

Article

The Relative Stability of Planktic Foraminifer Thermal Preferences over the Past 3 Million Years

Harry Dowsett ^{1,*}, Marci Robinson ¹, Kevin Foley ¹, Timothy Herbert ², Stephen Hunter ³,
Carin Andersson ⁴ and Whitney Spivey ¹

¹ U.S. Geological Survey, Florence Bascom Geoscience Center, Reston, VA 20192, USA

² Department of Earth, Environmental and Planetary Sciences, Brown University, Providence, RI 02912, USA

³ School of Earth and Environment, University of Leeds, Leeds LS2 9JT, UK

⁴ NORCE Norwegian Research Centre, Bjerknes Centre for Climate Research, N-5007 Bergen, Norway

* Correspondence: hdownsett@usgs.gov

Abstract: Stationarity of species' ecological tolerances is a first-order assumption of paleoenvironmental reconstruction based upon analog methods. To test this and other assumptions used in quantitative analysis of foraminiferal faunas for paleoceanographic reconstruction, we analyzed paired alkenone unsaturation ratio (U_{37}^K) sea surface temperature (SST) estimates and relative abundances of planktic foraminifera within Late Pliocene assemblages. We established Pliocene temperature preferences for nine species in the North Atlantic: *Dentoglobigerina altispira*, *Globorotalia menardii*, *Globoconella puncticulata*, *Neogloboquadrina atlantica*, *Neogloboquadrina incompta*, *Neogloboquadrina pachyderma*, *Trilobatus sacculifer*, *Globigerinita glutinata*, and *Globigerina bulloides*. We compared these to the temperature preferences of the same extant species, and in the three cases where the species are now extinct (*Dentoglobigerina altispira*, *Neogloboquadrina atlantica*, and *Globoconella puncticulata*), comparisons were made to either the descendant species or other modern species commonly used as analogs. In general, the taxa tested show similar temperature responses in both Late Pliocene and present-day (core-top) distributions. The data from these comparisons are mostly encouraging, supporting past paleoceanographic conclusions, and are otherwise valuable for testing previous taxonomic grouping decisions that are often necessary for interpreting the paleoenvironment based upon Pliocene foraminiferal assemblages.

Keywords: Pliocene; planktic foraminifera; thermal niche; sea surface temperature; alkenones; uniformitarianism



Citation: Dowsett, H.; Robinson, M.; Foley, K.; Herbert, T.; Hunter, S.; Andersson, C.; Spivey, W. The Relative Stability of Planktic Foraminifer Thermal Preferences over the Past 3 Million Years.

Geosciences **2023**, *13*, 71.

<https://doi.org/10.3390/geosciences13030071>

geosciences13030071

Academic Editor: Spencer G. Lucas

Received: 1 February 2023

Revised: 23 February 2023

Accepted: 27 February 2023

Published: 2 March 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Uniformitarianism, simply stated as “the present is the key to the past”, is based upon the seminal work of James Hutton and was popularized by Charles Lyell [1,2]. This principle has had far-reaching effects on the geological sciences in general and specifically on paleontology and the interpretation of ancient environments through modern analogs. Taxonomic uniformitarianism as used here refers to the stationarity of a species' ecological preference over time. Here we focus on planktic foraminifera, ubiquitous in the world's oceans today and throughout the Cenozoic, and their relationship to sea surface temperature (SST). Temperature is the dominant driver of planktic foraminiferal species distributions, often overwhelming all other ecological factors, especially in the North Atlantic Ocean [3–8].

Planktic foraminiferal census data have been routinely used to quantitatively estimate paleoceanographic SSTs since the 1970s, when a method for deriving factor analytic transfer functions was introduced [9]. The Imbrie–Kipp method (IKM) relates modern species abundance data to present-day physical oceanographic parameters. Equations are then derived that can be applied to fossil assemblages to make quantitative estimates of paleoenvironments. This technique was used extensively in the CLIMAP reconstruction

of the Last Glacial Maximum [10] and later the Last Interglacial [11]. The IKM and other methods such as the Modern Analog Technique (MAT), in which fossil assemblages are assigned the SST of the most analogous assemblage within a modern dataset [12], and methods using artificial neural networks to discover patterns within data [13,14] all rely upon the basic assumption that modern foraminiferal faunas can be used as analogs to interpret Quaternary assemblages. For example, Late Pleistocene glacial and interglacial SSTs have been reconstructed from planktic foraminiferal assemblages [10,15–17]. Indeed, Antell et al. [18] have shown that the 100,000-year glacial–interglacial SST cycle over the last 700,000 years has not affected the temperature preferences of planktic foraminifera.

Kucera and Schonfeld [19] documented that the modern foraminiferal fauna was established by ~4 Ma, suggesting that calibration of species tolerances in sediments older than the initiation of Northern Hemisphere glaciation might not be valid. Thus, extending these methods to deeper time settings means perhaps inappropriately applying the concept of taxonomic uniformitarianism for the temporal range of the species, up to several million years and across notable paleoclimate transitions. It also requires additional assumptions to address extinction and evolution of species [20–26]. Nevertheless, the USGS Pliocene Research, Interpretation and Synoptic Mapping (PRISM) Project applied modern species–temperature associations to foraminiferal census data in the 3.3 Ma to 3.0 Ma interval within the Piacenzian Stage of the Pliocene [27]. The resulting temperature estimates, in combination with geochemical proxies for SST, have formed the cornerstone of several iterations of PRISM global paleoenvironmental reconstructions [28–32]. PRISM SST data, in turn, have been routinely used to initiate atmospheric general circulation model experiments and verify coupled ocean–atmosphere experiments [27,33–38]. Here, we test the validity of extending the assumption of taxonomic uniformity to the mid-Piacenzian by plotting Pliocene species abundances against independently derived SST data and then comparing these Pliocene temperature distributions to those of modern taxa.

This work utilizes the extensive PRISM planktic foraminiferal census dataset [39] and associated alkenone-based SST estimates to document the temperature preferences of Pliocene species, examine the assumption of species’ temperature range stability over millions of years, and address some additional assumptions required to extend quantitative assemblage methods to Pliocene-age faunas. We focus these initial tests on the North Atlantic Ocean where the dataset is of the highest temporal and geographical resolution and where the relationship between species distributions and SST is strong. We examine six extant Pliocene species: *Neogloboquadrina pachyderma*, *Neogloboquadrina incompta*, *Globigerina bulloides*, *Globorotalia menardii*, *Trilobatus sacculifer*, and *Globigerinita glutinata*; three extinct Pliocene species: *Dentoglobigerina altispira*, *Globoconella puncticulata*, and *Neogloboquadrina atlantica*; and the modern species *Globoconella inflata*, the descendant of *Gl. puncticulata*. Our results help to define the nature of taxonomic uniformity over millions of years and reinforce North Atlantic species’ temperature associations and their application to paleoceanography.

2. Materials and Methods

2.1. Geographic Distribution of Pliocene Samples

We focus on the North Atlantic Ocean because it is here that we have the highest concentration of sites. Moreover, the response of species distributions in the North Atlantic to SST is especially strong [40]. Our Pliocene dataset contains 341 paired samples from the mid-Piacenzian Stage of 18 localities where we have both alkenone SST estimates and faunal assemblage data (Figure 1, Table S1). To increase coverage in the tropics, we supplement the North Atlantic data with 23 mid-Piacenzian samples from an additional site (ODP Site 1115) in the western equatorial Pacific (Solomon Sea).

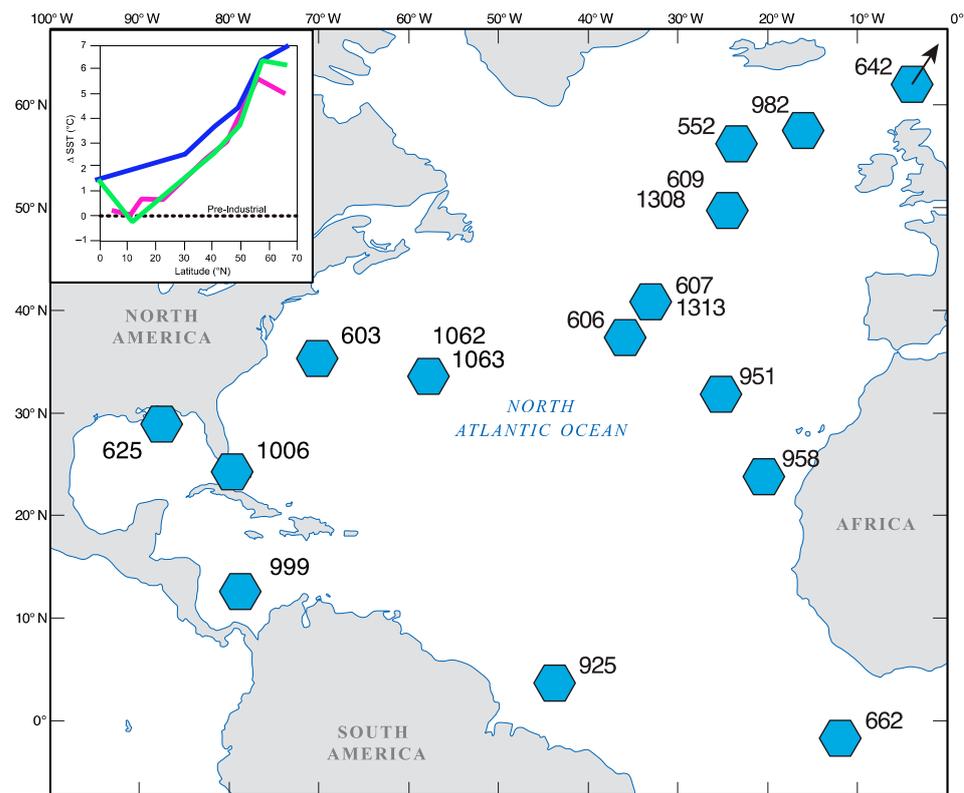


Figure 1. Map of Pliocene core sites. Geographic location of 18 North Atlantic sites used in this study. Inset figure shows North Atlantic temperature gradients as anomalies from the pre-industrial gradient (horizontal black dashed line). Multiproxy gradient from Dowsett et al. [41], pink; PRISM4 alkenone-based gradient from Dowsett et al. [42], green; PlioVAR (Pliocene Climate Variability over glacial–interglacial timescales) gradient based on alkenone SST estimates from McClymont et al. [43], blue. PRISM4 and PlioVAR gradients are based upon alkenone analyses calibrated to Müller et al. [44].

2.2. Faunal Census Data

Piacenzian faunal assemblage data were generated from the 19 Deep Sea Drilling Project, Ocean Drilling Program, Integrated Ocean Drilling Program, and International Ocean Discovery Program localities (Figure 1; Tables S1 and S2) in the Global Planktic Foraminifer dataset for the Pliocene ocean [39]. In most cases, 10–20 cc samples were acquired from a split core using a cylindrical plug, oven-dried at ≤ 50 °C, and then soaked and agitated in water with ~ 2 mL of dilute sodium hexametaphosphate solution (5 g to 1 L water) for 1–2 h. Samples were then washed over a 63μ sieve until clean, oven-dried at ≤ 50 °C, then dry-sieved to concentrate the $\geq 150 \mu$ fraction. Samples were split to obtain ~ 300 planktic foraminifer specimens and placed on a 60-cell faunal micropaleontology slide, identified into species, and counted. Taxa are reported in relative abundances within samples, and while this metric is affected by the diversity of each sample, we consider it the most meaningful representation of species temperature preference for this study. While the actual flux of various species may be more informative, many of the sites we incorporate do not have the data necessary to estimate mass accumulation rates and fluxes of planktic foraminifera to the sea floor.

Pre-industrial (core-top) planktic foraminiferal assemblage data were extracted from the ForCenS database of planktic foraminifer census counts [45]. We extracted 2068 samples designated as “Atlantic” from the original 6984 samples in ForCenS. Removing duplicates further reduced the number of North Atlantic core-top samples to 932. These core localities provide coverage of the full range of modern North Atlantic biogeographic zones (see also Figure S1).

2.3. Sea Surface Temperature

We use the Merged Hadley-OI SST and sea ice concentration dataset, Version 5.0 1-degree [46] to represent pre-industrial (PI) conditions. We extracted and averaged the monthly data from 1870–1899 and then used linear interpolation to derive mean annual SSTs and monthly means for each of the 932 ForCenS core-top sediment samples.

For Pliocene samples, alkenone temperature estimates are based upon the $U_{37}^{K'}$ paleotemperature index and derived from estimates provided in Dowsett et al. [47] except for data from Site 642, which are from Bachem et al. [48]. In all cases, SSTs are reported using the Müller et al. [44] calibration for mean annual temperature. The $U_{37}^{K'}$ index has an upper limit of ~ 28.5 °C [49] capping our Pliocene SST estimates and a calibration uncertainty of ± 1.38 °C [50]. The mid-Piacenzian North Atlantic was generally warmer than during the PI [42,43,51], and all Pliocene SST estimates exceed 10 °C, though lower temperatures are found in the PI dataset.

2.4. Chronology

Both the alkenone estimates and faunal census data are from the mid-Piacenzian intervals of all sites (~ 3.3 Ma to ~ 3.0 Ma), based on the published ages assigned to each sample. In most cases, both $U_{37}^{K'}$ SST estimates and relative abundance data were collected from the same samples. Where both data types were not available from the same samples, SST data series were interpolated to obtain values for the same depths as the faunal census data.

3. Results

3.1. Temperature Response of Pliocene Species

Relative abundances of nine taxa from the mid-Piacenzian are compared to SST estimates of the same age derived using alkenone paleothermometry (Figure 2). Figure 2 shows SSTs between 10 °C, the coolest estimate in our dataset, and 28.5 °C, the upper limit of the alkenone paleothermometer. Three types of temperature responses are revealed: taxa with maximum abundance at the warmest temperatures, at the coolest temperatures, and near the middle of the SST range (~ 20 °C).

Warm taxa include *D. altispira*, *T. sacculifer*, and *Gl. menardii*, which all show a preference for warm SSTs with maximum relative abundances at the upper end of the alkenone methodology (~ 28.5 °C). *Neogloboquadrina atlantica*, common in Pliocene North Atlantic sediments [26,52–56], is considered the cold endmember of the genus (see also Figure S1, Table S3). In the North Atlantic, *N. atlantica* has a temperature response opposite to the warm species with very few occurrences (relative abundance < 0.1) at temperatures > 22 °C and a rapid increase with decreasing temperature, so it often dominates Pliocene assemblages with relative abundance > 0.8 at temperatures ≤ 15 °C (Figure 2). The remaining species, *N. pachyderma*, *N. incompta*, *Gl. puncticulata*, *G. bulloides*, and *Gt. glutinata*, have maximum abundances (over the 10 °C to 28.5 °C range) in samples centered on ~ 20 °C. *Globigerinita glutinata* exhibits two maxima, one near 20 °C and a second skewed toward the warmest temperatures, similar to the warm species listed above (Figure 2).

3.2. Temperature Response of Pre-Industrial Core-Top Species

The thermal distributions of extant Pliocene taxa are shown in Figure 3 where North Atlantic core-top assemblage data are plotted against PI SSTs. The modern distribution patterns of extant taxa are largely like their mid-Piacenzian distributions in that the warm taxa *T. sacculifer* and *Gl. menardii* increase in abundance with temperature increase, while *N. incompta*, *G. bulloides*, and *Gt. glutinata* show maximum abundances in the middle of the 10 °C to 30 °C temperature range. *Neogloboquadrina pachyderma* shows a clear increase in relative abundance towards colder temperatures (< 10 °C). From the 10 °C to 30 °C range, the thermal responses of both Pliocene and PI *N. pachyderma* are similar (Figure 3). The warmer high-latitude temperatures of the mid-Piacenzian North Atlantic compared to

those of the PI are apparent in these plots, as minimum mid-Piacenzian SST estimates are $\sim 10^{\circ}\text{C}$, and PI estimates are as cool as $\sim 2^{\circ}\text{C}$.

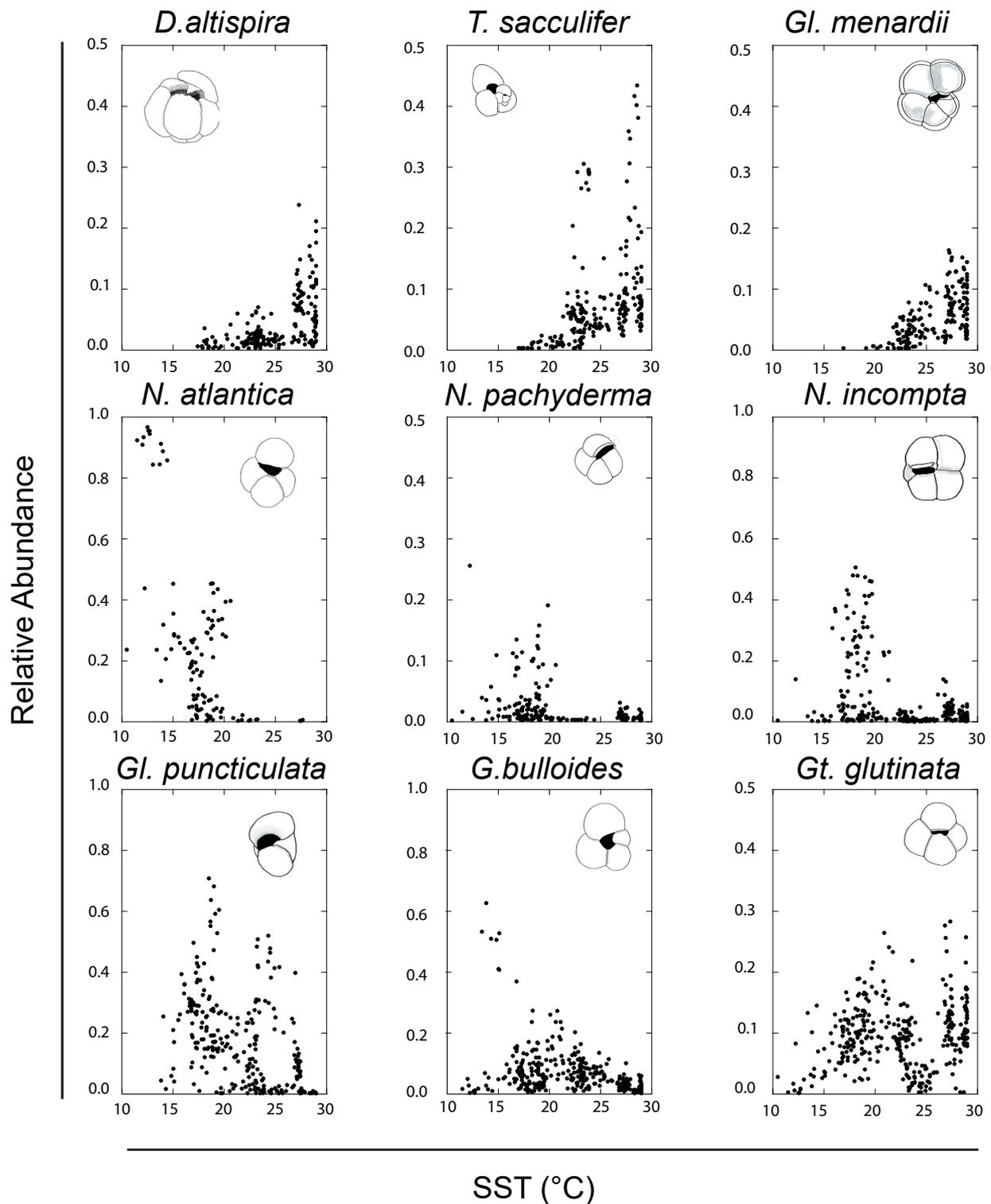


Figure 2. Temperature responses of nine species of Pliocene planktic foraminifera found in the North Atlantic. Sea surface temperatures derived using the $U_{37}^{K'}$ index range from 10°C to 30°C and are plotted against the relative abundance of species (0.0 to 1.0) within each sample. See text.

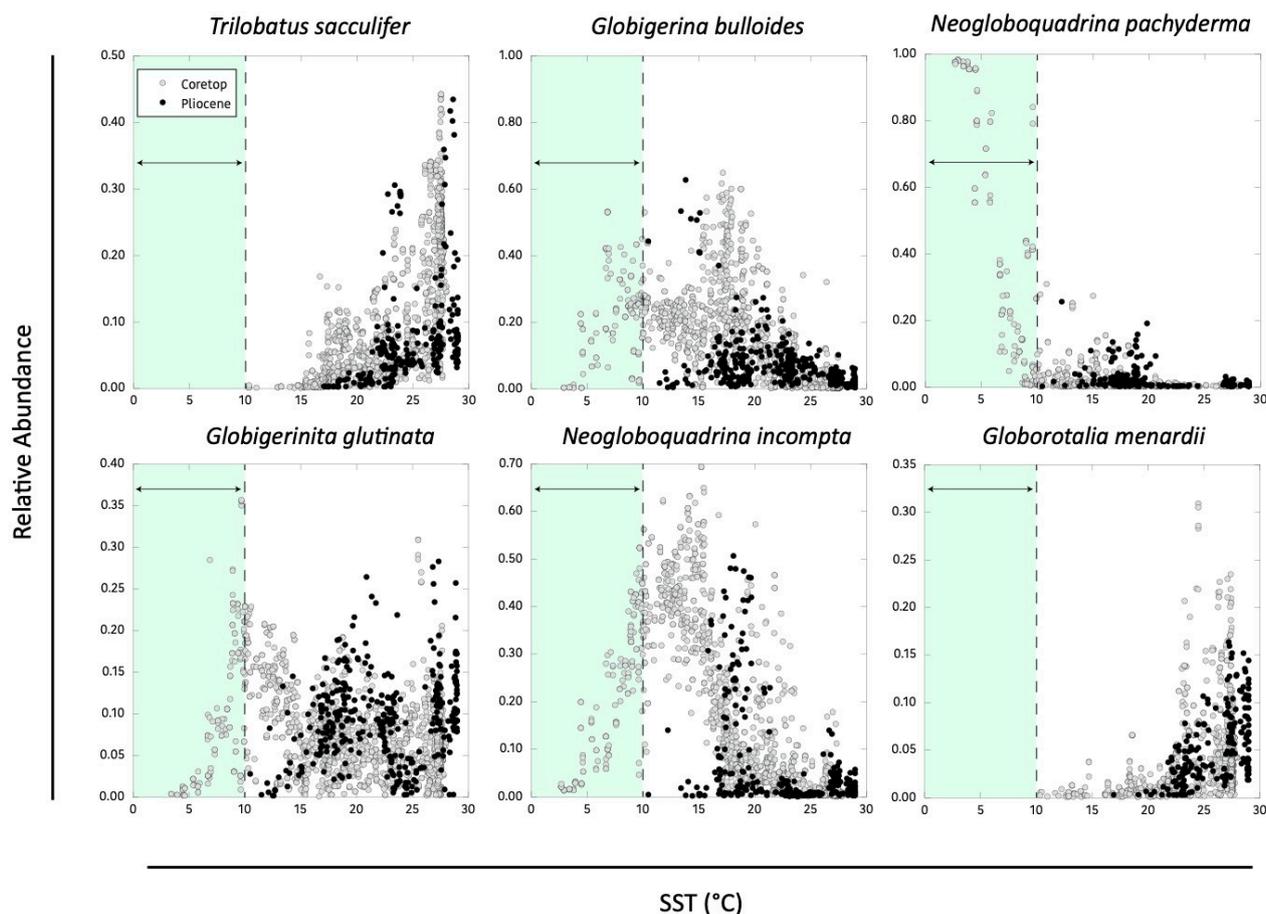


Figure 3. Comparison of extant species found in the North Atlantic. Scatter plots of relative abundance and alkenone-based SSTs for six extant species showing core-top (gray) and Pliocene (black) distribution. Dashed vertical lines at 10 °C indicate the lower temperature limit of Pliocene North Atlantic data. Horizontal arrows and green shading highlight the 0 °C to 10 °C region of only core-top data in each plot.

3.3. Comparison of Pliocene and PI Temperature Responses

The difference between mid-Piacenzian and PI North Atlantic latitudinal temperature gradients are shown in Figure 1. Mid-Piacenzian SSTs were warmer than during the PI, and the degree of additional warmth increases with increasing latitude [37,41–43]. These relatively warm high-latitude temperatures limit our ability to fully assess the thermal niche of species, especially those preferring cold temperatures. Therefore, the following results are restricted to the 10 °C–30 °C temperature responses of taxa.

3.3.1. Extant Taxa

Globigerina bulloides is a subpolar species [7] with a bimodal temperature distribution in the North Atlantic today (Figure 3). In warmer regions, it is usually associated with cooler surface waters and increased nutrients characteristic of upwelling. During the mid-Piacenzian, *G. bulloides* is associated with a wide range of SSTs with a broad response centered on ~20 °C within the range of the warmer modes recorded for this species in the core top. Since North Atlantic SSTs were warmer in the Pliocene, and since upwelling waters were also warmer, we do not record the lower temperature mode.

Globigerinita glutinata is present in core-top samples from subpolar through tropical regions. Our Pliocene data show a distribution that spans the range of temperature seen in core-top samples (Figure 3) with maxima near 20 °C and at the warm end of the range. Spatially, both core-top and Pliocene distributions show maximum abundances in the southwest and northeast North Atlantic (Figure S1).

Trilobatus sacculifer and *Gl. menardii* have core-top spatial distributions (Figure S1) that track gyre-margin (tropical-subtropical) conditions [40]. Both species have mid-Piacenzian and PI relative abundances that increase with temperature, indicating a preference for the warmest conditions (Figure 3). Each of these species shows a Pliocene temperature preference within the range of those recorded for the same species in the core top (Figure 3).

Neogloboquadrina pachyderma is a well-known polar species with affinities for cold temperatures at the core top [40,55,57]. Figure 3 shows PI *N. pachyderma* present in very low abundances at temperatures warmer than $\sim 10^{\circ}\text{C}$, rapidly increasing between 10°C and 5°C , where it routinely comprises nearly 100% of the core-top assemblage. In Pliocene samples between 10°C and 30°C , *N. pachyderma* shows abundances like those found in the core-top data at the same temperatures. *Neogloboquadrina pachyderma* had a more restricted range of preferred temperature during the Pliocene, and/or it was displaced relative to core-top distributions by other taxa. During the mid-Piacenzian, *N. atlantica* was the dominant cool species, rapidly increasing from a relative abundance of 0.4 near 20°C to 0.9 by 15°C (Figure 2). *Neogloboquadrina pachyderma* reaches maximum relative abundances of ~ 0.20 in both core-top and mid-Piacenzian datasets in samples between 10°C and 30°C (Figures 2 and 3).

Neogloboquadrina incompta is a common subpolar species today, reaching maximum core-top relative abundances of ~ 0.6 at temperatures of $\sim 15^{\circ}\text{C}$ (Figure 3). Our Pliocene data show similar relative abundances between 17°C and 30°C , but unlike the core-top data, Figure 3 shows a cluster of low-abundance samples near 15°C derived from sites 552 and 982. The relative abundances of this species and *N. pachyderma* during the Pliocene were influenced by the spatial distribution of *N. atlantica* (see below).

3.3.2. Extinct Taxa

The relative abundance data presented in Figure 4 allow us to estimate temperature preferences of some extinct taxa. Through comparisons to extant taxa, we can assess the taxonomic groupings used by PRISM when interpreting Pliocene planktic foraminiferal assemblages, specifically for SST estimation.

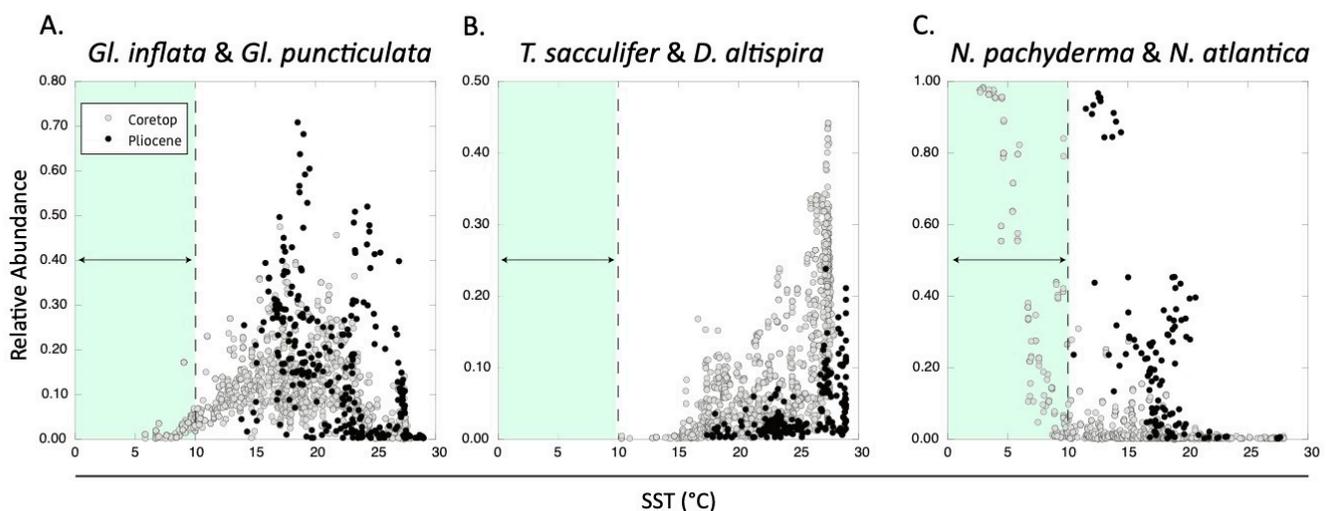


Figure 4. Assessment of previous taxonomic groupings of extinct planktic foraminifera taxa. (A) *Globoconella inflata* (core top) and *Globoconella puncticulata* (Pliocene), (B) *Trilobatus sacculifer* (core top) and *Dentoglobigerina altispira* (Pliocene), (C) *Neogloboquadrina pachyderma* (core top) and *Neogloboquadrina atlantica* (Pliocene). Pliocene data (black); core-top data (gray). Dashed vertical lines at 10°C indicate the lower temperature limit of Pliocene North Atlantic data. Horizontal arrows and green shading highlight the 0°C to 10°C region of only core-top data in each plot.

We compare *Gl. puncticulata* to *Gl. inflata*. *Globoconella puncticulata* occurs in Pliocene North Atlantic samples but disappears near the Piacenzian-Gelasian boundary [58–61]. *Globoconella inflata*, present in core tops, evolved from *Gl. puncticulata* during the Early Pliocene in the Southwest Pacific region [62]. The two species have similar biogeographic distributions in the North Atlantic (Figure S1) and have previously been considered to have similar environmental tolerances when interpreting paleoceanographic conditions [21,23,26]. *Globoconella puncticulata* has a very similar distribution to the core-top distribution of *Gl. inflata* (Figure 4).

We compare *D. altispira* to *T. sacculifer*. *Dentoglobigerina altispira* is present in North Atlantic Pliocene samples but became extinct at ~3 Ma [60]. Environmental preferences for this taxon have previously been based upon its negative $\delta^{18}\text{O}$ values compared to other elements of the assemblage [63–66] and its geographic distribution during the Pliocene (Figure S1), which shows greatest abundance in tropical regions [42,55]. The relative abundance of *D. altispira* in Pliocene samples increases with temperature, not unlike the response exhibited by Pliocene and PI *T. sacculifer* (Figures 3 and 4). The paired faunal abundance and alkenone SST data for *D. altispira* and *T. sacculifer* (Figure 4) add additional evidence for *D. altispira* being a tropical, warm-water surface dweller. These data support previous studies that grouped *D. altispira* in a *Globigerinoides* (warm) counting category for SST estimation based on mid-Piacenzian assemblage data [26].

Finally, we compare *N. atlantica* to *N. pachyderma*. *Neogloboquadrina atlantica* was widespread and dominant in high-latitude assemblages of the North Atlantic during the Pliocene [56,67–69]. Dowsett and Poore [26] considered *N. atlantica*, exhibiting sinistral coiling, to be the cold endmember of the genus during the Pliocene. Our paired Pliocene alkenone and foraminiferal abundance data show *N. atlantica* was extremely rare in waters with mean annual temperatures greater than ~20 °C. Below ~20 °C, abundance rapidly increased to where it became the dominant Pliocene species at high latitudes, in agreement with previous work (Figure 2). Our highest-latitude North Atlantic site (ODP Site 642) does not record temperatures below 10 °C for the Late Pliocene [48].

The present-day cold endmember of the genus *Neogloboquadrina* is *N. pachyderma*. This generally polar species is found most often in high latitudes and upwelling regions [5]. In the modern ocean, it shows a cool temperature response with a sharp increase in abundance occurring at ≤ 10 °C (Figure 3). As in the modern ocean, *N. pachyderma* is ubiquitous across the Pliocene North Atlantic (Figures 2, 3 and S1). Unlike the modern ocean, however, this species does not peak in the coldest Pliocene temperatures, possibly because the high-latitude North Atlantic was warmer in the Pliocene than it is today. Instead, *N. atlantica* dominates the coolest regions in the northeastern North Atlantic (Figure 4).

Our paired alkenone–abundance data suggest *N. atlantica* was present during the Pliocene at warmer temperatures than present-day *N. pachyderma*. Therefore, the effect of grouping both Pliocene taxa together for assemblage-based SST estimation and calibrating to the core-top temperature response of *N. pachyderma* would result in a cool-biased SST estimate. The implication is that in the absence of other factors, high-latitude PRISM temperature estimates based solely upon assemblage analysis underestimate warming while still clearly indicating mid-Piacenzian polar amplification.

The dominance of *N. atlantica* at cooler temperatures (Figure 4) affects the relative abundances of other Pliocene taxa. Figure 5 shows how the high relative abundance of *N. atlantica* between 10 °C–15 °C likely reduces the abundance of *N. incompta* and *N. pachyderma*, and perhaps *G. bulloides* and *Gt. glutinata*, from their core-top response in that same temperature interval. *Dentoglobigerina altispira* has the same effect in the warmer temperatures; it likely reduces the abundance of *T. sacculifer* above 25 °C.

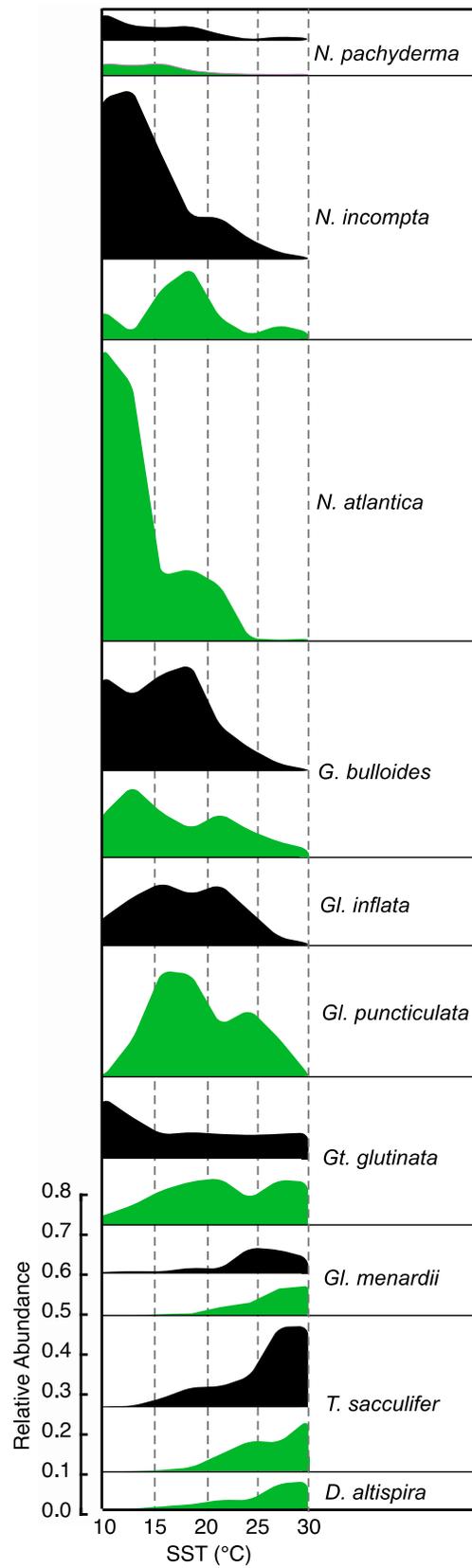


Figure 5. Comparison of mean relative abundances within 2.5 °C temperature bins ranging from 10 °C to 30 °C for seven extant species (*N. pachyderma*, *N. incompta*, *G. bulloides*, *Gl. inflata*, *Gt. glutinata*, *Gl. menardii*, *T. sacculifer*) and three extinct species (*N. atlantica*, *Gl. puncticulata*, *D. altispira*). Pliocene data are shown in green, core-top data in black.

4. Discussion

Our comparisons of Pliocene species' temperature distributions to those of modern taxa show relative stability in the thermal preferences of these taxa, though some differences are apparent. For example, our comparisons of Pliocene and core-top taxa (Figures 3 and 4) show warmer Pliocene maximum temperatures (28.5 °C) than are seen in core-top samples (27.9 °C). This offset is caused by the difference between the SST data used to calibrate the alkenones [70] and the PI SST data [46] used to assign temperatures to core-top samples. This 1 °C difference is within the range of alkenone calibration uncertainty.

Pliocene minimum temperatures could also be affected by calibration issues. While the $U_{37}^{K'}$ paleotemperature index is calibrated to mean annual SSTs [44], seasonal biases may exist due to changes in the timing of alkenone production by haptophyte algae [71]. If our alkenone-based SSTs are indicating late spring or summer productivity in high-latitude regions, the minimum temperatures in our Pliocene data could reflect summer rather than the mean annual SST.

The difference in the density of our Pliocene and PI datasets could also introduce bias. Our Pliocene dataset, limited to 18 North Atlantic sites, does not have the spatial coverage afforded by the 932 ForCenS core-top samples (Figure S1). Thus, the ForCenS core-top dataset possibly samples environments that are missed by the Pliocene dataset.

Conversely, there may be no-analog Pliocene environments. For example, very high Pliocene productivity could affect the relative abundance of species (e.g., the *Gt. glutinata* decreased abundance at ~25 °C; Figure 2). A small number of samples (10 samples from Sites 609 and 1308 at about 20 °C with relative abundances > 0.5, and a second group near 24–25 °C with abundances > 0.4 from Site 958) plot outside the core-top data, exhibiting very high abundances of *Gl. puncticulata* (Figure 4). Robinson et al. [72] suggested anomalously high abundances of *Gl. puncticulata* at Site 609 due to increased productivity that caused faunal assemblage-based SST estimates to be warmer than those estimated by other proxies. This is corroborated by available alkenone concentration data, interpreted as an indicator of productivity, from nearby Sites 607, 982, and 1313 [73,74]. Assemblages from eastern North Atlantic Site 958, influenced by the African margin, might also represent unique Pliocene environmental conditions not observed today.

Furthermore, core-top (and Pliocene) samples are, to some degree, temporally averaged over a range of timescales. Varying sedimentation rates, bioturbation, and especially at the core top, drilling disturbance, can distort or disguise temporal signals. Accumulation rates vary geographically and temporally, but a typical 1 cm sediment sample may represent between 50 and 500 years of accumulation. The faunal assemblage extracted from each sample, assuming accumulation rate was constant over those years, represents average conditions for that period. More likely, regional phytoplankton blooms and zooplankton patchiness result in uneven temporal and spatial fluxes. Bioturbation further compromises sediment chronology through mixing the sediment column, shifting elements of the fauna from their original levels [42,75,76]. This temporal mixing affects both the alkenone paleothermometer and the foraminiferal assemblage, undoubtedly at different scales and at different times. The ForCenS curated database, despite improvements over past core-top compilations, may still represent a range of different ages (and corresponding paleoceanographic conditions), rather than a true PI time slice.

Finally, while it appears to not be an issue, we accept that our exploration of the thermal habitat preferences of planktic foraminifera is dependent upon the stability of the $U_{37}^{K'}$ paleotemperature index through time [49]. Even with the potential introduction of noise into our comparisons, we see similarities in thermal responses of the selected species that approximate stability of thermal preferences in planktic foraminifera over the past 3 million years.

We recognize that the species niche is a multidimensional space. While temperature is often a first-order control on the abundance of Pliocene and pre-industrial (core-top) taxa, other environmental variables (e.g., salinity, nutrients, dissolved oxygen, chlorophyll concentrations, etc.) are also factors [77]. The core-top data provide a more complete spatial

sampling of North Atlantic environmental conditions than does our Pliocene dataset. Some disagreement between core-top and Pliocene temperature responses may be attributable to incomplete Pliocene sampling of the environmental space and/or the existence of no-analog Pliocene environments (Figures S1 and S2). Overlap between Pliocene and core-top temperature responses, assuming other factors are negligible, are taken as evidence of similar temperature preferences. Even when the spatial density of paired Pliocene temperature–abundance data increases, it may not be possible to definitively determine the existence of stationarity/lability of a species thermal niche. The degree to which stationarity of thermal preferences can be approximated is dependent upon both application and scale.

Thermal niches of planktic foraminifera have been shown to be static over the past 700,000 years [18] with SSTs as the first-order driver of assemblage composition [57]. Strac et al. [78] documented changes in North Atlantic assemblages in response to deglacial warming (equivalent in scale to what is expected by the end of this century), though that response may not have been uniform.

5. Conclusions

Our work suggests that thermal niches may have been stable over the past 3 million years. We have documented Pliocene (Piacenzian) thermal preferences for nine species of planktic foraminifera in the North Atlantic Ocean using alkenone paleothermometry as an independent source of temperature data. We found that planktic foraminiferal species temperature responses appear qualitatively similar between the Pliocene and PI in many of the planktic foraminiferal species we investigated. However, the results depend upon our definition of “similar.” For our purposes, we feel planktic foraminifer thermal niches are stable enough to support the use of assemblage-based temperature estimates on Pliocene assemblages.

Beyond the evaluation of stationarity, our results provide a direct assessment of thermal habitat preferences for Pliocene planktic foraminifera. This information can be used to evaluate paleoenvironments and, in conjunction with other proxy methods, can be used to identify situations where environmental variables other than temperature may be exhibiting a first-order control on faunal assemblages, thereby highlighting important aspects of the paleoenvironment. This strengthens our ability to reconstruct past environments and thereby validate model experiments, which in turn affords a more robust understanding of the effects of future climate change on biodiversity, ecosystems, and natural resources.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/geosciences13030071/s1>, Figure S1: Relative abundance of species; Figure S2: Pliocene SST estimates by core site; Table S1: Summary SST statistics for localities; Table S2: Summary SST statistics for taxa; Table S3: Pliocene sites shown in Figure S1; Table S4: Unpublished faunal census data from ODP Site 642; Taxonomy.

Author Contributions: Conceptualization, H.D.; Data curation, K.F. and W.S.; Formal analysis, H.D., M.R., K.F. and T.H.; Investigation, H.D., M.R., K.F., T.H., S.H. and C.A.; Methodology, H.D., M.R., K.F. and T.H.; Resources, H.D., M.R., K.F., T.H., S.H., C.A. and W.S.; Supervision, H.D.; Visualization, H.D. and K.F.; Writing—original draft, H.D.; Writing—review and editing, H.D., M.R., K.F., T.H., S.H. and C.A. All authors have read and agreed to the published version of the manuscript.

Funding: Funding for this work was provided by the USGS Climate R&D Program. TH acknowledges support from NSF 1545859 and NSF 1459280. SH was supported by FP7 Ideas: European Research Council (grant no. PLIO-ESS, 278636). CA was supported by Earth System Modeling, NFR project 221712 (OCCP) and the Centre for Climate Dynamics at the Bjercknes Centre through the DYNAWARM project.

Data Availability Statement: Foraminiferal census data used in this study are available at <https://doi.org/10.25921/yjwg-qc25>, <https://doi.org/10.25921/5wnk-kr52>, and <https://doi.org/10.1594/PANGAEA.873570>. Site 642 assemblage data are included in the supplement (Table S4). Pliocene alkenone data can be obtained from <https://doi.org/10.5066/F7959G1S> and <https://doi.pangaea.de/10.1594/PANGAEA.85894>. The SST data used to produce PI SST estimates for ForCens

North Atlantic surface sediment samples can be found at https://gdex.ucar.edu/dataset/158_asphilli.html (accessed on 11 May 2022).

Acknowledgments: This research used samples and/or data provided by the International Ocean Discovery Program (IODP), Ocean Drilling Program (ODP), and Deep Sea Drilling Project (DSDP). The authors thank T. Cronin, L. Wingard, and three anonymous individuals for helpful reviews of earlier versions of this work. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Hutton, J. Theory of the Earth; or an investigation of the laws observable in the composition, dissolution, and restoration of land upon the Globe. *Trans. R. Soc. Edinb.* **1788**, *1*, 209–304. [[CrossRef](#)]
2. Lyell, C. *Principles of Geology, Being an Attempt to Explain the Former Changes of the Earth's Surface, by Reference to Causes Now in Operation*; John Murray: London, UK, 1830; Volume 1.
3. Giamali, C.; Kontakiotis, G.; Koskeridou, E.; Ioakim, C.; Antonarakou, A. Key Environmental Factors Controlling Planktonic Foraminiferal and Pteropod Community's Response to Late Quaternary Hydroclimate Changes in the South Aegean Sea (Eastern Mediterranean). *J. Mar. Sci. Eng.* **2020**, *8*, 709. [[CrossRef](#)]
4. Bé, A.W.H. An ecological, zoogeographic and taxonomic review of recent planktonic foraminifera. In *Oceanic Micropaleontology*; Ramsay, A.T.S., Ed.; Academic Press: London, UK, 1977; Volume 1, pp. 1–100.
5. Schiebel, R.; Hemleben, C. *Planktic Foraminifers in the Modern Ocean*; Springer: Berlin, Germany, 2017; p. 358.
6. Morey, A.E.; Mix, A.C.; Pisias, N.G. Planktonic foraminiferal assemblages preserved in surface sediments correspond to multiple environment variables. *Quat. Sci. Rev.* **2005**, *24*, 925–950. [[CrossRef](#)]
7. Bé, A.W.H.; Tolderlund, D.S. Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans. In *The Micropaleontology of Oceans*; Funnell, B.M., Riedel, W.R., Eds.; Cambridge University Press: London, UK, 1971; pp. 105–149.
8. Tolderlund, D.S.; Bé, A.W.H. Seasonal distribution of planktonic foraminifera in the Western North Atlantic. *Micropaleontology* **1971**, *17*, 297–329.
9. Imbrie, J.; Kipp, N.G. A New Micropaleontological method for paleoclimatology: Application to a Late Pleistocene Caribbean core. In *The Late Cenozoic Glacial Ages*; Turekian, K.K., Ed.; Yale University Press: New Haven, CT, USA, 1971; pp. 71–181.
10. Cline, R.M.; Hays, J.D. *Investigation of Late Quaternary Paleooceanography and Paleoclimatology*; Geological Society of America: Boulder, CO, USA, 1976; Volume 123, p. 464.
11. Cline, R.M.L.; Hays, J.D.; Prell, W.L.; Ruddiman, W.F.; Moore, T.C.; Kipp, N.G.; Molino, B.E.; Denton, G.H.; Hughes, T.J.; Balsam, W.L.; et al. The last interglacial ocean. *Quat. Res.* **1984**, *21*, 123–224. [[CrossRef](#)]
12. Hutson, W.H. The Agulhas Current during the Late Pleistocene: Analysis of Modern Faunal Analogs. *Science* **1980**, *207*, 64–66. [[CrossRef](#)]
13. Malmgren, B.A.; Nordlund, U. Application of artificial neural networks to paleoceanographic data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **1997**, *136*, 359–373. [[CrossRef](#)]
14. Malmgren, B.A.; Kucera, M.; Nyberg, J.; Waelbroeck, C. Comparison of statistical and artificial neural network techniques for estimating past sea surface temperatures from planktonic foraminifer census data. *Paleoceanography* **2001**, *16*, 520–530. [[CrossRef](#)]
15. MARGO Project Members. Constraints on the magnitude and patterns of ocean cooling at the Last Glacial Maximum. *Nat. Geosci.* **2009**, *2*, 127–132. [[CrossRef](#)]
16. CLIMAP. *Seasonal Reconstructions of the Earth's Surface at the Last Glacial Maximum*; Geological Society of America: Boulder, CO, USA, 1981; p. 18.
17. Sarnthein, M.; Gersonde, R.; Niebler, S.; Pflaumann, U.; Spielhagen, R.; Thiede, J.; Wefer, G.; Weinelt, M. Overview of Glacial Atlantic Ocean Mapping (GLAMAP 2000). *Paleoceanography* **2003**, *18*, 1030. [[CrossRef](#)]
18. Antell, G.S.; Fenton, I.S.; Valdes, P.J.; Saupé, E.E. Thermal niches of planktonic foraminifera are static throughout glacial–interglacial climate change. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2017105118. [[CrossRef](#)]
19. Kucera, M.; Schonfeld, J. The origin of modern oceanic foraminiferal faunas and Neogene climate change. In *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*; The Micropaleontological Society: London, UK, 2007; pp. 409–425.
20. Keigwin, L.D. Late Cenozoic planktonic foraminiferal biostratigraphy and paleoceanography of the Panama Basin. *Micropaleontology* **1976**, *22*, 419–442.
21. Thunell, R.C. Pliocene–Pleistocene paleotemperature and paleosalinity history of the Mediterranean Sea: Results from DSDP Sites 125 and 132. *Mar. Micropaleontol.* **1979**, *4*, 173–187. [[CrossRef](#)]
22. Dowsett, H.J.; Poore, R.Z. Pliocene sea surface temperatures of the North Atlantic Ocean at 3.0 Ma. *Quat. Sci. Rev.* **1991**, *10*, 189–204. [[CrossRef](#)]

23. Sabaa, A.T.; Sikes, E.L.; Hayward, B.W.; Howard, W.R. Pliocene sea surface temperature changes in ODP Site 1125, Chatham Rise, east of New Zealand. *Mar. Geol.* **2004**, *205*, 113–125. [[CrossRef](#)]
24. Dowsett, H.J.; Robinson, M.M. Application of the modern analogue technique (MAT) of sea surface temperature estimation to middle Pliocene North Pacific planktic foraminifer assemblages. *Palaeontol. Electron.* **1998**, *1*, 22.
25. Andersson, C. Transfer function vs. modern analog technique for estimating Pliocene sea-surface temperatures based on planktic foraminiferal data, western Equatorial Pacific Ocean. *J. Foraminifer. Res.* **1997**, *27*, 123–132. [[CrossRef](#)]
26. Dowsett, H.J.; Poore, R.Z. A new planktic foraminifer transfer function for estimating Pliocene—Holocene paleoceanographic conditions in the North Atlantic. *Mar. Micropaleontol.* **1990**, *16*, 1–23. [[CrossRef](#)]
27. Dowsett, H.J.; Foley, K.M.; Stoll, D.K.; Chandler, M.A.; Sohl, L.E.; Bentsen, M.; Otto-Bliesner, B.L.; Bragg, F.J.; Chan, W.-L.; Contoux, C.; et al. Sea Surface Temperature of the mid-Piacenzian Ocean: A Data-Model Comparison. *Sci. Rep.* **2013**, *3*, 1–8. [[CrossRef](#)]
28. Dowsett, H.; Barron, J.; Poore, R. Middle Pliocene sea surface temperatures: A global reconstruction. *Mar. Micropaleontol.* **1996**, *27*, 13–25.
29. Dowsett, H.J. The PRISM palaeoclimate reconstruction and Pliocene sea-surface temperature. In *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*; Williams, M., Haywood, A.M., Gregory, J., Schmidt, D.N., Eds.; Micropalaeontological Society (Special Publication), Geological Society of London: London, UK, 2007; pp. 459–480.
30. Dowsett, H.; Robinson, M.; Haywood, A.; Salzmann, U.; Hill, D.; Sohl, L.; Chandler, M.; Williams, M.; Foley, K.; Stoll, D. The PRISM3D paleoenvironmental reconstruction. *Stratigraphy* **2010**, *7*, 123–139.
31. Dowsett, H.J.; Chandler, M.A.; Cronin, T.M.; Dwyer, G.S. Middle Pliocene sea surface temperature variability. *Paleoceanography* **2005**, *20*, 1–8. [[CrossRef](#)]
32. Dowsett, H.; Dolan, A.; Rowley, D.; Moucha, R.; Forte, A.M.; Mitrovica, J.X.; Pound, M.; Salzmann, U.; Robinson, M.; Chandler, M.; et al. The PRISM4 (mid-Piacenzian) paleoenvironmental reconstruction. *Clim. Past* **2016**, *12*, 1519–1538. [[CrossRef](#)]
33. Chandler, M.A.; Rind, D.; Thompson, R. Joint investigations of the middle Pliocene climate II: GISS GCM Northern Hemisphere results. *Glob. Planet. Change* **1994**, *9*, 197–219. [[CrossRef](#)]
34. Sloan, L.C.; Crowley, T.J.; Pollard, D. Modeling of middle Pliocene climate with the NCAR GENESIS general circulation model. *Mar. Micropaleontol.* **1996**, *27*, 51–61. [[CrossRef](#)]
35. Haywood, A.M.; Valdes, P.J.; Sellwood, B.W. Global scale palaeoclimate reconstruction of the middle Pliocene climate using the UKMO GCM: Initial results. *Glob. Planet. Chang.* **2000**, *25*, 239–256. [[CrossRef](#)]
36. Haywood, A.; Valdes, P. Modelling Pliocene warmth: Contribution of atmosphere, oceans and cryosphere. *Earth Planet. Sci. Lett.* **2004**, *218*, 363–377. [[CrossRef](#)]
37. Dowsett, H.J.; Robinson, M.M.; Haywood, A.M.; Hill, D.J.; Dolan, A.M.; Stoll, D.K.; Chan, W.-L.; Abe-Ouchi, A.; Chandler, M.A.; Rosenbloom, N.A.; et al. Assessing confidence in Pliocene sea surface temperatures to evaluate predictive models. *Nat. Clim. Chang.* **2012**, *2*, 365–371. [[CrossRef](#)]
38. Haywood, A.M.; Hill, D.J.; Dolan, A.M.; Otto-Bliesner, B.L.; Bragg, F.; Chan, W.L.; Chandler, M.A.; Contoux, C.; Dowsett, H.J.; Jost, A.; et al. Large-scale features of Pliocene climate: Results from the Pliocene Model Intercomparison Project. *Clim. Past* **2013**, *9*, 191–209. [[CrossRef](#)]
39. Dowsett, H.; Robinson, M.; Foley, K. A global planktic foraminifer census data set for the Pliocene ocean. *Sci. Data* **2015**, *2*, 150076. [[CrossRef](#)]
40. Kipp, N.G. New transfer function for estimating past sea-surface conditions from sea-bed distribution of planktonic foraminiferal assemblages in the North Atlantic: Investigations of late Quaternary Paleoclimatology and Paleoclimatology. *Geol. Soc. Am. Mem.* **1976**, *145*, 3–41.
41. Dowsett, H.J.; Cronin, T.M.; Poore, R.Z.; Thompson, R.S.; Whatley, R.C.; Wood, A.M. Micropaleontological Evidence for Increased Meridional Heat Transport in the North Atlantic Ocean During the Pliocene. *Science* **1992**, *258*, 1133–1135. [[CrossRef](#)] [[PubMed](#)]
42. Dowsett, H.J.; Robinson, M.M.; Foley, K.M.; Herbert, T.D.; Otto-Bliesner, B.L.; Spivey, W. The mid-Piacenzian of the North Atlantic Ocean. *Stratigraphy* **2019**, *16*, 119–144. [[CrossRef](#)]
43. McClymont, E.L.; Ford, H.L.; Ho, S.L.; Tindall, J.C.; Haywood, A.M.; Alonso-Garcia, M.; Bailey, I.; Berke, M.A.; Littler, K.; Patterson, M.O.; et al. Lessons from a high-CO₂ world: An ocean view from ~3 million years ago. *Clim. Past* **2020**, *16*, 1599–1615. [[CrossRef](#)]
44. Müller, P.J.; Kirst, G.; Ruhland, G.; von Storch, I.; Rosell-Melè, A. Calibration of the alkenone paleotemperature index U_{37K'} based on core-tops from the eastern South Atlantic and the global ocean (60°N–60°S). *Geochim. Et Cosmochim. Acta* **1998**, *62*, 1757–1772. [[CrossRef](#)]
45. Siccha, M.; Kucera, M. ForCenS, a curated database of planktonic foraminifera census counts in marine surface sediment samples. *Sci. Data* **2017**, *4*, 170109. [[CrossRef](#)] [[PubMed](#)]
46. Shea, D.; Hurrell, J.; Phillips, A. *Merged Hadley-OI Sea Surface Temperature and Sea Ice Concentration Data Set*; Version 5.0; NCAR: Boulder, CO, USA, 2022. [[CrossRef](#)]
47. Dowsett, H.J.; Foley, K.M.; Robinson, M.M.; Herbert, T.D. PRISM late Pliocene (Piacenzian) alkenone—derived SST data. In *U.S. Geological Survey Data Release*; USGS: Reston, VA, USA, 2017. [[CrossRef](#)]
48. Bachem, P.E.; Risebrobakken, B.; McClymont, E.L. Sea surface temperature variability in the Norwegian Sea during the late Pliocene linked to subpolar gyre strength and radiative forcing. *Earth Planet. Sci. Lett.* **2016**, *446*, 113–122.

49. Herbert, T.D. 6.15—Alkenone Paleotemperature Determinations. In *Treatise on Geochemistry*; Holland, H.D., Turekian, K.K., Eds.; Pergamon: Oxford, UK, 2003; pp. 391–432.
50. Lawrence, K.T.; Herbert, T.D.; Dekens, P.S.; Ravelo, A.C. The application of the alkenone organic proxy to the study of Plio-Pleistocene climate. In *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*; Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N., Eds.; Micropalaeontological Society (Special Publication), Geological Society of London: London, UK, 2007; pp. 539–562.
51. Foley, K.M.; Dowsett, H.J. Community sourced mid-Piacenzian sea surface temperature (SST) data. *U.S. Geol. Surv. Data Release* **2019**. [[CrossRef](#)]
52. Berggren, W.A. Cenozoic biostratigraphy and paleobiogeography of the North Atlantic. *Initial Rep. Deep Sea Drill. Proj.* **1972**, *12*, 965–1001.
53. Poore, R.Z. Oligocene through Quaternary planktonic foraminiferal biostratigraphy of the North Atlantic: DSDP Leg 49. *Initial Rep. Deep Sea Drill. Proj.* **1978**, *49*, 447–517. [[CrossRef](#)]
54. Weaver, P.P.E. Late Miocene–Recent planktonic foraminifers from the North Atlantic: Deep Sea Drilling Project Leg 94. *Initial Rep. Deep Sea Drill. Proj.* **1987**, *94*, 703–727. [[CrossRef](#)]
55. Dowsett, H.J.; Robinson, M.M. Mid-Pliocene planktic foraminifer assemblage of the North Atlantic Ocean. *Micropaleontology* **2007**, *53*, 105–126. [[CrossRef](#)]
56. Flower, B.P. Data Report: Planktonic foraminifers from the subpolar North Atlantic and Nordic Seas: Sites 980–987 and 907. *Proc. Ocean Drill. Program* **1999**, *162*, 19–34. [[CrossRef](#)]
57. Rillo, M.C.; Woolley, S.; Hillebrand, H. Drivers of global pre-industrial patterns of species turnover in planktonic foraminifera. *Ecography* **2022**, *2022*, 1–11. [[CrossRef](#)]
58. Poore, R.Z.; Steinmetz, J.C.; Schrader, H.J. Biostratigraphic summary of DSDP Leg 49. *Initial Rep. Deep Sea Drill. Proj.* **1978**, *49*, 851–858. [[CrossRef](#)]
59. Weaver, P.P.E.; Clement, B.M. Magnetobiostratigraphy of planktonic foraminiferal diatoms. *Initial Rep. Deep Sea Drill. Proj.* **1986**, *94*, 815–829. [[CrossRef](#)]
60. Dowsett, H.J. Application of the Graphic Correlation method to Pliocene marine sequences. *Mar. Micropaleontol.* **1989**, *14*, 3–32. [[CrossRef](#)]
61. Brombacher, A.; Wilson, P.A.; Bailey, I.; Ezard, T.H.G. The Dynamics of Diachronous Extinction Associated with Climatic Deterioration Near the Neogene/Quaternary Boundary. *Paleoceanogr. Paleoclimatology* **2021**, *36*, e2020PA004205. [[CrossRef](#)]
62. Malmgren, B.; Kennett, J. Phyletic gradualism in a Late Cenozoic planktonic foraminiferal lineage; DSDP Site 284, southwest Pacific. *Paleobiology* **1981**, *7*, 230–240. [[CrossRef](#)]
63. Norris, R.D.; Corfield, R.M.; Cartlidge, J.E. Evolution of depth ecology in the planktic foraminifera lineage Globorotalia (Fohsella). *Geology* **1993**, *21*, 975–978. [[CrossRef](#)]
64. Prentice, M.L.; Bockheim, J.G.; Wilson, S.C.; Burckle, L.H.; Hodell, D.A.; Schluchter, C.; Kellogg, D.E. Late Neogene Antarctic glacial history: Evidence from Central Wright Valley. In *The Antarctic Paleoenvironment: A Perspective on Global Change*; Kennett, J.P., Warnke, D.A., Eds.; Antarctic Research Series American Geophysical Union: Washington, DC, USA, 1993; Volume 60, pp. 207–250.
65. Savin, S.M.; Abel, L.; Barrera, E.; Hodell, D.; Kennett, J.P.; Murohy, M.; Keller, G.; Killingley, J.; Vincent, E. The evolution of Miocene surface and near-surface marine temperatures: Oxygen isotope evidence. In *The Miocene Ocean: Paleooceanography and Biogeography, Geological Society of America Memoir 163*; Kennett, J.P., Ed.; Geological Society of America: Boulder, CO, USA, 1985; pp. 49–82.
66. Birch, H.; Coxall, H.K.; Pearson, P.N.; Kroon, D.; O'Regan, M. Planktonic foraminifera stable isotopes and water column structure: Disentangling ecological signals. *Mar. Micropaleontol.* **2013**, *101*, 127–145. [[CrossRef](#)]
67. Spiegler, D.; Jansen, E. Planktonic Foraminifer Biostratigraphy of Norwegian Sea Sediments: ODP Leg 104. *Ocean Drill. Program Sci. Results* **1989**, *104*, 681–696. [[CrossRef](#)]
68. Poore, R.Z. Temporal and spatial distribution of ice-rafted mineral grains in Pliocene sediments of the North Atlantic: Implications for Late Cenozoic climatic history. In *The Deep Sea Drilling Project: A Decade of Progress*; Warme, J.E., Douglas, R.G., Winterer, E.L., Eds.; Society of Economic Paleontologists and Mineralogists Special Publication: Tulsa, OK, USA, 1981; Volume 32, pp. 505–515.
69. Poore, R.Z.; Berggren, W.A. The morphology and classification of Neogloboquadrina atlantica (Berggren). *J. Foraminifer. Res.* **1975**, *5*, 76–84. [[CrossRef](#)]
70. Levitus, S.; Boyer, T.P. World ocean atlas 1994 (vol. 4): Temperature. In *NOAA Atlas NESDIS*; US Department of Commerce: Washington, DC, USA, 1994; Volume 4.
71. Bova, S.; Rosenthal, Y.; Liu, Z.; Godad, S.P.; Yan, M. Seasonal origin of the thermal maxima at the Holocene and the last interglacial. *Nature* **2021**, *589*, 548–553. [[CrossRef](#)] [[PubMed](#)]
72. Robinson, M.M.; Dowsett, H.J.; Dwyer, G.S.; Lawrence, K.T. Reevaluation of mid-Pliocene North Atlantic sea surface temperatures. *Paleoceanography* **2008**, *23*, PA3213. [[CrossRef](#)]
73. Lawrence, K.T.; Sigman, D.M.; Herbert, T.D.; Riihimaki, C.A.; Bolton, C.T.; Martinez-Garcia, A.; Rosell-Mele, A.; Haug, G.H. Time-transgressive North Atlantic productivity changes upon Northern Hemisphere glaciation. *Paleoceanography* **2013**, *28*, 740–751. [[CrossRef](#)]

74. Naafs, B.D.A.; Voelker, A.H.L.; Karas, C.; Andersen, N.; Sierro, F.J. Repeated Near-Collapse of the Pliocene Sea Surface Temperature Gradient in the North Atlantic. *Paleoceanogr. Paleoclimatol.* **2020**, *35*, e2020PA003905. [[CrossRef](#)]
75. Soltwedel, T.; Hasemann, C.; Vedenin, A.; Bergmann, M.; Taylor, J.; Krauß, F. Bioturbation rates in the deep Fram Strait: Results from in situ experiments at the arctic LTER observatory HAUSGARTEN. *J. Exp. Mar. Biol. Ecol.* **2019**, *511*, 1–9. [[CrossRef](#)]
76. Hülse, D.; Vervoort, P.; van de Velde, S.J.; Kanzaki, Y.; Boudreau, B.; Arndt, S.; Bottjer, D.J.; Hoogakker, B.; Kuderer, M.; Middelburg, J.J.; et al. Assessing the impact of bioturbation on sedimentary isotopic records through numerical models. *Earth-Sci. Rev.* **2022**, *234*, 104213. [[CrossRef](#)]
77. Hemleben, C.; Spindler, M.; Anderson, O.R. *Modern Planktonic Foraminifera*; Springer: New York, NY, USA, 1989; p. 363.
78. Strack, A.; Jonkers, L.C.; Rillo, M.; Hillebrand, H.; Kucera, M. Plankton response to global warming is characterized by non-uniform shifts in assemblage composition since the last ice age. *Nat. Ecol. Evol.* **2022**, *6*, 1871–1880. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.