

**A model-data  
comparison of the  
Holocene global sea  
surface temperature**

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# A model-data comparison of the Holocene global sea surface temperature evolution

G. Lohmann<sup>1</sup>, M. Pfeiffer<sup>1</sup>, T. Laepple<sup>1</sup>, G. Leduc<sup>2</sup>, and J.-H. Kim<sup>3</sup>

<sup>1</sup>Alfred Wegener Institute for Polar and Marine Research, Bussestrasse 24,  
27570 Bremerhaven, Germany

<sup>2</sup>Kiel University, Institute of Earth Sciences, Ludewig-Meyn-Str. 10, 24118 Kiel, Germany

<sup>3</sup>Royal Netherlands Institute for Sea Research, P.O. Box 59,  
1790 AB Den Burg, Texel, The Netherlands

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Correspondence to: G. Lohmann (gerrit.lohmann@awi.de)

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## Abstract

We compare the ocean temperature evolution of the Holocene as simulated by climate models and reconstructed from marine temperature proxies. We use transient simulations from a coupled atmosphere-ocean general circulation model, as well as an ensemble of time slice simulations from the Paleoclimate Modelling Intercomparison Project. The proxy dataset comprises a global compilation of marine alkenone- and Mg/Ca-derived sea surface temperature (SST) estimates. Independently of the choice of the climate model, we observe significant mismatches between modelled and estimated SST amplitudes in the trends for the last 6000 yr. Alkenone-based SST records show a similar pattern as the simulated annual mean SSTs, but the simulated SST trends underestimate the alkenone-based SST trends by a factor of two to five. For Mg/Ca, no significant relationship between model simulations and proxy reconstructions can be detected. We tested if such discrepancies can be caused by too simplistic interpretations of the proxy data. We therefore considered the additional environmental factor changes in the planktonic organisms' habitat depth and a time-shift in the recording season to diagnose whether invoking those environmental factors can help reconciling the proxy records and the model simulations. We find that invoking shifts in the living season and habitat depth can remove some of the model-data discrepancies in SST trends. Regardless whether such adjustments in the environmental parameters during the Holocene are realistic, they indicate that when modeled temperature trends are set up to allow drastic shifts in the ecological behavior of planktonic organisms, they do not capture the full range of reconstructed SST trends. These findings challenge the quantitative comparability of climate model sensitivity and reconstructed temperature trends from proxy data.

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# 1 Introduction

A serious problem of future environmental conditions is how increasing human industrialisation with growing emissions of greenhouse gases will induce a significant impact on the Earth's climate. Information beyond the instrumental record covering the last 150 yr can be obtained mainly from two strategies: on the one hand by deriving from proxies which record past climate and environmental conditions, and on the other hand by simulating climate, using comprehensive models of the climate system under appropriate external forcing. Numerical climate models are clearly unequalled in their ability to simulate a broad suite of phenomena in the climate system (Jansen et al., 2007), but their reliability on longer timescales requires additional evaluation. Only climate records derived from paleo-environmental proxies enable the test of these models because they provide records of climate variations that have actually occurred in the past. However, well-known uncertainties in the proxy-derived paleo-climate records exist, e.g. age control, signal formation, or calibration issues (Bradley, 1999).

Performing model-data comparisons can help reducing uncertainties in both model simulations and reconstruction of past climate change, and thus provide a test for climate projections as derived from climate models (e.g. Schmidt, 2010). In this perspective, the climate evolution from the mid-Holocene to the preindustrial (PI) conditions is an ideal test bed for models, as the main forcing for temperature trends (insolation) for this period is known from astronomical theory (Berger, 1978), and a relatively large number of high-resolution and well-dated proxy records are available (e.g. Leduc et al., 2010a). Such records constrain the climate response to changes in external forcing (e.g. Hansen et al., 2007). However, uncertainties remain regarding important variables, such as temperature responses, the amplitude and feedbacks on long time scales and on large spatial scales (Köhler et al., 2010; Rohling et al., 2012).

There have been several studies focused on model-data comparisons of the mid-Holocene climate evolution devoted to identify and explain model-data mismatches. For example, Masson et al. (1999) and Guiot et al. (1999) compared mid-Holocene

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pollen- and lake status-based reconstructions of European climate to an ensemble of atmosphere general circulation model (AGCM) climate simulations. They found little coherency among different models in the simulations of European climate change during the Holocene, and concluded that the North Atlantic sea surface temperature (SST) evolution that was not considered in those atmosphere-only simulations may be crucial to adequately simulate European climate evolution. A more recent analysis of Brewer et al. (2007) compared the output of 25 atmosphere-ocean general circulation model (AOGCM) simulations of the mid-Holocene period with a set of paleo-climate reconstructions based on over 400 fossil pollen sequences, distributed across the European continent. They found an improvement in the model-data agreement for the newer generation of climate models but still faced difficulties for models in capturing the magnitude of climate change. Sundqvist et al. (2010) provided an overview of northern high-latitude temperature change, and found that most proxies were terrestrial, and summer biased. By taking simple arithmetic averages over the available data, the reconstructions indicated that the northern high-latitudes were 2 °C warmer in the annual mean temperature at the mid-Holocene compared to the recent pre-industrial. This compilation (Sundqvist et al., 2010) and modelling studies (Lorenz and Lohmann, 2004; Zhang et al., 2010) indicate that the strongest warming in the Arctic Ocean realm is in autumn which is closely related to sea ice effects.

Previous data compilation based on SST reconstructions during the mid-to-late Holocene mainly focused on large-scale pattern in the North Atlantic realm (Marchal et al., 2002; Rimbu et al., 2003), Pacific-Atlantic teleconnections (Kim et al., 2004), linkages between high and low latitudes (Rimbu et al., 2004) and global trends (Lorenz et al., 2006; Leduc et al., 2010a). The set of Holocene SST records that we use here is derived from alkenones and Mg/Ca, two proxies that are well established and thus largely applied over the last two decades (e.g. Brassell et al., 1986; Prah1 and Wakeham, 1987; Prah1 et al., 1988; Rosell-Melé et al., 1995; Nürnberg et al., 1996; Schneider et al., 1996; Bard et al., 1997; Conte et al., 1998; Herbert et al., 1998; Müller et al., 1998; Rosenthal et al., 2004; Greaves et al., 2008). For alkenones synthesized by

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5 a small number of Haptophyceae phytoplankton of which the coccolithophorids *Emiliana huxleyi* and *Gephyrocapsa oceanica* are the two most common sources in the present oceans and for contemporary sediments, we consider mainly two parameters that might influence estimations of Holocene SST trends: changes in the seasonality of coccolithophorids (e.g. Rosell-Melé et al., 1995; Sikes et al., 1997; Ternois et al., 1997; Davis and Brewer, 2009), and in their habitat depth (e.g. Ternois et al., 1997; Bentaleb et al., 1999; Ohkouchi et al., 1999). Alkenones record a temperature signal that reflects the surrounding water temperature during the algae's lifetime. This recorded signal can be influenced by species-dependent ecological preferences, hence, the reconstructed temperature signal may depend on the seasonality of the alkenone-producing organisms and the depth of its living habitat (e.g. Müller et al., 1998; Baumann et al., 2000; Andruleit et al., 2003). As for alkenones, planktonic foraminifera calcifying their tests from which Mg/Ca SST estimates are derived thrive over wide ranges of seasons and water depths (e.g. Fairbanks et al., 1982; Deuser and Ross, 1989; Mohtadi et al., 2009; Regenberg et al., 2009; Fallet et al., 2010).

15 Here, we specifically address this issue by presenting a comparison of simulated and reconstructed ocean temperatures for the mid-to-late Holocene (6 to 0 kyr BP – before present). We compared model data from an ensemble of transient simulations of the Holocene, performed with the ECHO-G model (Lorenz and Lohmann, 2004), to marine alkenone- and Mg/Ca-based temperature reconstructions. Previous model-data comparison studies indicated an agreement in the tendency between marine proxy reconstructions and model simulations of the temperature evolution, but a mismatch with respect to the amplitude of the temperature trends (Lorenz et al., 2006; Schneider et al., 2010). Therefore, it has been speculated that taking into account proxy specificities associated with the ecological behavior of planktonic organisms from which SST are derived can remove parts of the observed mismatches. Such possibility was however not explicitly addressed by extracting from the model the variables that may have affected the proxy data. For instance, changes in surface water stratification and in seasonality of the planktonic organisms' living season could affect environmental factors

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influencing proxy reconstructions, which may establish a diagnostic of why model-data mismatch is observed.

Here, we use our extended GHOST database (Leduc et al., 2010a), which comprises marine SST proxy records based on alkenones and Mg/Ca. We compare these data to ensemble simulations from a transient experiment as well as to a selection of climate model simulations for the mid-Holocene period. We then systematically reduce the model-data mismatches by considering changes in seasonality and water depth structure from model outputs at marine core locations within the limit of basic ecological requirements to identify marine sites where model-data mismatch may potentially be caused by a misinterpretation of the proxy record, rather than by a real deviation between observed temperatures and model simulations. By quantifying the potential influence of seasonality and habitat depth on the alkenone- and Mg/Ca-derived temperature, we evaluate possible reasons for the misfit of simulated Holocene SST trends with the proxies.

## 2 Data and methods

The marine alkenone-based temperature reconstructions are from the GHOST database (Kim and Schneider, 2004). We use an updated version of this database (Leduc et al., 2010a), which comprises marine proxy records for SST based on alkenones and Mg/Ca. The temperature reconstructions used here cover the mid-Holocene (6 kyr BP) to the last millennium (0 kyr to 1 kyr BP, depending on the record), and consist of 52 alkenones-based SSTs (Fig. 1) and 19 Mg/Ca-based SST records (Fig. 2). These are unevenly distributed over the world ocean and are mainly located in the North Atlantic Ocean and in coastal areas (Fig. 3). In order to fulfill minimal statistical requirements, we only consider records that have at least 10 incorporated values. As our main interest is the pattern of SST evolution, we determine the linear temperature trends between 6 kyr BP and 0 kyr BP at every core location. These temperature

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trends show the spatial pattern of temperature evolution since the mid-Holocene, as recorded by the marine temperature proxies.

Simulated temperatures are based on the ensemble mean of two transient experiments spanning 7 to 0 kyr BP, using the ECHO-G model (Lorenz and Lohmann, 2004).

The model is described in Legutke and Voss (1999). It consists of the atmosphere model ECHAM4 (Roeckner et al., 1996) and the ocean general circulation model HOPE including a dynamical-thermodynamical model for sea ice (Wolff et al., 1997). Only the orbital forcing has been applied in this experiment, and other parameters (e.g. CO<sub>2</sub>) have been set to PI values. Calculation of the orbital parameters follows the orbital solution of Berger (1978) and is accelerated by a factor of ten (Lorenz and Lohmann, 2004). The same model has been applied for the Eemian and glacial inception (Felis et al., 2004; Lohmann and Lorenz, 2007).

The ocean model grid consists of 120 unequally spaced grid cells in poleward direction, and 128 equally spaced grid cells in longitudinal direction; the equatorial latitudes between  $\pm 10^\circ$  latitude have a resolution of  $0.5^\circ$  in order to resolve the equatorial wave guide, this resolution gradually decreases polewards until  $30^\circ$  to approximately  $2.7^\circ$ . As for the proxy reconstruction, we calculate the linear trends of the temperature simulation from the mid-Holocene to the present (6 to 0 kyr BP).

In order to gain insight into the way how different climate models perform when simulating the temperature evolution during the Holocene, we also analyze the modeled SST anomalies between 6 and 0 kyr BP from simulations performed in the framework of paleoclimate modelling intercomparison project phase II (PMIP2) (Braconnot et al., 2007a,b). Assuming linearity of the mid- to late-Holocene temperature trends, the PMIP2 temperature anomalies can be compared to the reconstructed temperature trends. Our comparison comprises 14 experiments from 9 AOGCMs, of which some models performed two experiments, i.e. with and without interactive vegetation (Braconnot et al., 2007a,b). The models participating in PMIP2 represent coupled atmosphere-ocean models: CCSM3 (Otto-Bliesner et al., 2006), ECBilt-CLIO-VECODE (Renssen et al., 2005), FGOALS-g1.0 (Yu et al., 2002, 2004), FOAM (Jacob

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et al., 2001), GISSmodelE (Schmidt et al., 2006), MIROC3.2 (K-1 Model Developers, 2004), MRI-CGCM2.3.4 (Yukimoto et al., 2006), and UBRIS-HadCM3M2 (Gordon et al., 2000). Three models (ECBilt-CLIO-VECODE, FOAM, and UBRIS-HadCM3M2) have been also used including a vegetation representation. For more detailed information on the setup we refer to Braconnot et al. (2007b).

In the first step of our analysis, we compare the observed proxy-based temperature trends to the simulated temperature trends at the core positions. As the habitat depth and the seasonality of the proxy recorder are unknown, we perform this comparison for simulated annual and seasonal mean temperatures and extract the temperature trends at each model level of the upper 100 m water depth of the ECHO-G model. In a second step, we estimate the sensitivity of the observed temperature trends to potential transient changes in the ecological behavior of planktonic organisms: shifts in seasonality or habitat depth.

For seasonality, we first extract the maximum seasonal temperature gradient ( $^{\circ}\text{C day}^{-1}$ ) from the PI climate simulation for each core position. A lower limit of the seasonal shift that is needed to reconcile model simulation and proxy reconstruction is then calculated by dividing the residual between the simulated and reconstructed Holocene temperature trend by the maximum temperature gradient described above. Such procedure only estimates the absolute value of the seasonality shift required to reconcile models and data, but its direction cannot be determined as a result of a lack of knowledge on the seasonality of the planktonic organisms. To derive a lower estimate for the shift in habitat depth we analyze the vertical temperature gradient between the first two levels of the ocean in the PI climate model output at the core positions. We retrieve the shift in habitat depth similarly to the procedure of the time shift calculation, by dividing the difference between the simulated and reconstructed temperature trends by the vertical temperature gradient.

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## 3 Results

### 3.1 Holocene trends: data and model

We compare the annual mean SST trends from the mid-Holocene to the present as simulated by the ECHO-G model and as estimated from alkenone and Mg/Ca temperature proxies for the same time period (Fig. 3). We find that the general temperature pattern recorded by the alkenones is a warming in the tropics and the North Pacific Ocean. Cooling predominates in mid- and high-latitudes of the North Atlantic Ocean and in the Southern Hemisphere mid-latitudes. In many regions, such as the North Atlantic Ocean, the Mediterranean Sea, the northern Indian Ocean, and the western North Pacific Ocean, there is a good agreement between the model and alkenone data with respect to the spatial pattern of the temperature trend (Fig. 3). Globally, the alkenone and simulated SST trends are significantly correlated ( $R = 0.49$ ,  $p < 0.05$ ). Yet, the amplitudes of recorded and simulated temperature trends often differ, with proxies generally showing larger SST changes during the Holocene. A scatter plot of the modeled SST trends as simulated by the ECHO-G model versus alkenone-based SST trends (Fig. 4a) shows that only at few locations the alkenone reconstructions and the model simulations bear comparable temperature trends. The correlation between the modeled and Mg/Ca-based SST trends is not significant ( $R = -0.31$ ,  $p > 0.05$ ). To analyze the potential influence of the seasonality on the model-data comparison, seasonal variations of the simulated temperature trends are shown as vertical bars in Fig. 4. Of the 52 alkenone records, only 22 (~42% of the total number of records) are in agreement with the model trend at some time during the year (Fig. 4a). Out of the other 30 (~58%) data markers, 9 (~17% of the total number of records) show a difference of more than 2°C (red data markers, Fig. 4a).

A similar analysis for Mg/Ca-based SSTs indicates that approximately 53% of the cores agree with the model simulation at some time during the year (Fig. 4b). Of the 9 (~47%) data markers that do not match with the model simulation, 2 (~11%) differ by more than 2°C (Fig. 4b). Temperature trends are larger in the alkenone (-4°C to

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2°C) than in the Mg/Ca (−2°C to 2°C) reconstructions. This might be also caused by the different core positions of both proxies. In our dataset, alkenone records are more abundant at high latitudes while Mg/Ca records are more abundant in low latitudes. The magnitude of the modeled SST trends at core locations is however limited to −1°C to 1°C which means that the model underestimates the trends as compared to both the alkenone and Mg/Ca reconstructions.

A comparison of SST trends of each proxy with local summer, local winter and annual mean SST trends, as simulated by ECHO-G, indicates which season shows the best agreement between model and proxy reconstruction (Fig. 3). The local summer and winter is defined by the warmest and coldest month. In the North Atlantic Ocean, the best agreement is given for local summer model temperatures (Fig. 3). In other areas, there is no clear evidence for a preferred season. Some cores in close proximity with each other show the best agreement for different seasons in the model. This suggests that the best agreement with a specific season might not always be caused by the seasonality in the recording process.

Figure 5 compares the temperature trends derived from alkenone and Mg/Ca records to those calculated from the evolution of the warmest (local summer) and coldest (local winter) month of each year from the mid-Holocene to the present. The correlation between the alkenone proxy record and the climate simulation is higher for local summer ( $R = 0.44$ ,  $p < 0.05$ ) than for winter ( $R = 0.14$ ,  $p > 0.05$ ), but lower than for the annual mean ( $R = 0.49$ ,  $p < 0.05$ ). In the North Atlantic Ocean, the agreement between the reconstructed and the simulated SST trends is still stronger for the local summer than for the annual mean, because the simulated cooling trend is much more pronounced for summer than for the annual mean (Fig. 5b). For Mg/Ca, there is a higher correlation for the winter mean ( $R = 0.17$ ,  $p > 0.05$ ) than for the summer mean ( $R = -0.56$ ,  $p < 0.05$ ) and the annual mean ( $R = -0.31$ ,  $p > 0.05$ ).

The analyses described so far focused on the model-data comparison at the sea surface. Planktonic organisms are however known to be able to move in the water column. In order to depict whether deeper model layers would be in better agreement

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with the temperature reconstruction, the proxy records were compared to the model for different layers of the upper 100 m of the ocean (10 m, 20 m, 52 m, 75 m, and 100 m). Layers below these depths can be ignored, since alkenone-producing organisms require sunlight for photosynthesis and are therefore strictly restricted to the euphotic zone. For the Mg/Ca ratio, we also consider only the upper layers, since the species that are represented in the proxy database used in our study (*Globigerinoides ruber*, *Globigerina bulloides*, and *Neogloboquadrina pachyderma*) are considered in the literature as being surface-dwelling foraminifera (Ostermann et al., 2001; Schiebel et al., 1997; Wang et al., 1995).

Figure 6a shows the depths of best fit between the modeled SST trends and the alkenone- and Mg/Ca-based SST trends. For alkenones, about a third of the records best agree with the upper level of the ocean, with the highest correlations being present in the upper 10 m (~33%). The other ~67% of the records best agree with deeper layers, of those 38% are located between 10 and 75 m. In general, the number of cores that agree with modeled temperature trends decreases with depth (Table 1).

For Mg/Ca-ratios, ~32% of the records fit best to the modeled temperature trends at 10 m depth. The remainder of 68% fit best to deeper layers, of which 32% show best agreement with layers between 10 to 75 m. Figure 6b shows a common pattern of the preferred depth for alkenones, which might be linked to the depth where annual average nitrate concentrations reach high levels (Conkright and Boyer, 2002). Although Fig. 6b and c does not account for zonal oceanic heterogeneities, they capture at first order the ecological preference for algae's ecological niches found close to the surface at low and high latitudes (due to the influences of upwelling and of penetration of sunlight into the subsurface layers, respectively), while the mid-latitudes regions where the nutricline is found deeper show an increase in the depth where model and data agree best (Fig. 6b). Both estimates are optimistic as they are based on the maximum seasonal and vertical gradient.

While choosing specific depths and seasons in the model simulations decreases the mismatch between reconstructed and simulated trends, the amplitude of the simulated

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trends is still smaller than of the reconstructed trends (Fig. 4a and b). We therefore evaluate two potential parameters that might be able to partly explain the misfits found in the model-data comparison: a time-shift in the recording season and a change in the habitat depth of the recorder (Figs. 7 and 8). The model-alkenone data disagreement could be relaxed for up to 37 % of the records by considering a potential vertical shift of the habitat depth of the proxy-producing organism in the water column by less than 20 m. For up to 52 % of the alkenone records, a shift in the blooming season of less than 14 days could explain the model-data mismatch. In total, up to 62 % of the records can be explained by at least one of the two shifted parameters, whereas the remaining 38 % of the cores cannot be explained by any of these potential parameters. We further note that for 38 % of the records, the ambient temperature exceeds the calibration range 6 °C–25 °C for which alkenones are most sensitive to SST (e.g. Conte et al. 2006). In tropical warm pools and polar regions, the ambient water temperature induces only small changes in the UK'37 index, reducing the sensitivity of alkenone paleothermometry for these regions (Sonzogni et al., 1997; Mix et al., 2000; Conte et al., 2006), therefore the recorded temperature proxy at those locations might be problematic. However, as the sensitivity of UK'37 on temperature changes seems to be reduced in these tails of the calibration, we do not expect that this mechanism leads to an overestimation of the trends.

The same analysis performed for the Mg/Ca records (Fig. 8) shows that up to ~26 % of the records could potentially be reconciled with the model simulation if we consider a shift in habitat depth of up to 20 m. For up to 21 % of the records a shift in recording season of less than 14 days could explain the disagreement between model simulation and data reconstruction. The remainder of 58 % of the Mg/Ca records cannot be explained by any of these two parameters. For an overview on the agreement between model and proxy data we refer to Table 2.

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## 3.2 PMIP simulations – comparison with proxy-derived SST trends

To test whether the above-described relation between proxy-derived and modeled SSTs are model-dependent we analyze simulations from the PMIP2 multi-model experiment. Therefore, we compare the difference between the mid-Holocene and PI simulated SST fields to the alkenone- and Mg/Ca-based SST trends (Fig. 9), as described above for the transient ECHO-G simulations.

In general, the Holocene trends simulated by the models participating in PMIP2 and the ECHO-G transient runs are comparable. We perform this comparison on a global scale for modeled vs. alkenone-derived SSTs (Fig. 9a) and modeled vs. Mg/Ca-based SSTs (Fig. 9b) separately. Only a few data markers are close to the unity slope line (Fig. 9). The agreement between the models and the SST reconstructions is similar to the case of the ECHO-G model (Figs. 3 and 10). Because of space limitations, we do not show all individual model anomalies and their agreement/disagreement with the alkenone-derived SST trends. Instead, the median is evaluated as a useful mean quantity. It is defined as the value of the 12th ensemble member, out of 24 members are ordered according to ranked values. This serves as a dynamic filter to reduce features that vary amongst the members and are therefore likely to be regarded as model specific and less reliable. Any of these features that have been removed are not lost but re-enter as probabilities. Indeed, the model-data agreement is largest for the ensemble median as compared to each individual member. All of the considered models underestimate the temperature trends when compared to the SST trends as recorded by the alkenones by more than a factor of two (Fig. 9a). Mg/Ca shows again no relationship to the simulated SST anomalies (Fig. 9b).

## 4 Discussion

Our analyses show that, in general, the model and alkenone based Holocene SST trends show a similar pattern, but the amplitude of the modeled temperature trends are

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weaker when compared to the proxy records. The Mg/Ca-reconstructed temperature trends do not show a positive relation to the simulated trend pattern. The observed mismatch between the proxy records and the model simulations might be caused by model deficiencies as well as by biased and/or misinterpreted proxy records. In the following, we will discuss several hypotheses.

#### 4.1 Recorder system: potential seasonal biases

The origin of the deviation between climate simulations and proxy records can be attributed to the way by which proxies record the temperature signal, and how this information is interpreted. Systematic changes in the living season over the course of the Holocene might cause a biased temperature reconstruction. Since, in our study, the alkenone- and Mg/Ca-based SST reconstructions cannot be reconciled with an annual mean temperature signal as simulated by the climate models, we further consider potential seasonal biases of the proxies. When comparing local summer/local winter (Fig. 5a and b) to the temperature trends derived from alkenone and Mg/Ca records we get a higher correlation between the alkenone proxy record and the climate simulation for the summer mean ( $R = 0.44$ ,  $p < 0.05$ ) than for the winter mean ( $R = 0.14$ ,  $p > 0.05$ ), but the correlation with the annual mean is still highest ( $R = 0.49$ ,  $p < 0.05$ ). In the case of Mg/Ca, we observe a higher correlation for the winter mean ( $R = 0.17$ ,  $p > 0.05$ ) than for the summer mean ( $R = -0.56$ ,  $p < 0.05$ ) and the annual mean ( $R = -0.31$ ,  $p > 0.05$ ). However, considering local seasons does not decrease the disagreement between model temperature trends and alkenone SST trends. For Mg/Ca we find an improvement for winter mean but still the correlation is weak. This is likely caused by a regional dependency of the seasonal skewing. However, even allowing a different seasonality for each core leaves a mismatch to the simulated trends for more than 50 % of the alkenone cores and about 50 % for Mg/Ca cores (Fig. 4).

The degree of seasonal skewing might be spatially dependent since the biogeographical properties of the ocean differ from one location to another (Prahl et al., 2010, and references therein). Lorenz et al. (2006) summarized previous studies,

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which suggested that in high latitudes the maximum production of phytoplanktic coccolithophorides occurs in summer (Baumann et al., 1997; Baumann et al., 2000), which supports that alkenones record summer temperatures (Sikes et al., 1997; Leduc et al., 2010a; Prahl et al., 2010). Satellite data further supports the theory of summer-biased alkenone records (Iglesias-Rodriguez et al., 2002).

## 4.2 Recorder system: regional seasonal biases

It has been argued that high-latitude alkenone production may be light-limited (Leduc et al., 2010a; Schneider et al., 2010) and therefore record the summer season, which may explain why alkenone-derived SST trends in the North Atlantic Ocean follow the Northern Hemisphere summer insolation. Indeed, we find a good agreement between modelled summer temperatures and the proxy reconstruction for the North Atlantic Ocean (Fig. 5b), but we still observe a disagreement between the amplitudes of the trends. There is also a clear mismatch between modelled and reconstructed SST trends in the eastern and western Pacific Ocean (Fig. 5b). In the southern high latitudes, alkenones were proposed to be skewed toward summer as well (Sikes et al., 2002). Alkenone SST located in the southern mid- to high-latitudes indicate a Holocene SST cooling which is reproduced by the modeled summer SST evolution, even though the magnitudes of SST changes are still larger in the proxy records (Fig. 5b).

Seasonality in phytoplankton production is generally less pronounced in tropical and subtropical regions (Jickells et al., 1996) and alkenone-derived SSTs from low latitude sites are therefore more likely to be representative of temperatures close to the annual mean values (Müller and Fischer, 2001; Kienast et al., 2012). It also has been argued that at low latitudes alkenones might record a boreal winter signal when a decrease in the surface ocean stratification reduces SST and enhances primary productivity (Bijma et al., 2001; Leduc et al., 2010a). In our study, we find best agreement between reconstruction and annual mean temperatures in low latitudes (Fig. 3). This might be just related to the fact that seasonality at low latitudes is very weak. We still have a considerable number of records (~52%) at low latitudes that agree best with either

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local summer (~35 %) or local winter (17 %), but the spatial patterns of these matches are featureless. In the eastern South Atlantic Ocean, only one record fits best to the mean annual SST while the nearby cores show a local summer signal. For Mg/Ca in tropical regions the large heterogeneity in Mg/Ca and modelled SST trends does not allow to draw any firm conclusion on where and how model and data disagree (Fig. 5).

Schneider et al. (2010) employed marine temperature proxies for a model-data SST comparison, using results from an AOGCM for three time slices (9.5 kyr BP, 6 kyr BP and PI). In their study, they made several assumptions on how proxy records might be seasonally biased by defining four different filters. They estimate which seasonal bias might be represented in a certain proxy record, and identify regions where proxy records are biased towards a specific season, by applying these filters to the simulated SST trend. Schneider et al. (2010) defined a seasonal index weighting that relies on the modern relationship between net primary production (NPP) and SSTs. We do not assume a constant PI relationship between NPP and SST and refrain from considering such filter. Similar to our study, Schneider et al. (2010) found that the North Atlantic Ocean is mostly influenced by a local summer bias in alkenone-based SSTs, while records in the western Pacific Ocean preferably represent a winter signal. The correlation values between proxy records and filtered model simulations that Schneider et al. (2010) estimate are higher than those that we find, this might be attributed to the pre-selection of proxy-records that Schneider et al. (2010) applied prior to the correlation estimation.

### 4.3 Recorder system: habitat depth

In the same way, a change in the habitat depth of the SST carriers over the Holocene could create deviations between proxy records and model simulations. Such changes in habitat depth and recording season could have been caused by changes in insolation over the Holocene or by related changes in the ocean temperature and nutrient distribution that the alkenone-producing organisms and the foraminifera are exposed to.

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Comparing the reconstructed Holocene temperature trends to the model levels of the upper 100 m neither does remove much of the discrepancy between models and proxies. For Mg/Ca-ratios, ~32 % of the records fit best to the model trends at 10 m depth and the remainder of 68 % fit best to lower layers (Table 1). For alkenones, we find best agreement in the upper 10 m (~34 %), while the other ~66 % of the records best agree with deeper layers (Table 1). Thus, we find that the highest agreement between proxy-recorded and simulated temperature trend is in the most upper ocean layer. This is in agreement with results from Rosell-Melé et al. (1995), who compared core-top alkenone-derived SSTs from the surface sediments to SSTs from overlying waters for different depths and found best agreement of alkenone SSTs with temperature at the ocean surface.

Our calculations of seasonality and upper ocean stratification are based on model output. They do not provide any diagnostic on the real ecological behavior of planktonic organisms. However, they do provide a mapping of oceanic regions where even small changes in the planktonic organisms' ecology can have large consequences on the reconstructed local SST trends. It reinforces the idea that alkenones and Mg/Ca may be affected by ecological specificities (Leduc et al., 2010a).

#### 4.4 Recorder system: shifts in seasonal preferences and habitat depth

Since neither seasonal nor habitat depth preferences of the proxy recorder can resolve the model data mismatch, we allow for shifts in the habitat depth and the blooming season from the mid-Holocene to the present as a potential mechanism that might cause the model-data disagreement. To explain the model-data mismatch by those mechanisms, summer sensitive proxy-recording species in the northern high latitudes would have to record summer temperatures in the mid-Holocene, and temperatures that are biased toward spring or autumn in the present day climate. If the organisms changed their recording behavior over the Holocene in such a way, this would increase the recorded temperature trend. Consequently, a respectively corrected proxy-based SST trend would be in better agreement with the model simulations of the Holocene.

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On the one hand it is questionable whether proxy-recording species really behave in such a way, as the organisms would likely try to keep their preferred ecological conditions by shifting their living seasons in a way that mitigates the changes in the climate (Mix, 1987). Fraile (2008, 2009) analyzed the seasonality of the foraminifera species using a planktonic foraminifera model and showed that the organisms record an underestimated temperature signal if a change in global temperature is applied. They performed a model sensitivity study by decreasing the global temperature by 2° and 6 °C and found a shift in the maximum planktonic foraminifera abundance towards warmer seasons, which would decrease the temperature trend captured in Mg/Ca records (Fraile et al., 2008).

On the other hand, planktonic organisms are subject to several limiting factors, e.g. temperature as well as light- and nutrient-availability. If those factors change in opposite directions, the organisms might change their living season without bypassing their basic ecological requirements. For example, food or nutrient availability might shift towards spring or autumn so that the living season might shift accordingly. This in the end would represent a possible mechanism explaining overestimated temperature trends in the proxy record, which would exceed a real climate trend. To be able to explain such shifts, more studies using complex ecosystem models of the planktonic organisms need to be done, such as e.g. ecophysiological models reproducing the growth of planktonic foraminifera (Lombard et al., 2011).

It is not obvious which amplitude a seasonal shift realistically might have had during the Holocene. Our results show that indeed 48 % of the alkenone records cannot be reconciled with the model simulation when considering a shift of less than 14 days over the last 6 kyr. For nearly all the records (47 out of 52) the mismatch between model and data can be removed by allowing a higher time shift of the recording season of up to 60 days (Fig. 7b). In the case of Mg/Ca, up to ~21 % of the records could be reconciled with the model simulation if we consider a potential shift in the recording season of less than 14 days (Fig. 8b and c), but only 1 out of 19 records would require a shift of more than 60 days.

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We also find a latitudinal-dependent depth profile of alkenones which might be linked to the nitrate concentration (Fig. 6b). This suggests that the best fitting model-depth indeed might depend on the location, which may reflect a coupling between surface ocean biogeochemistry and stratification. For Mg/Ca we do not detect a relationship (Fig. 6c), although we did not take into account species-specific ecological behavior in this present study. While the low-latitude Mg/Ca records derived from the symbiont-bearing foraminifer *G. ruber* require those records to be restricted to the euphotic zone, the mid- to high-latitudes records derived from *G. bulloides* and *N. pachyderma* may integrate to some extent a subsurface signal.

If such a preference for a certain habitat depth changed with time, this would allow for another mechanism that might explain the mismatch between model simulation and proxy-reconstruction linked to planktonic organisms' migrations in the water column. Such a shift in living depth is supported by the indication that the detachment of coccoliths on coccolithophores plays a role in the regulation of buoyancy (Fritz and Balch, 1996). The non-detachment of the coccoliths would allow the alkenone-producing organisms to migrate by as much as 100 m in the euphotic zone in about 75 days (Fritz and Balch, 1996), facilitating access to the subsurface nutricline (Munk and Riley, 1952).

The needed vertical shift that might eliminate the disagreement between proxy recorder and model simulation can reconcile up to 37 % of the records with the modelled SST trends if a vertical shift of less than 20 m is allowed. About 46 % of the cores would require a shift of more than 50 m to be in agreement with modelled SSTs. Considering the annual cycle of the maximum alkenone concentration reported by Ternois et al. (1997), the possibility of a vertical shift of about 20 m seems to be a reasonable assumption. Therefore, a significant proportion of the proxy records may be reconciled with the model simulation by assuming a vertical shift of the alkenone-producing organism's habitat depth. Yet, in our study shifts in seasonality seem to have greater potential to explain the model-proxy disagreement. It is possible that biases in the paleothermometers may add further degrees of freedom to reconcile models and data.

We however do not believe that those biases would be systematic enough to be responsible for the observation we made that models seem to underestimate Holocene SST trends as alkenone and Mg/Ca records suggest.

#### 4.5 Climate models: coarse resolution

Climate models are limited in their spatial resolution (computational constraints) and necessary approximations. Therefore, they cannot represent the full complexity of the earth system. The proxy records used in this study (and many others) are mostly located in coastal areas. These regions are not well represented by climate models due to their low resolution. Coastal areas may be especially sensitive to external forcing, since their thermal inertia may be lower than that of the open ocean due to land-ocean interactions. Other local feedbacks operating in upwelling systems might also complicate the SST model-data comparison, since local cooling can take place within regions where in general widespread warming is observed (Leduc et al., 2010b). In a similar way, mismatches can be due to difficulties in capturing changes in oceanic fronts in the models.

The similarity of the results when using the transient ECHO-G simulation and the ensemble of PMIP simulations shows that the deviation between proxy data and model simulations does not seem to be a problem of specific climate models, but seems to be a robust feature of Holocene climate simulations with global coupled climate models. One testable hypothesis is that proxy records can therefore correctly record local temperature trends that cannot be simulated by the models. A possible way to examine this effect can be through a new ocean model which has high resolution of up to 7 km in deep water formation areas and in coastal areas where a higher sensitivity is expected (Scholz et al., 2012). A logical next step is the application of this model for the Holocene.

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## 4.6 Spatial representativeness of the data

Paleoclimate information gathered from model-data comparisons are difficult to be put into a context which goes beyond a description of observed model-data discrepancies, as both climate models and proxy reconstructions are imperfect and have very different characteristics. Proxy reconstructions are sparse and patchy, and can be affected by local processes and/or proxy specificities, which are not always considered in paleoclimate reconstructions. Usually, paleoclimatologists tend to obtain data in regions where sedimentation allows it and where the signal is a clear. Therefore, it could be that the SST signals are overestimated due to the selection of the sites. Climate models have coarse spatial and temporal resolutions, but can resolve changes in climatic features with a global perspective and thus help identifying the mechanisms of climate variations. Spatial heterogenous patterns provide an additional uncertainty for our data-model comparison. Here, we discuss large-scale pattern of the temperature evolution only. Furthermore, we cannot exclude that part of the signal is due to differential degradation of alkenones under contrasting bottom water oxygen conditions (Hoefs et al., 1998; Gong and Hollander, 1999). We will follow this hypothesis in a further study to examine if and how redox conditions during early organic matter diagenesis can also be determined.

Additional biases may also complicate the interpretation of Mg/Ca and alkenone paleothermometers. In particular, alkenones can be transported over long distances along with fine-grained particles (Ohkouchi et al., 2002), while Mg/Ca may be impacted by dissolution (Tachikawa et al., 2008). Alkenone advection over long distances can question those records as local SST indicators (Sicre et al., 2005). However, we expect that advection would in general tend to reduce the signal when propagating through different water masses. It is therefore not likely that advection plays the dominant role for the large-scale reconstructed temperature signal based on alkenones.

As we cannot monitor the two above-mentioned processes for our database, we consider them as having not affected the Holocene SST records we analyze here. We

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however do not expect those biases to have had an impact on the reconstructed SST trend as represented in our database as a whole, but in frontal system and dynamically active regions it can strongly affect the interpretation (e.g. Rühlemann and Butzin, 2006).

#### 5 4.7 Calibration of the proxy data

In regional and global core-top calibrations, UK'37 correlates best to the annual mean of surface water temperature SST (Rosell-Melé et al., 1995; Herbert et al., 1998; Müller et al., 1998) but this finding could be limited to the spatial relationship and does not imply that UK'37 individually record annual mean surface temperatures. Indeed, high-  
10 latitude core-top studies suggest that the alkenones are skewed toward summer temperatures (Sikes et al., 1997; Prahl et al., 2010). At low latitudes, it is also unclear whether alkenone-based SST estimates reflect mean annual SST or are skewed toward seasons during which temperatures are below the mean annual SST. A study of regional sediment-traps has shown that low-latitude alkenones most likely record  
15 annual mean temperatures (Müller and Fischer, 2001) despite the fact that alkenone-producing coccolithophorids mostly thrive during winter to spring (Müller and Fischer, 2001; Cortés et al., 2001; Bijma et al., 2001), or more generally when nutrients are abundant (Baumann et al., 2000). A recent core-top study from the eastern equatorial Pacific Ocean seems to confirm this hypothesis (Kienast et al., 2012). Such obser-  
20 vations may be materialized in the mismatch recorded between the SST calibration curves as derived from alkenone-based SST derived from water samples (that best fit with ambient temperature through a non-linear calibration curve) and from core top sediments (that best fit with the mean-annual SST overlying core-tops through a linear calibration curve) (Conte et al., 2001, 2006). Conte et al. (2006) argued that such  
25 mismatch can at least partly be explained by seasonality and water depth of coccolithophorids, suggesting that ecological effects may somewhat be embedded in modern sedimentary material.

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The uncertainties embedded in seasonal signals of Mg/Ca-based SST data may be more identifiable since available SST records and calibrations are species-specific (e.g. Anand et al., 2003). It means that refining Mg/Ca interpretation in light of the foraminiferal seasonal preferences may theoretically be undertaken by field studies.

5 Yet, seasonal preferences for a given species can also vary from site to site. For example, fluxes of the surface-dwelling planktonic foraminifer *G. ruber*, the species most represented in the updated version of the GHOST database, were found to be maximum during summer in the Panama Basin when surface waters are well stratified (Thunell et al., 1983), but during winter South of Java when upwelling occurs (Mohtadi  
10 et al., 2009). *G. bulloides* is, on the other hand, usually associated with upwelling events and tends to flourish whenever primary productivity increases since it needs abundant food to develop (e.g. Lombard et al., 2011).

### 4.8 Model-data comparison: ecological requirements

15 Model-data comparisons of Holocene temperature evolution induced by insolation changes have independently proposed that seasonality of coccolithophorids blooms can explain part of the reconstructed temperature signal at low latitudes (Lorenz et al., 2006; Schneider et al., 2010). However, beyond the firm limits of basic ecological requirements of planktonic organisms, there is still a lack of a conceptual model for explaining the season and water depth embedded in SST signal carriers that can glob-  
20 ally explain how and where ecological optima are reached for a given foraminifera or coccolithophorid species. Our study goes beyond the work of Schneider et al. (2010) in that we quantify the amplitude of the biases that the proxy records might include. Additional to seasonal shifts of the recording season, we also include and quantify shifts in the habitat depth.

25 The dependence of the temperature record on the habitat depth has not been as much studied as seasonality. For the Mediterranean Sea, Bentaleb et al. (1999) suggested that alkenones are essentially synthesized at levels of highest primary production, and therefore may record a signal which integrates subsurface temperature where

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a chlorophyll maximum can develop seasonally. Another study from the Arabian Sea indeed demonstrated that alkenone-synthesizing coccolithophorids are several orders of magnitude more abundant at subsurface as compared to the surface (Andruleit et al., 2003). Vertically, this integration is of course strictly restricted to the euphotic zone, which sets a lower firm limit on where alkenones are being synthesized. As for coccolithophorids, foraminifera are subject to changes in the depth habitat (see e.g. Fairbanks et al., 1982). Even though *G. ruber* and *G. bulloides* are both considered as surface ocean dwellers, only *G. ruber* must thrive in the euphotic zone to allow the photosynthesis of their symbiont-bearing organisms. Recent studies indeed suggest that the *G. bulloides* life cycle associated with gametogenesis involves calcification of its test within subsurface and may significantly affect its resulting Mg/Ca value (Marr et al., 2011). In summary, it appears that potential changes in seasonality and upper water column structure, likely accompanying Holocene changes in ocean dynamics, provide two degrees of freedom which have the potential to explain the model-data mismatch and which warrant further investigations.

### 4.9 Forcing and internal variability

Besides the insolation forcing, changes in greenhouse gases may play a role. However, the radiation effect due to CO<sub>2</sub> is rather small and has a negligible influence on our results (not shown). Internal variability is expected to have a minor effect on the overall hemispheric temperature trends. However, it was concluded that part of the regional Holocene SST trend can be attributed to a pattern which resembles the Arctic Oscillation/North Atlantic Oscillation (Rimbu et al., 2003) and modulations of the Icelandic Low (Lohmann et al., 2005) showing opposite SST trends at one latitude. Such features are more difficult to assess in data and models because of their spatial heterogeneity and atmospheric dynamics.

One particular example how complex the temperature trend in the North Pacific and Atlantic oceans are, can be seen in Fig. 3. The inverse long-term SST trends between the northeastern Pacific and the northeastern Atlantic Oceans during the Holocene

has been attributed to inter-oceanic teleconnections during the Holocene related to Pacific-North Atlantic mode of variability (Kim et al., 2004). Such features have not been sufficiently tested in climate models on long time scales.

In alkenone SSTs, the millennial variability seems to be a robust feature though the Holocene (Rimbu et al., 2004). Wirtz et al. (2010) report furthermore on change in climate variability in the early to mid-Holocene which might influence regional temperature. However, Moros et al. (2004) report on case studies from the northern North Atlantic Ocean that planktonic  $\delta^{18}\text{O}$  shows a “rather flat early- to mid-Holocene and a marked increase in amplitude and decrease in mean values from about 4 kyr BP” which could be linked to pronounced variations in the recorder system associated to different seasons and water depths. Large millennial variability in the data can mask the temperature trend and other factors as insolation may affect the climate (Bond et al., 2001; Sundqvist et al., 2010). Because we have taken the temperature trends only, we eliminated to a large extent the effect of millennial climate variability in our analysis (Figs. 1 and 2).

#### 4.10 Climate models: sensitivities to long-term changes

Climate sensitivity is defined in the sense of Charney (1979), in which fast feedback processes are allowed to operate, but long-lived atmospheric gases, ice sheet area, land area and vegetation cover are considered as fixed forcings. Fast feedbacks include changes of water vapor, clouds, climate-driven aerosols, sea ice, and snow cover. The inference, that models do not capture the Holocene trends with respect to the amplitude found in the records could raise doubt about the correct representation of climate sensitivity in the climate models on long time-scales.

Laepple and Lohmann (2009) calculated empirically the Holocene temperature evolution based on the analogy with the temperature response to the seasonal cycle. It turned out that the climate patterns resemble the large-scale features of the modeled Holocene trend (Lorenz and Lohmann, 2004), but the amplitude and regional changes associated with circulation changes are not well captured. By construction, long-term

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5 feedbacks are missing in such an approach. It is conceivable that present climate models neglect in a similar way long-term feedbacks amplifying the obliquity forcing. Future sensitivity studies shall identify potential missing positive feedbacks in the system. Indeed, experiments indicate potential positive feedback amplifying external forcing which is related to details in the representation of vegetation and albedo in the models (O'ishi and Abe-Ouchi, 2011). Their warming is due to direct amplification of warming over high latitude land through increases in vegetation and reduced albedo during the summer and indirect amplification through sea-ice feedback in autumn and winter and snow albedo feedback in spring. Further model studies are necessary to  
10 examine whether the climate sensitivity has been underestimated at least in the coastal areas.

We have to identify the model-data discrepancy in order to have a reliable estimate of simulated temperature trends of the past, their error bars, as well as an estimate of climate sensitivity on long time scales. It could be that current climate simulations underestimate the full range of climate warming on centennial to millennial time scales that might arise as a result of anthropogenic greenhouse gas emissions. The concept of climate sensitivity relies on the responses of slow feedback processes to forcing and subsequent involved feedback mechanism (Hansen et al., 2007). It is therefore  
15 likely that the climate sensitivity (to greenhouse gas forcing and orbital forcing) is much greater than that due to fast feedbacks.  
20

## 5 Conclusions

Our study shows that model simulations of the Holocene temperature evolution largely agree with respect to the trend pattern recorded in alkenones but are unrelated to the trend pattern recorded in Mg/Ca. In general, the amplitudes of the simulated trends  
25 are significantly smaller than the reconstructed temperature trends. This deviation persists for all considered models, even if we take into account seasonality and different water depths at which the recording organisms may have lived. This raises important

questions as to whether climate models have deficiencies, and/or whether our understanding of the recorder system linked to the proxy records still needs to be refined.

We evaluate several mechanisms that can be responsible for the observed mismatch between the reconstructed and the modeled magnitude of the Holocene SST trends.

5 These are systematic changes in the living season over the course of the Holocene and a varied habitat depth of the SST signal carriers. In many cases (up to 62 % for alkenones and 42 % for Mg/Ca in our study) the mismatch between proxy and simulation may be removed if these mechanisms are considered. The amount of vertical shift of the recorder depth, or of the shift of the living season, that are needed to remove the model-proxy mismatch, is within ranges that we consider realistic for climatic changes  
10 over the last 6 kyr.

We consider the model-data mismatch of Holocene temperature trends as being indicative of either model deficiencies or data particularities with respect to the planktonic organisms' ecology. When interpreting the proxy records two assumptions regarding  
15 the stationary of seasonality and habitat depth can be made. First, one could assume that the seasonality and the habitat depth of planktonic organisms did not change under varying climate conditions during the Holocene. Such assumption is generally applied while interpreting paleo-reconstructions because it is difficult to assess how hydrographical changes occurred over contrasting seasons and habitat depths in the  
20 past. In such case, a good knowledge of the modern seasonality and living depth of coccolithophorids and foraminifera would be sufficient for the interpretation of the temperature record. Second, one could assume that living season and the habitat depth may have changed over time. In such a likely situation, the interpretation of the proxy record becomes more difficult. However, considering ecological limits of seasonality and habitat depth, the model simulations can be used to extract the range of  
25 possible proxy trends consistent with the simulated climate. Ecophysiological models accounting for planktonic foraminifera ecology capture most of the first-order seasonal and depth habitat preferences of the most commonly used species for Mg/Ca-based reconstructions (Fraile et al., 2009a; Lombard et al., 2011). These models have further

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pointed out that any past climate change affecting surface ocean characteristics may alter foraminifera-derived SST climatic signals by modulating environmental characteristics for which planktonic foraminifera have optimal living conditions (Fraile et al., 2009b; Bassinot et al., 2011). It is also conceivable that oceanic vertical mixing caused by atmospheric circulation and synoptic storms can affect the coccolith bloom period (Moros et al., 2004).

Our work shows that the model under- and/or the data overestimation of the Holocene temperature evolution is indeed a global and persistent feature that might be weakened, but not completely removed, if we consider proxies through their ecological prism. We show that differences in the magnitude of Holocene SST trends between model simulations on the one hand, and a global data set of alkenone- and Mg/Ca-derived paleo-temperatures on the other hand, can be reconciled to some degree by considering shifts in seasonality and habitat depth – two parameters known to be relevant for understanding alkenone and Mg/Ca paleothermometry in the modern ocean.

This suggests that the discrepancy between our proxy database and the considered climate models is not only caused by a specific problem of the marine records used in this study, but a general problem that also occurs in other model-data comparisons (Brewer et al., 2007; Sundqvist et al., 2010; Zhang et al., 2010; O'ishi and Abe-Ouchi, 2011). At northern high latitudes, Sundqvist et al. (2010) report an annual mean 2°C cooling from the mid Holocene to preindustrial values, again larger than the model trends. A similar systematic deviation is also found for  $\delta^{18}\text{O}$ -derived temperature trends from Greenland and Antarctic ice cores (Masson-Delmotte et al., 2006). They found that most models capture the correct sign of the reconstructed temperature change on Greenland, but underestimate its amplitude by a significant factor (e.g. Vinther et al., 2009).

It is therefore conceivable that the observed mismatch between modeled and reconstructed Holocene climate evolution is related to the representativeness of long-term temperature trends in climate models. The models may be not sensitive enough with

respect to insolation, may not be able to fully capture the natural range of climate variability, or might have regional biases linked to the fact that the proxy data records used in this study are located in coastal areas which are challenging to simulate with global climate models. Further studies are required to examine possible feedback mechanisms affecting the long-term climate sensitivity.

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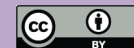
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**Table 1.** Best fit for alkenone and Mg/Ca records for different layers of the ocean.

Depth (m)	10	10–30	30–50	50–75	75–100	Below 100
Alkenone records %	~33	~12	~10	~17	~6	~21
Mg/Ca records %	~32	~5	~11	~16	~11	~26

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**Table 2.** Overview on the agreement between model and proxy data. We list cores that agree with the model simulation at some time during the year and summarize the number of cores that could be reconciled with the model simulation by assumed shifts of <20 m of the habitat depth and <14 days of the blooming season. We also list cores that show a difference of more than 2 °C to the model simulation, and note cores that might be biased by calibration uncertainties.

Filters	Cores that agree during annual cycle	Shift in depth of <20 m	Shift in time of <14 days	Shifts <20 m and <14 days	Model-data difference >2 °C	Calibration uncertainties
Alkenone records %	~42	~37	~52	~62	~17	~38
Mg/Ca records %	~53	~26	~21	~42	~11	N. A.

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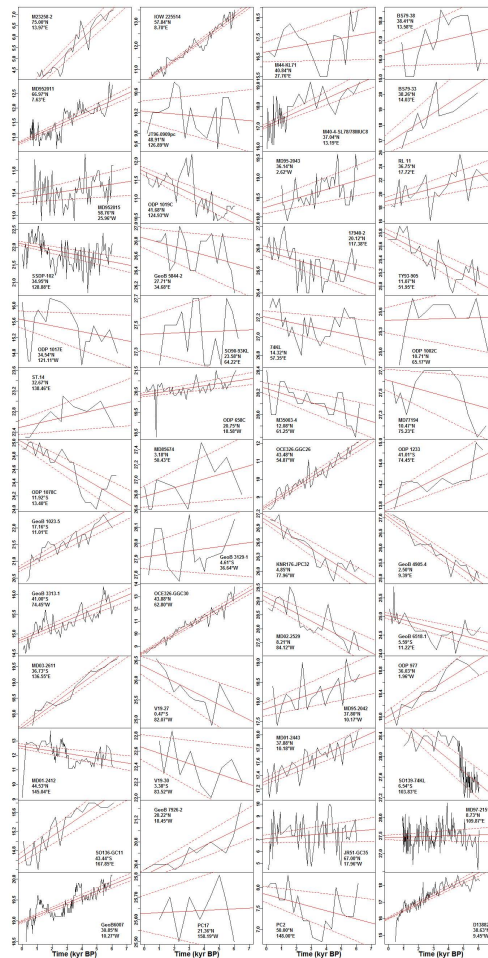
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**Fig. 1.** Alkenone SST Holocene reconstruction (black) of the 52 cores considered in this study: linear fitted trend and standard error ranges (red), calculated using a linear model. Units are °C. Name and position are included in the panels.



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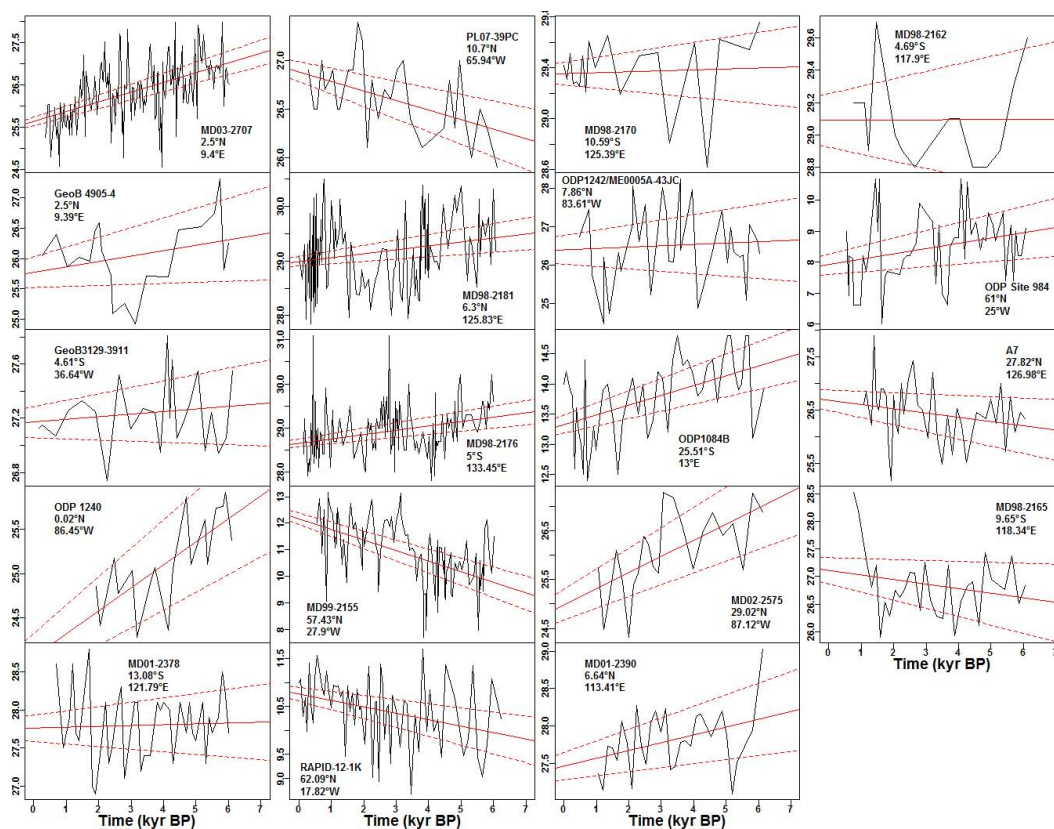


Fig. 2. As Fig. 1, but for Mg/Ca records.

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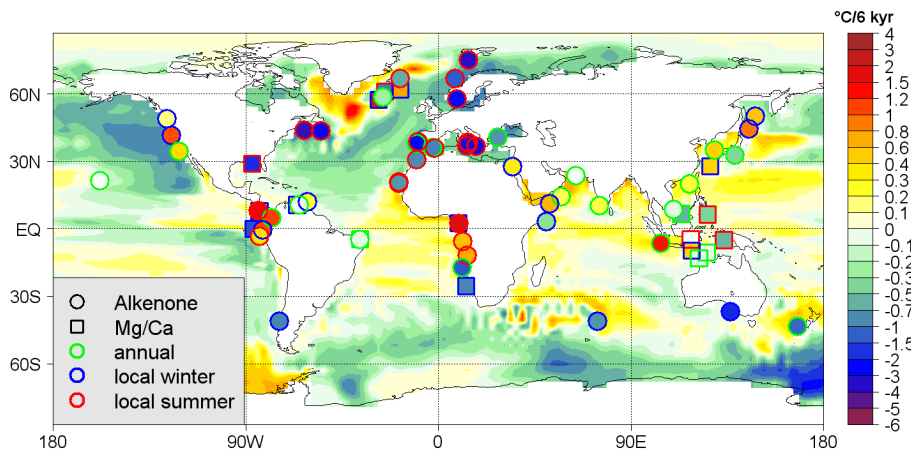
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**Fig. 3.** Global SST trends of the annual mean ECHO-G model output, and local temperature trends based on alkenone and Mg/Ca reconstructions. The circles and squares localize the alkenone and Mg/Ca records, respectively, the colors that fill the circles/squares show the temperature trend they record. The border colors of the circles/squares represent the annual mean/season in which the reconstruction agrees best with the model simulation.

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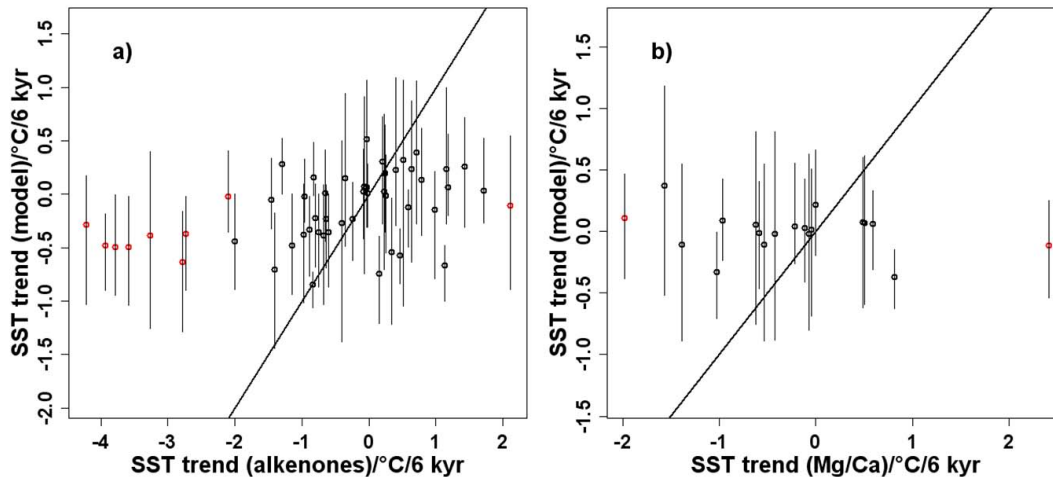
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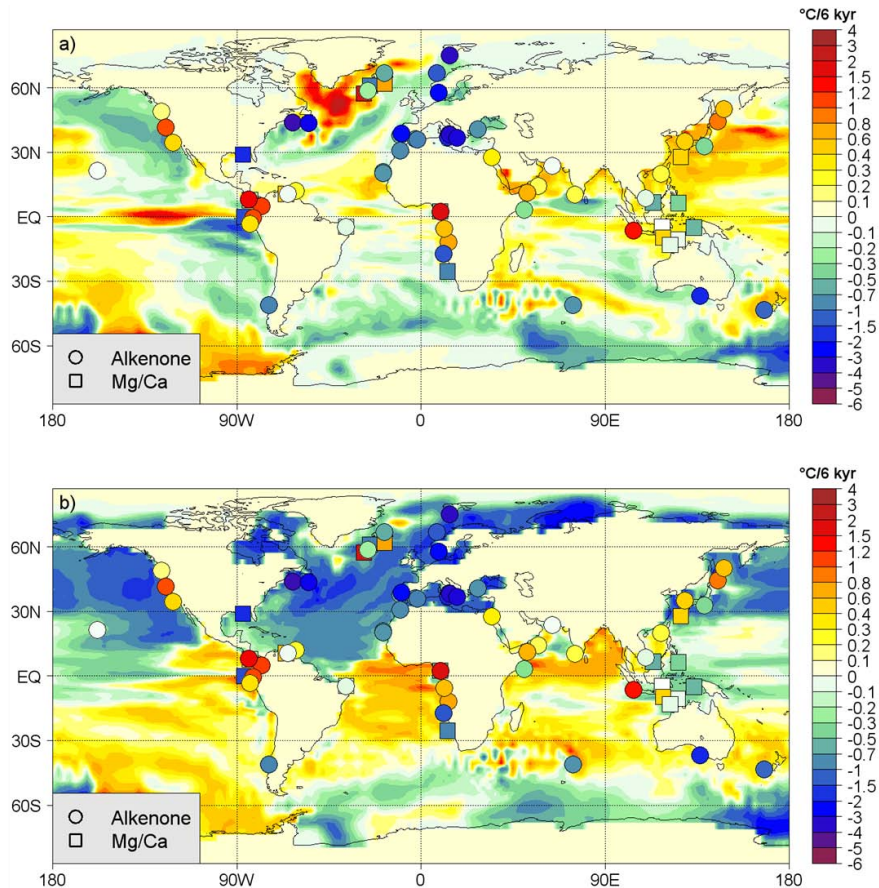
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**Fig. 4.** (a) Alkenone-based temperature trends plotted against annual mean SST trends derived from the ECHO-G model. The red data markers represent cores for which the difference to the climate model simulation exceeds 2 °C. The bars show the range of intra-seasonal variation within the ECHO-G model during the year at the respective location. (b) As (a), but for Mg/Ca-based temperature trends.

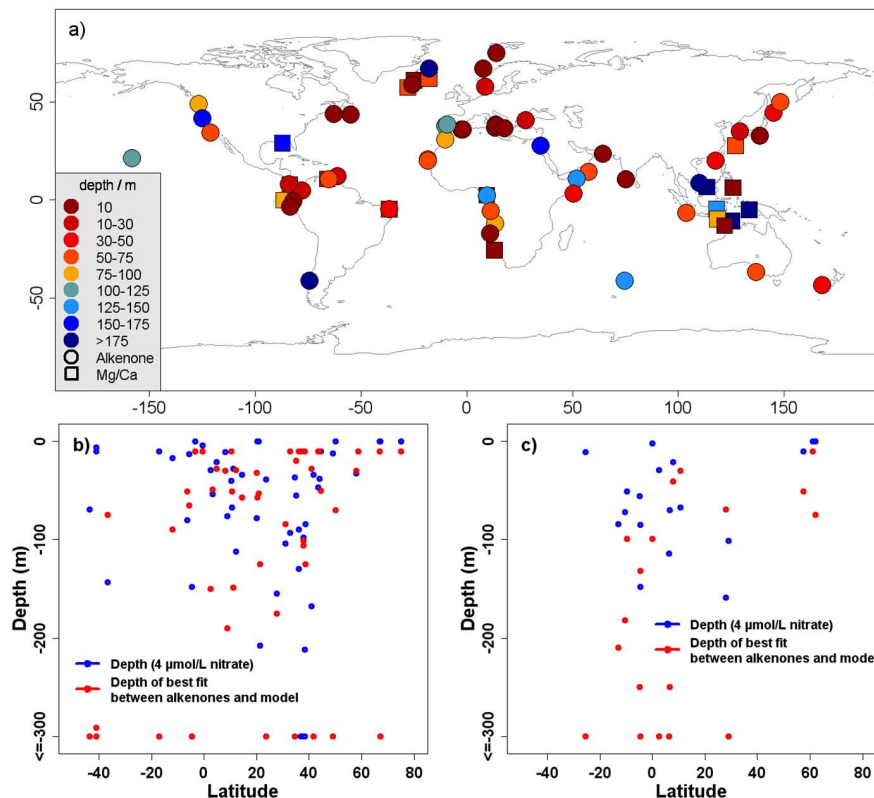
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**Fig. 5.** Local temperature trends based on proxy reconstructions and seasonal SST trends taken from the ECHO-G climate simulation for (a) local winter and (b) local summer. The circles and squares represent the locations of alkenone and Mg/Ca records, respectively; the fill-color of the data marker represents the recorded temperature trend.

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**Fig. 6.** (a) Depth for best agreement between alkenone and Mg/Ca temperature reconstructions and model simulation. The filled circles/squares the depth interval in which the best fit falls. (b) Depth of best fit between alkenone and model temperature trend (red dots) and depth where nitrate concentration is  $4 \mu\text{mol l}^{-1}$  (blue dots). (c) As (b), but for Mg/Ca-based temperature trends.

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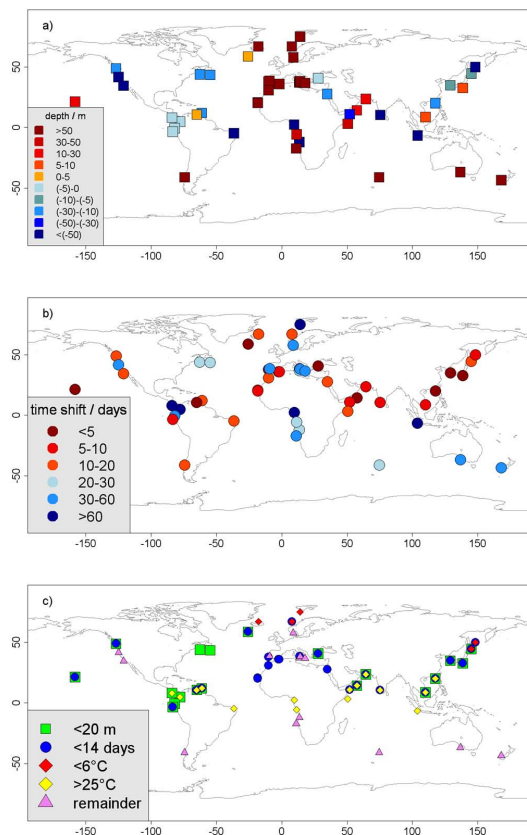
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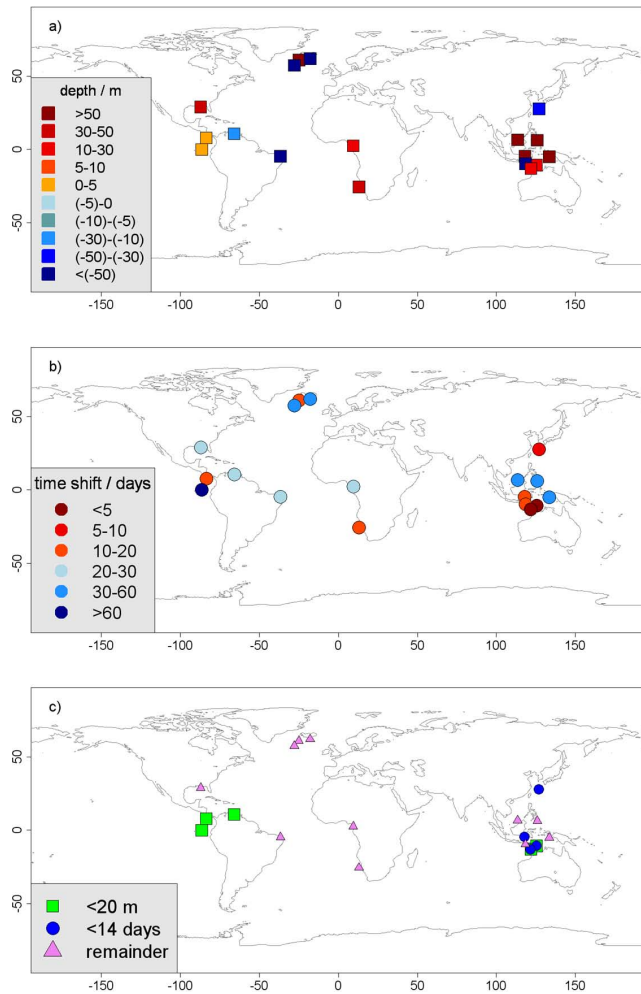
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**Fig. 7.** (a) Vertical shift that is needed to minimize model-data disagreement. (b) Time shift that is needed to minimize model-data disagreement. (c) Global SST trends of the annual mean model output. The icons indicate the location of alkenone-proxy records and the time- or vertical- shift that is needed to minimize the disagreement between the model simulation and data reconstruction.



**Fig. 8.** As Fig. 7, but for Mg/Ca-based temperature trends.

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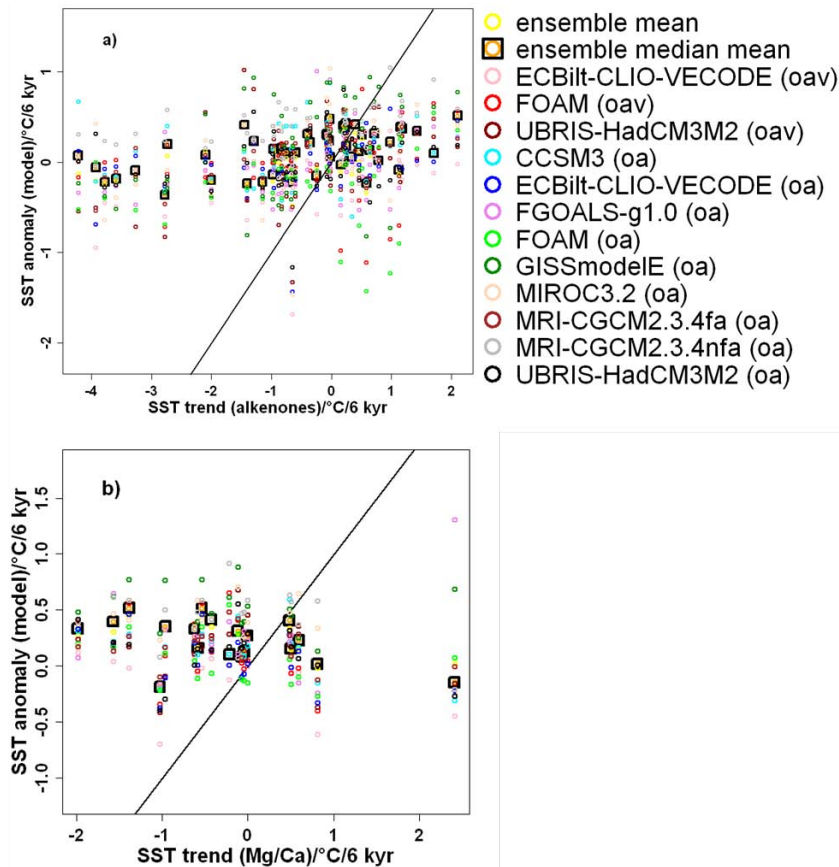
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**Fig. 9.** (a) Global alkenone-based SST trends compared to simulated annual mean SST anomalies in the models listed in PMIP2. The black squares represent the ensemble mean and the colors correspond to a specific model. (b) Global Mg/Ca- based SST trends compared to the models of the PMIP2 annual mean SST anomalies.

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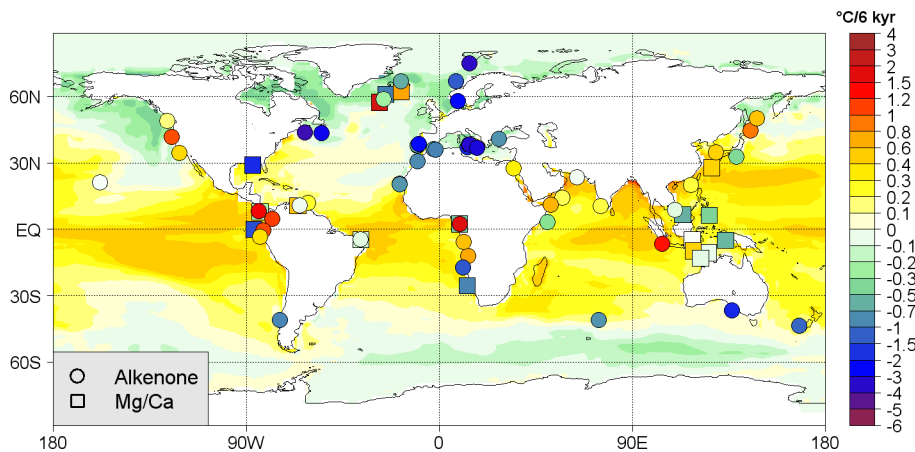
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**Fig. 10.** Global alkenone-based SST trends compared to simulated annual mean SST anomalies as calculated from the ensemble median mean of the models listed in PMIP2.

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