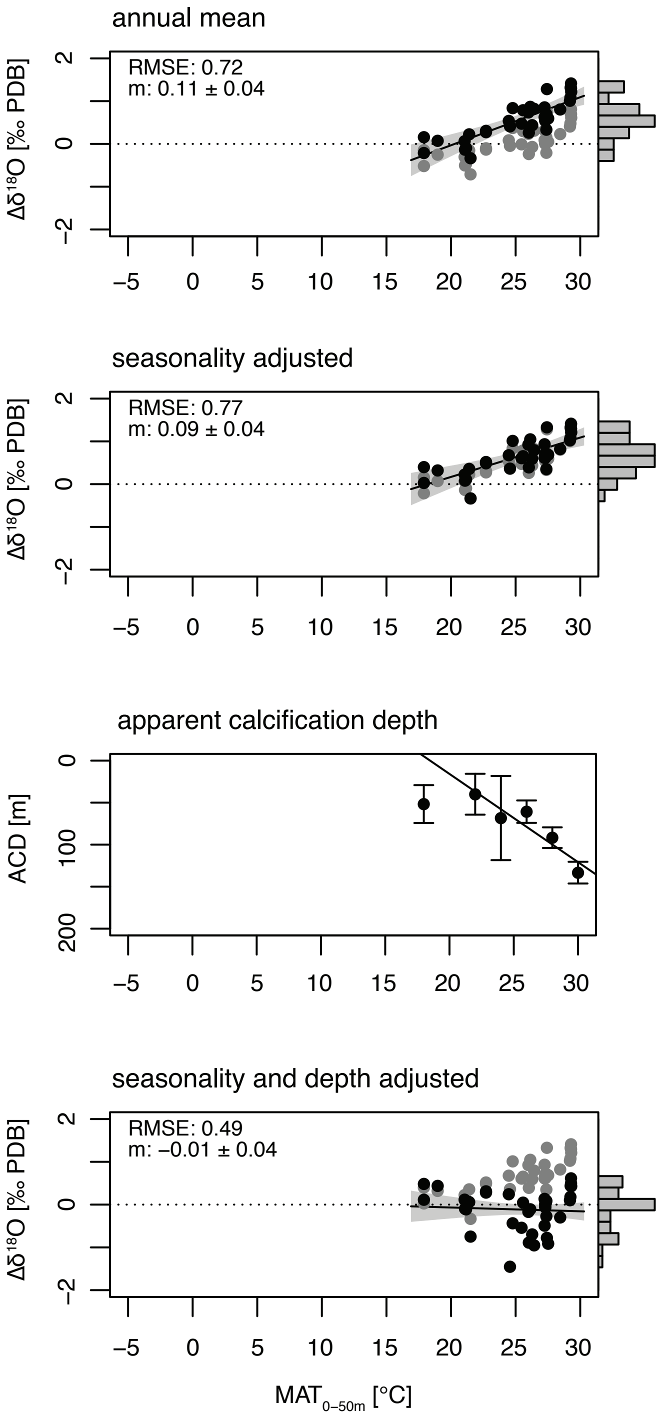

annual mean
RMSE: 0.72
m: 0.11 ± 0.04
Δδ18O [‰ PDB]
2
0
−2
−5
0
5
10
15
20
25
30
seasonality adjusted
RMSE: 0.77
m: 0.09 ± 0.04
Δδ18O [‰ PDB]
2
0
−2
−5
0
5
10
15
20
25
30
apparent calcification depth
ACD [m]
0
100
200
−5
0
5
10
15
20
25
30
seasonality and depth adjusted
RMSE: 0.49
m: −0.01 ± 0.04
Δδ18O [‰ PDB]
2
0
−2
−5
0
5
10
15
20
25
30
MAT0–50m [°C]

Fig. 9

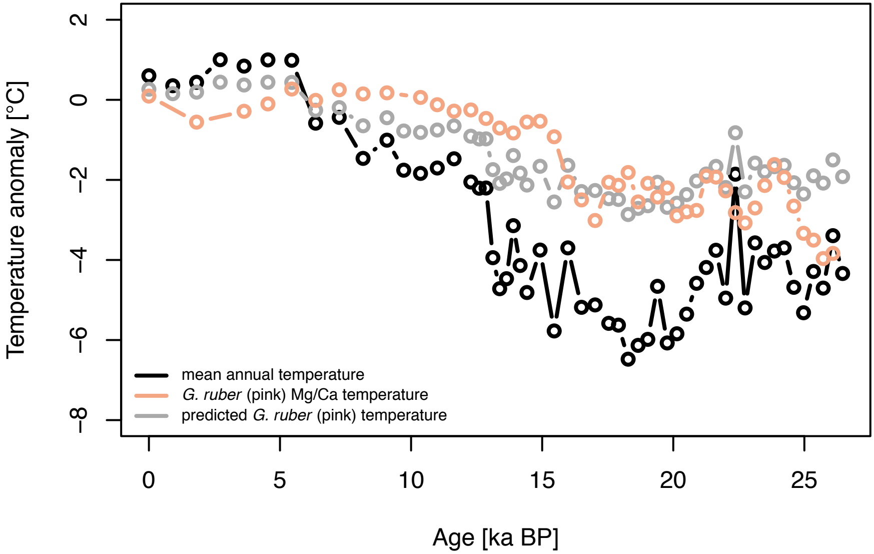
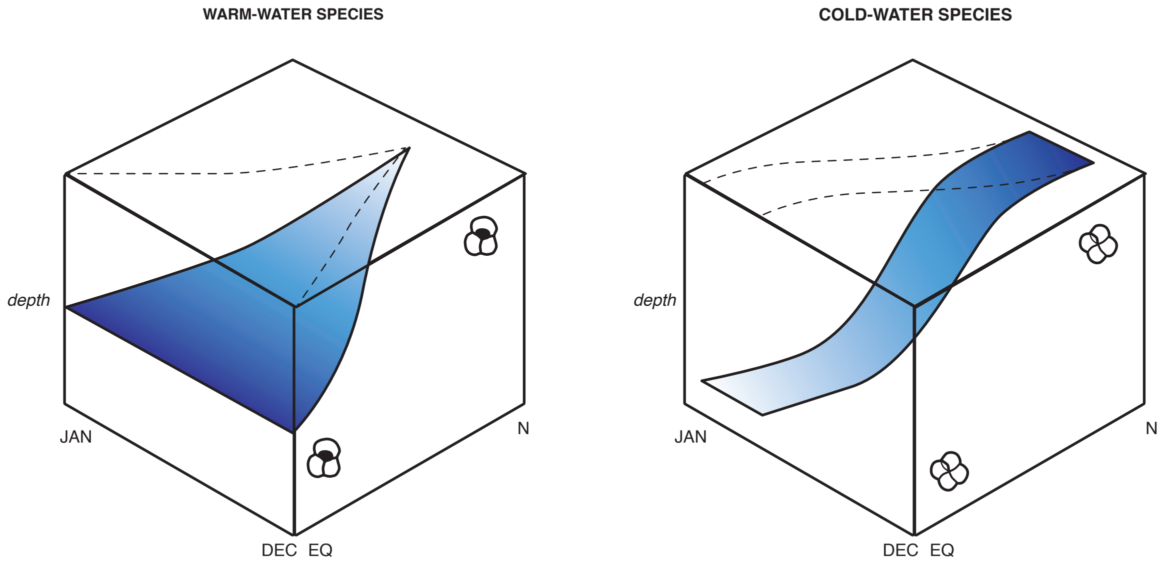

Temperature anomaly [°C]
2
0
−2
−4
−6
−8
0
5
10
15
20
25
Age [ka BP]
mean annual temperature
G. ruber (pink) Mg/Ca temperature
predicted *G. ruber* (pink) temperature

Fig. 10


WARM-WATER SPECIES
depth
JAN
DEC
EQ
N
COLD-WATER SPECIES
depth
JAN
DEC
EQ
N