

## Foraminiferal faunal estimates of paleotemperature: Circumventing the no-analog problem yields cool ice age tropics

Alan C. Mix, Ann E. Morey, and Nicklas G. Pisias

College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis

Steven W. Hostetler

U.S. Geological Survey, Corvallis, Oregon

**Abstract.** The sensitivity of the tropics to climate change, particularly the amplitude of glacial-to-interglacial changes in sea surface temperature (SST), is one of the great controversies in paleoclimatology. Here we reassess faunal estimates of ice age SSTs, focusing on the problem of no-analog planktonic foraminiferal assemblages in the equatorial oceans that confounds both classical transfer function and modern analog methods. A new calibration strategy developed here, which uses past variability of species to define robust faunal assemblages, solves the no-analog problem and reveals ice age cooling of 5° to 6°C in the equatorial current systems of the Atlantic and eastern Pacific Oceans. Classical transfer functions underestimated temperature changes in some areas of the tropical oceans because core-top assemblages misrepresented the ice age faunal assemblages. Our finding is consistent with some geochemical estimates and model predictions of greater ice age cooling in the tropics than was inferred by Climate: Long-Range Investigation, Mapping, and Prediction (*CLIMAP*) [1981] and thus may help to resolve a long-standing controversy. Our new foraminiferal transfer function suggests that such cooling was limited to the equatorial current systems, however, and supports *CLIMAP*'s inference of stability of the subtropical gyre centers.

### 1. Introduction

The Climate: Long-Range Investigation, Mapping, and Prediction (*CLIMAP*) [1981] reconstruction of the ice age world suggested relatively little change in the low latitudes. An array of newer data from low latitudes, including reconstructions of mountain glacier advances and tropical ice core records [Thompson *et al.*, 1995], Sr/Ca ratios in corals at a few locations [Guilderson *et al.*, 1994], the rare gas chemistry of lowland groundwaters [Stute *et al.*, 1995], and inferences about glacier advances from atmospheric circulation models [Rind and Peteet, 1985], suggest greater tropical cooling but do not constrain the regional distribution or mechanisms of such cooling. Other geochemical data from the ocean, however, such as the alkenone  $U^k_{37}$  index [Sikes and Keigwin, 1994; Roselle-Melé *et al.*, 1998], and Mg/Ca data [Hastings *et al.*, 1998] are to first approximation consistent with *CLIMAP* [1981] in many locations. Point-by-point comparisons of the *CLIMAP* data and atmospheric model output suggest the mismatches are smaller than originally thought [Broccoli and Marciniak, 1996].

Four recent ocean models, some coupled to the atmosphere with varying degrees of sensitivity, yield significantly different responses in the tropical oceans, perhaps because of different degrees of linkage between the atmosphere and ocean in each model [Bigg *et al.*, 1998; Bush and Philander, 1998; Ganopolski *et al.*, 1998; Weaver *et al.*, 1998]. Thus the range of

cooling in ice age reconstructions from both models and data is large, and the controversy about sensitivity of tropical climate to change remains unresolved. Progress requires resolving the extent, mechanisms, and regional distribution of ice age cooling. If the *CLIMAP* [1981] reconstruction based on faunal transfer functions was biased in the tropics, we need to know why.

### 2. Methods

#### 2.1. Classical Transfer Functions

In the now traditional use of transfer functions, common practice is to find empirical assemblages of a fossil fauna in modern (core-top) sediments. The core-top fauna is converted into orthogonal  $Q$ -mode factors rotated with a varimax criterion [Klovan and Imbrie, 1971].  $Q$ -mode factor analysis defines each fossil assemblage as a linear combination of input species. The weighting of each species in a factor is indicated by a factor score. The weighting of each factor in describing a sample is referred to as a factor loading.

The next step is to calibrate an equation that predicts a useful property, such as sea surface temperature (SST), by regressing core-top faunal factor loadings against modern oceanographic properties [Imbrie and Kipp, 1971]. This is usually done with multiple linear regression methods, allowing squared and cross-product terms of the factor loadings to enter the equation to account for moderate nonlinearity in the faunal response to the environment. Finally, the modern factor definitions and calibrated equations are applied to species census data from ancient samples to make estimates of environmental properties in the past.

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Calibration of a transfer function is meaningful only if an oceanographic property is chosen that either controls, or is consistently correlated to other processes that control, species distributions. A variety of statistical tests suggests that temperature is indeed a dominant control but perhaps not the only control on foraminiferal species assemblages [Parker and Berger, 1971; Coulbourn et al., 1980; Loubere, 1982; Mix, 1989]. Andreassen and Ravelo [1997] argue for upper ocean mixed layer depth as a primary control of tropical foraminiferal faunas, although Watkins and Mix [1998] note that mixed layer depth and biological productivity may be difficult to distinguish from each other because they are highly correlated in the modern ocean [Herbland and Voituriez, 1979].

Multiple oceanic properties may influence faunal assemblages, either independently or in combination. It is possible that transfer functions may still work in such situations as long as the statistical relationships between the various controls remain constant through time. However, it is also possible for transfer functions to be biased by the interactions of multiple processes. For example, Watkins and Mix [1998] suggest that pycnocline depth, upper ocean temperature, and biological productivity may all influence the living fauna and show examples of bias induced by productivity on temperature estimates (and vice versa) in an array of plankton-tow samples from the equatorial Pacific Ocean. Thus, in any application of transfer functions, possible bias effects must be considered.

A key assumption in the classical transfer function approach is that modern variations of the fauna through space (i.e., in an array of sediment core tops) simulate past variations through time. If processes that modify the ecological groupings of the past are not well expressed in the modern ocean, then this assumption would break down, and paleotemperature estimates would likely be in error. Here we test this assumption and find that it is sufficiently in error to bias the CLIMAP [1981] temperature estimates of the equatorial zones.

It has long been known that ice age samples from the eastern equatorial Pacific and Atlantic are not well described by modern core-top assemblages [Moore et al., 1981; Mix et al., 1986]. Faunal factors defined using only tropical Atlantic core tops explain just 35% of the variance in Last Glacial Maximum samples from the same region [Ravelo et al., 1990]. This so-called no-analog problem [Hutson, 1977] either could reflect the response of past faunas to climate changes outside the range experienced by the present fauna or could be an artifact of empirical core-top assemblages that are not true ecological assemblages in the tropics. In either case the traditional transfer function would yield erroneous answers. Such errors would not be easily detectable in core-top calibrations; that is, the calibration statistics of the transfer function might appear precise, but the transfer functions might still be inaccurate when applied to ancient samples.

## 2.2. Modern Analog Technique

Some workers have attempted to circumvent this problem by using various versions of the modern analog technique (MAT) [Hutson, 1980; Prell, 1985; Pflaumann et al., 1996; Ortiz and Mix, 1997; Waelbroeck et al., 1998]. This method finds a selection of modern (core-top) samples that are statistically most similar to ancient samples and then estimates the temperature of

the ancient sample as an average (or in some cases an average weighted by geographic distance) of those modern samples.

The MAT may also underestimate tropical climate changes. As with the classical transfer function method, temperatures calculated with the MAT are limited to the range of modern variability. Also, if there is no good modern analog of ancient conditions, then the modern analog cannot find an appropriate modern sample to match the ancient sample. Because its estimate of precision is based on variability within the array of modern samples chosen as best analogs, it may yield apparently precise estimates that are inaccurate. Prell [1985] shows that the MAT and classical transfer function methods yield roughly similar results in the tropics.

The primary issue for both transfer functions and MATs is whether the modern (core-top) faunas adequately represent the range of past variations in faunas within an oceanographic setting. If not, then it is unlikely that either the classical transfer function or the MAT method would predict the past range of temperatures correctly. The result of either method would be to underestimate the range of changes in the environment. Such errors would not be detected in modern calibration statistics, which can only test the success of the methods in the modern world. In short, temperature estimates must be accurate as well as precise.

## 2.3. A Revised Transfer Function Method

Our primary purpose is to address the no-analog problem. We examine whether the foraminiferal species within the tropics combine through time to form assemblages in subtly different ways than are observed through space in modern core-top sediments. Instead of solving for fossil assemblages in core-top samples, we define assemblages based on *Q*-mode factors of planktonic foraminifera in ancient samples from the equatorial Atlantic and Pacific Oceans<sup>1</sup>. This procedure guarantees that the assemblages are based on species that covary in the past, and samples a larger range of variation than is observed in the core tops. Because they are defined entirely from tropical samples, these assemblages better describe the total faunal variations within the regional context of tropical oceanographic processes.

Samples used here to define the factor assemblages span the past 300,000 years, a time long enough to capture the large range of climate variations of the late Pleistocene. Samples come from 10 sediment cores in the tropical Atlantic and Pacific Oceans (Figure 1). Four of these cores (1057 samples) are from the tropical Atlantic Ocean, and six of the cores (715 samples) are from the eastern tropical Pacific Ocean. Core names and locations are tabulated by Mix and Morey [1996].

Two other features of our factor analysis differ from common practice. First, after some experimentation to minimize species percentage artifacts associated with selective dissolution at great water depths we excluded the dissolution resistant species *Globorotalia tumida*, *Globorotalia menardii*, and *Globorotalia menardii neoflexuosa*. Mix and Morey [1996] test and document potential dissolution effects on these assemblages.

<sup>1</sup>Data are available electronically at World Data Center-A for Paleoclimatology, NOAA/NGDC, 325 Broadway, Boulder, Colorado (e-mail: paleo@mail.ngdc.noaa.gov; URL: <http://www.ngdc.noaa.gov/paleo>).

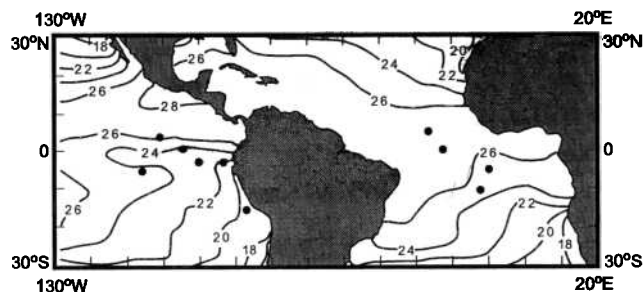


Figure 1. Core sites (dots) containing downcore foraminiferal species census data used here to define tropical faunal factors for transfer function calibration. Details of locations and data sources are provided elsewhere [Mix and Morey, 1996]. Contours are modern annual sea surface temperature (SST) [Levitus, 1982].

Exclusion of these species also eliminates a problem in Atlantic Ocean reconstructions as all three are absent from the Atlantic for long periods of the late Pleistocene and episodically repopulate the Atlantic only when they are advected around South Africa [Ericson, 1968].

Second, our analyses are based on the  $\ln(\text{species percentage} + 1)$ . Lognormal distributions of species relative abundances are commonly observed in many ecosystems, and are consistent with biological theory (MacArthur, 1960). In the factor analysis, log transforms amplify the importance of less abundant species (and thus minimize the dominance of the analysis by a few abundant species) and makes the species distributions more Gaussian, an assumption inherent in multiple regression techniques. One is added to each percentage value to avoid taking the log of zero. The log transform is applied to all species percentage data (downcore and core-top samples) prior to calculation of factor loadings or scores.

Our analysis is closed (100%) around 26 species and morphotypes, listed in Table 1. Only species without significant taxonomic controversies are included. We included specimens referred to by Kipp [1976] as "P-D" intergrade with *Neogloboquadrina duterrei*, as this is how much of the Pacific core-top data set was counted. Also, *Globorotalia theyeri* is grouped with *Globorotalia scitula* because the former species was not widely recognized in earlier studies. Morphotypes of *Globigerinoides sacculifer* with and without a terminal chamber are

Table 1. Q-mode, Varimax-Rotated Factor Scores for the Downcore Foraminiferal Faunas and for the Core-Top Climate: Long-Range Investigation, Mapping, and Prediction (CLIMAP) FA-20 Solution, Three of Five Factors Shown

Species <sup>a</sup>	Downcore Factor Scores (This Paper)			CLIMAP FA-20 Factor Scores		
	Factor 1 Warm Tropical	Factor 2 Upwelling	Factor 3 E. Boundary	Factor 1 Tropical	Factor 4 Gyre Margin	Factor 2 Transitional
<i>Globigerinoides ruber</i> (total)	0.56	-0.03	0.09	---	---	---
<i>Globigerinoides ruber</i> (white)	---	---	---	0.93	-0.12	0.03
<i>Globigerinoides ruber</i> (pink)	---	---	---	0.11	0.07	0.01
<i>Globigerinoides sacculifer</i> (total)	0.47	-0.09	0.13	---	---	---
<i>Globigerinoides sacculifer</i> (with sac)	---	---	---	0.10	0.24	0.00
<i>Globigerinoides sacculifer</i> (no sac)	---	---	---	0.21	0.33	-0.05
<i>Globigerinita glutinata</i>	0.38	0.09	-0.17	0.20	-0.02	-0.06
<i>Globigerinella aequilateralis</i>	0.22	-0.06	0.01	0.10	0.04	0.01
<i>Pulleniatina obliquiloculata</i>	0.23	-0.02	-0.08	0.01	0.26	-0.01
<i>Globigerina rubescens</i>	0.20	-0.07	-0.15	0.03	-0.02	-0.00
<i>Globigerinoides tenellus</i>	0.18	-0.06	-0.14	0.05	-0.03	0.01
<i>Globigerina falconensis</i>	0.14	-0.05	-0.03	0.06	-0.12	0.32
<i>Globigerinoides conglobatus</i>	0.10	-0.05	0.02	0.02	0.02	0.01
<i>Globigerinella calida</i>	0.11	0.05	0.00	0.03	-0.00	0.02
<i>Globorotalia scitula</i> + <i>Globorotalia theyeri</i>	0.09	-0.02	-0.02	0.01	-0.02	-0.00
<i>Globigerina digitata</i>	0.03	0.00	0.02	0.01	0.02	0.01
<i>Neogloboquadrina duterrei</i>	0.17	0.77	-0.16	0.00	0.60	0.05
<i>Globigerina bulloides</i>	-0.01	0.47	0.10	-0.03	0.08	0.03
<i>Orbulina universa</i>	0.05	0.10	0.10	0.02	0.04	0.03
<i>Globorotalia menardii</i>	---	---	---	0.06	0.46	-0.00
<i>Globorotalia tumida</i>	---	---	---	-0.01	0.37	-0.01
<i>Globorotalia inflata</i>	0.06	-0.06	0.68	-0.03	0.06	0.90
<i>Neogloboquadrina pachyderma</i> (dextral)	-0.11	0.34	0.46	-0.01	-0.06	0.11
<i>Globorotalia truncatulinoides</i> (dextral)	0.14	-0.10	0.30	0.05	-0.04	0.07
<i>Globorotalia crassaformis</i>	0.12	-0.02	0.24	0.01	0.07	0.01
<i>Neogloboquadrina pachyderma</i> (sinistral)	-0.01	0.02	0.09	-0.01	-0.11	0.01
<i>Globigerina quinquiloba</i>	0.00	0.01	0.04	-0.00	-0.01	-0.06
<i>Globorotalia truncatulinoides</i> (sinistral)	0.03	-0.01	0.01	0.03	-0.02	0.13
<i>Sphaeroidinella dehiscens</i>	0.02	0.00	-0.03	-0.00	0.04	0.00
<i>Globoquadrina conglomera</i>	0.02	0.04	-0.12	---	---	---
<i>Globoquadrina hexagona</i>	0.07	0.03	-0.11	---	---	---
<i>Globorotalia hirsuta</i>	0.00	0.00	0.00	0.02	-0.02	0.10
P-D intergrade <sup>b</sup>	---	---	---	-0.01	-0.01	0.14

<sup>a</sup>Species are grouped by their dominant factor scores in the downcore solution. Larger absolute values of scores indicate greater weighting in the factor index.

<sup>b</sup>P-D intergrade is combined with *N. duterrei* in the downcore solution.

grouped together as are pink and white varieties of *Globigerinoides ruber*.

### 3. Results

#### 3.1. Faunal Factors

*Q*-mode factor analysis of the downcore faunas in the 10 sites used as input here resolves three significant faunal factors [Mix and Morey, 1996]. Core-top studies typically resolve five or more factors [Imbrie and Kipp, 1971; Kipp, 1976; Imbrie et al., 1989]. Our results indicate that just three factors are sufficient to describe temporal variability in the eastern equatorial current systems (Table 1).

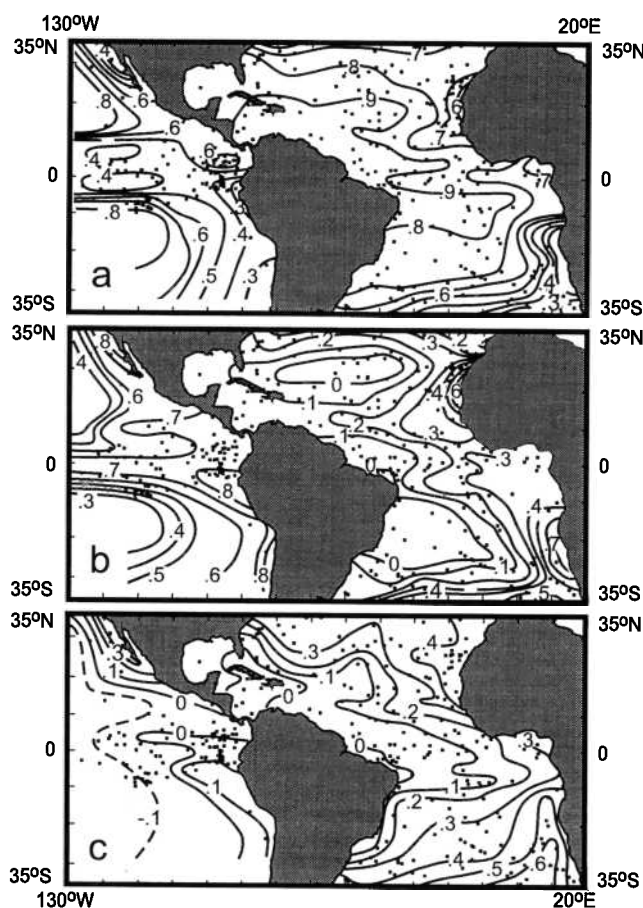
In all cases our downcore samples are well described by our three faunal factors. Communalities in the downcore samples analyzed here are always >0.7 and average 0.9; that is, the factors account for 90% of the downcore fauna. This contrasts with the application of tropical core-top factors to ice age samples, which accounts for just 35% of the population variance in downcore samples from the tropics [Ravelo et al., 1990]. Thus oceanographic changes in the tropical water masses are reflected better by variations of the factors we present here than by the core-top assemblages of CLIMAP [1981] or Ravelo et al. [1990].

To gain insight into the environmental meaning of the three downcore faunal factors, we applied them to core-top samples between 40°N and 40°S. Problems with no-analog conditions are apparent as low communalities in core-top samples. Because these anomalous samples can be examined in the context of modern oceanographic data, they can be understood more clearly and excluded from the paleoenvironmental calibration. Core-top samples used here come from the database assembled by Prell [1985] with additional samples from Atlantic and Pacific core tops [Coulbourn et al., 1980; Sverdrlove, 1983; Mix, 1986; Mix and Morey, 1996]. This analysis yields three maps of loadings (strengths) of the three downcore factors (Figure 2).

When mapping the factor loadings, we excluded any core-top samples with factor communalities <0.6 as these were not well described by the fauna present in the equatorial oceans. None of these low-communality samples come from the equatorial Pacific or Atlantic Oceans. The Pleistocene assemblages are thus good analogs for the modern fauna in much of the tropical oceans. This may seem surprising as we previously noted that the modern assemblages were not good analogs for the ancient fauna. The explanation is that ice age assemblages in the tropics reflect a larger range of conditions than occur at present within the tropics. Our downcore calibration of factors captures this broader dynamic range and thus succeeds in simulating both modern and ancient samples with good fidelity.

In nearly all cases the low-communality core-top samples are from distant regions such as the NW Pacific and Antarctic, which have little relevance to interpretation of the tropical data. This is important as it reveals the likely reason for the no-analog problem in CLIMAP studies. Core-top factors attempted to simulate the cool ice age foraminiferal assemblages in the tropics with modern cool water assemblages that were inappropriate because they were from high latitudes.

For comparison, Table 1 also notes the three most relevant CLIMAP Atlantic core-top factors used for equation FA-20 reported by Mix [1989]. McIntyre et al. [1989] document the



**Figure 2.** Downcore faunal factors applied to core-top samples. Values contoured are factor loadings of samples with communality >0.60: (a) factor 1, the warm tropical assemblage, (b) factor 2, the upwelling assemblage, and (c) factor 3, the eastern boundary assemblage.

contributions of these factors to tropical Atlantic planktonic foraminiferal assemblages. In all cases the major species that identify the CLIMAP factors are also strong contributors to our downcore factors. In detail, however, the weighting of species in the downcore factors differ from that in the core-top factors. It is these subtle differences that allow us to capture better the faunal patterns in ice age samples.

Factor 1 contains seven abundant species: *G. ruber*, *G. sacculifer*, *Globigerinita glutinata*, *Globigerinella aequilateralis*, *Pulleniatina obliquiloculata*, *Globigerina rubescens*, and dextral-coiling *Globorotalia truncatulinoides*, in order of importance. All of these species are common in warm tropical and subtropical environments [Kipp, 1976; Parker and Berger, 1971]. In core-top samples this factor is clearly associated with warm, salty subtropical and tropical water masses where the thermocline is deep in the western Atlantic Ocean and in the Pacific Ocean (Figure 2a). Factor 1 also dominates the Panama Basin, where SSTs are warm, salinities are low, and the thermocline is shallow [Levitus, 1982]. Warm temperature is the variable common to all these locations, so we refer to factor 1 as the “warm tropical factor”. This is the relatively warm end member against which the other two factors, with cooler aspect, contrast.

The second factor is dominated by *N. dutertrei*, with secondary contributions from *Globigerina bulloides* and dextral-coiling *Neogloboquadrina pachyderma*. These species are common in tropical upwelling environments and at high latitudes [Kipp, 1976; Parker and Berger, 1971; Prell and Curry, 1981]. The core-top projection of factor 2 is associated with the equatorial upwelling zone in the Pacific Ocean and is also present in the eastern tropical Atlantic Ocean and in the Benguela upwelling system (Figure 2b). We infer that this assemblage records the strength of cool upwelling systems of relatively high biological productivity and refer to it as the "upwelling factor".

In the third factor, *Globorotalia inflata* is the most important contributor, followed by dextral-coiling *N. pachyderma* (which is shared with factor 2), dextral-coiling *G. truncatulinoides* (which is shared with factor 1), and *Globorotalia crassaformis*. The high-latitude species sinistral-coiling *N. pachyderma* also is associated with factor 3 but is not dominant because it is relatively rare in the tropical samples that define the assemblages. The equatorial species *N. dutertrei*, which is common in factor 2, has a significantly negative score in factor 3. This implies that tropical samples with high loadings of factor 3 have both high concentrations of high-latitude species such as *G. inflata* or *N. pachyderma* and low concentrations of *N. dutertrei*. In the core-top samples, factor 3 penetrates into the low latitudes in the eastern boundary currents (Figure 2c). This factor is not strongly associated with productive coastal upwelling centers. Where present near the equator (i.e., with positive factor loadings), it appears to reflect advection off the eastern boundary. Thus we refer to it as the "eastern boundary factor".

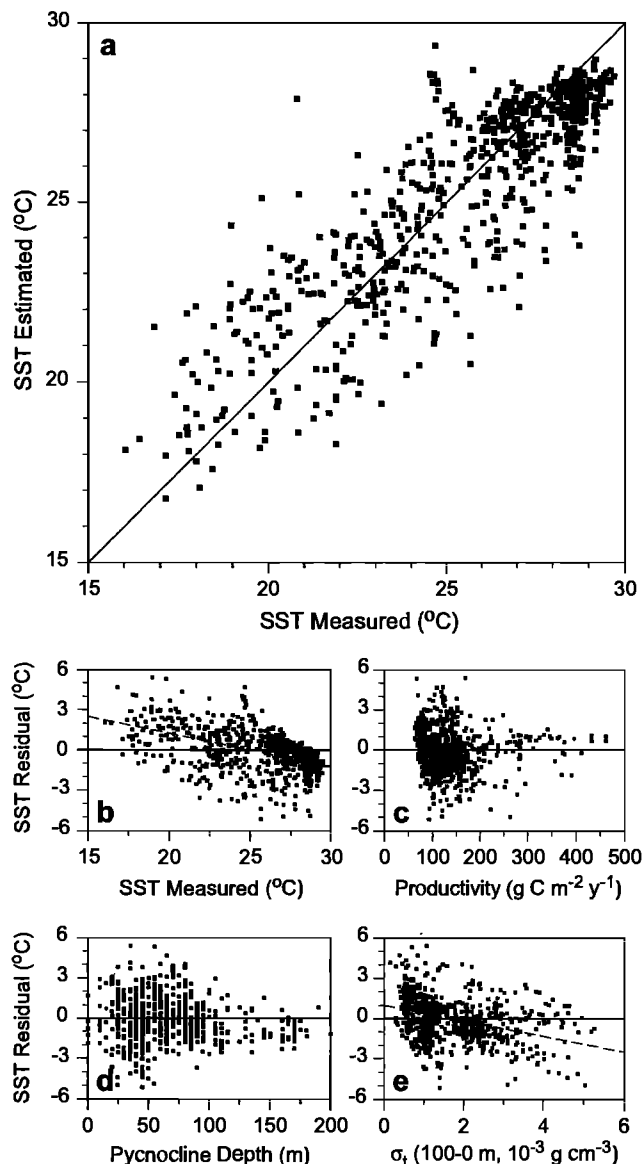
A potential worry in all faunal analyses is selective preservation. If dissolution modifies the relative weighting of faunal assemblages, transfer function equations operating on the assemblage weightings will produce biased estimates. Mix and Morey [1996] consider this possibility in detail and demonstrate no significant correlation in the modern ocean between the assemblage loadings and water depth (related to dissolution through a pressure effect) or in ancient samples to indices of shell fragmentation, an empirical measure of dissolution intensity [Le and Shackleton, 1992]. Thus, although some effects of dissolution may remain in the data set, with the factors defined here dissolution artifacts are relatively minor.

### 3.2. Temperature Estimates

We calibrate the three downcore foraminiferal assemblages, as expressed in core tops, to annual average SST [Levitus, 1982] following standard procedures of multiple linear regression essentially identical to those of CLIMAP [1981]. Terms only enter the transfer function equation if they are above the 95% confidence level (based on partial *F* statistic). The resulting transfer function, which accounts for 72% of the variance in modern SST from 15° to 30°C is

$$T = 27.0 + 4.81 (F_3)^2 + 12.59 (F_1)(F_2) - 5.02 (F_1)(F_3) - 10.50 (F_2) - 8.66 (F_3) \quad (1)$$

where *T* is the SST (in degrees Celsius), and *F*<sub>1</sub>, *F*<sub>2</sub>, and *F*<sub>3</sub> are the loadings of factors 1, 2, and 3, respectively (Figure 3). The statistical error (1  $\sigma$  standard deviation of residuals) of estimated mean annual SSTs in this equation is  $\pm 1.7^\circ\text{C}$ , somewhat larger



**Figure 3.** Transfer function calibration and analysis of residuals. (a) Annual average SST (degrees Celsius) estimated (this paper) versus measured [Levitus, 1982]. (b) SST residuals (estimated minus measured, degrees Celsius) versus SST measured. The dashed line is a linear regression ( $r^2=0.23$ ). (c) SST residuals (degrees Celsius) versus primary productivity ( $\text{g C m}^{-2} \text{y}^{-1}$ , estimated at each site from satellite imagery [Antoine et al., 1997]). (d) SST residuals (degrees Celsius) versus annual average pycnocline depth (m, calculated for each core site from Levitus [1982]). (e) SST residuals versus the upper ocean density contrast from 0 to 100 m ( $\sigma_t$  units,  $10^{-3} \text{g cm}^{-3}$ , calculated for each core site from Levitus [1982]). The dashed line is a linear regression ( $r^2=0.11$ ). The lack of significant correlation between temperature residuals and productivity or pycnocline depth suggests that these variables do not bias the temperature estimates. Significant correlation of temperature residuals to the upper ocean density contrast suggests the possibility of bias associated with the availability of different ecological niches within the euphotic zone.

than the seasonal precision of  $\pm 1.2^\circ$  to  $1.3^\circ\text{C}$  reported for the FA-20 equation calibrated on Atlantic core tops [Molfini et al., 1982].

There are several reasons for this apparent difference in preci-

sion. First, because our definitions of the faunal assemblages are based on ancient samples, our factors are not specifically tuned to fit the core-top samples used for the temperature calibration. Statistical errors that might occur in applying the assemblages to unknown samples are thus realistically revealed within our core-top calibration. The traditional CLIMAP approach, in which the factor analysis and temperature calibration are done on the same samples, cannot reveal such errors.

Second, our equation and statistical errors were calculated from a global array of samples (within the latitude range 40°N to 40°S), while the FA-20 equation statistics were calculated for Atlantic samples only. When we apply the FA-20 equations to the global core-top database and average the warm and cold season estimates, the statistical error of FA-20 for same set of core-top samples we used (between 15° and 30°C) is  $\pm 2.2^\circ\text{C}$ , significantly worse than the transfer function developed here. This finding is consistent with *Prell's* [1985] demonstration that transfer functions calibrated within a single ocean degrade when applied to another ocean.

Third, we have purposely designed a relatively simple equation, with just three faunal factors and six terms in the equation. In contrast, foraminiferal equation FA-20 includes six factors and 28 terms in each seasonal equation [*Imbrie et al.*, 1989]. A global foraminiferal transfer function [*Ortiz and Mix*, 1997] calculated with traditional core-top calibration of seven faunal assemblages and 21 equation terms gave a statistical error of  $\pm 1.9^\circ\text{C}$ , somewhat worse than our result using downcore calibration of faunal assemblages.

Summarizing, we believe our method of calculating faunal assemblages from Pleistocene samples gives a more realistic view of statistical errors in the transfer function while minimizing the no-analog problem inherent in CLIMAP's approach. Biases and misfits that remain in the calibration are apparent in the application of downcore factors to core-top sediments, where they can be examined and understood.

### 3.3. Evaluating Transfer Function Bias

To assess potential biases in our transfer function, which might yield an inaccurate result, we consider the relationship of estimated temperatures to measured (calibration) temperatures and the relationship of temperature residuals (the difference of estimated minus measured SST) to measured temperature and other oceanographic variables. We focus on variables that previous work suggests might bias the temperature estimates: biological primary productivity, pycnocline depth, and upper ocean density gradients [*Ravelo et al.*, 1990; *Andreasen and Ravelo*, 1997; *Watkins and Mix*, 1998]

A significant correlation exists between temperature residuals and measured temperatures ( $r^2=0.23$ ). At temperatures  $<18^\circ\text{C}$ , SST estimates tend to be too high (Figure 3b). These samples in the core-top calibration are located mostly at latitudes poleward of 35° north and south. The faunal factors derived from the tropics do not represent the core-top faunas well here. Future improvements in these regions may come from including higher-latitude samples in the factor analysis. Communalities in these anomalous samples are relatively low, averaging 0.7, compared to the samples at higher temperatures in which communalities average 0.9.

At temperatures  $>28^\circ\text{C}$ , temperature estimates appear to be too low. This suggests that the transfer function developed here

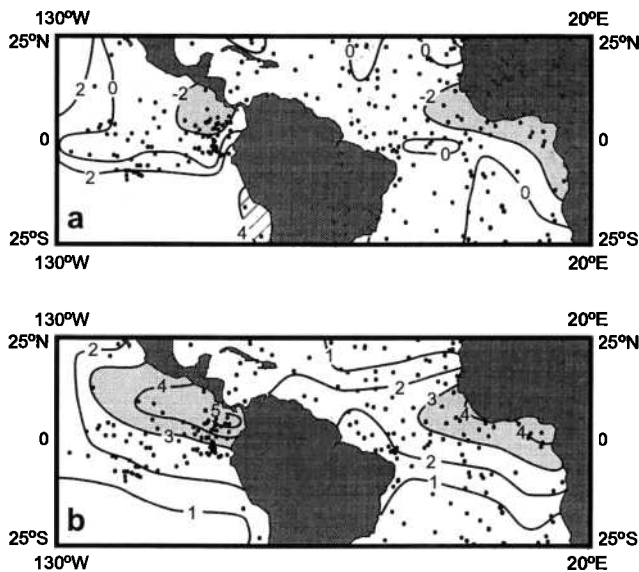
may tend to underestimate the full range of SST changes through time. One possible reason for this bias is that at colder locations, foraminiferal productivity is biased toward the warmer summer months [*Sautter and Thunell*, 1989], while at lower latitudes, foraminifera are more abundant during cooler seasonal upwelling events [*Thunell and Reynolds*, 1984]. The biased samples are not, however, associated with areas of strongest seasonal upwelling. This leads us to examine other oceanographic variables that may bias the transfer function.

Comparison of the temperature residuals to modern biological productivity (Figure 3c) and to pycnocline depth (Figure 3d) at the core sites reveals no significant correlations, suggesting that these variables do not bias the transfer function estimates of temperature. Primary productivity is calculated here at each site by averaging 12 monthly values of primary productivity estimated from satellite color data and binned in 1.2° latitude by 1.2° longitude blocks [*Antoine et al.*, 1997]. Pycnocline depth is defined here as the depth of maximum rate of change in density as a function of depth for annual average water column profiles of temperature and salinity. The rate of change in density was calculated at a resolution of  $\pm 5$  m from a spline fit of atlas data [*Levitus*, 1982].

Although the correlations between temperature residuals, productivity, and pycnocline depth (Figures 3c and 3d) are not significantly different from zero, some relationships are apparent. The total range of residuals is higher in regions where productivity is low and the pycnocline is shallow. This provides an important hint about where biases may exist in our new transfer function. These samples are anomalous compared to the situation prevalent in the tropics, where areas of shallow pycnocline are generally associated with higher primary productivity [*Herbland and Voituriez*, 1979]. The anomalous areas in which productivity is relatively low in spite of a shallow pycnocline are generally associated with low-salinity surface waters (for example west of the Panama Isthmus in the Pacific Ocean and in the Gulf of Guinea in the Atlantic Ocean). In these areas local precipitation greatly exceeds evaporation. The systematic nature of this apparent bias is revealed by comparing SST residuals and the density contrast within the euphotic zone (calculated from the difference of annual average densities at the sea surface and 100 m, Figure 3e). This correlation is weak but significantly different from zero ( $r^2=0.11$ ).

The geographic distribution of temperature residuals in the eastern Pacific and tropical Atlantic Oceans supports the correlation between transfer function temperature residuals and upper ocean density contrast (Figure 4). If the anomalous areas with high vertical density gradients ( $>3 \times 10^{-3} \text{ g cm}^{-3}$ ), such as Panama Basin and the Gulf of Guinea are excluded, the standard error of estimate for (1) is reduced to  $\pm 1.5^\circ\text{C}$  and the trend of temperature residuals compared to measured temperatures is reduced (i.e., within the statistical error). Thus, in areas that have moderate density gradients within the euphotic zone, (1) estimates SSTs accurately with a precision that warrants application to ancient samples in the tropics.

Note that none of the downcore samples included in the factor analysis that defined the faunal assemblages came from the areas of anomalously high vertical density gradients (Figure 1). Given more downcore faunal data from those areas, it is possible that the faunal descriptions and temperature estimates of such areas would improve.



**Figure 4.** (a) SST residuals (estimated minus measured, degrees Celsius) at core-top locations in the eastern Pacific and tropical Atlantic Oceans. (b) The upper ocean density contrast ( $\sigma_t$ , units,  $10^{-3} \text{ g cm}^{-3}$ ) calculated from 0 to 100 m (i.e., across the euphotic zone). Areas of strongest density contrast in the Pacific Ocean (west of the Panama Isthmus) and in the Atlantic Ocean (Gulf of Guinea) are associated with anomalously low surface water salinities. In these areas the foraminiferal transfer function estimates temperatures lower than those measured at the sea surface.

Summarizing, the depth of the pycnocline and biological productivity do not appear to induce systematic bias in the transfer function developed here. There is a weak tendency for bias induced by the strength of the density gradient within the euphotic zone. Transfer function temperature estimates tend to be too low in areas of very strong vertical density gradients. We speculate that such underestimates of SST in these areas are associated with the availability of significantly different ecological niches within the euphotic zone, exploited by different foraminiferal populations but averaged in the geologic record [Fairbanks *et al.*, 1982]. Although we have not attempted to make corrections for such an effect here, additional information on the strength of the pycnocline, perhaps based on the oxygen isotopic difference between shallow-dwelling and deep-dwelling foraminifera [Mullitza *et al.*, 1997], might improve transfer functions of SST.

### 3.4. The Last Glacial Maximum

The CLIMAP [1981] reconstruction (recalculated here as annual temperature anomalies by averaging the CLIMAP August and February estimates) suggested little change in the tropics. For example, CLIMAP [1981] estimated Last Glacial Maximum (LGM) cooling of  $2^\circ\text{C}$  in the equatorial Atlantic and slight warming relative to modern averages in the eastern equatorial Pacific (Plate 1a).

To compare our new transfer function to that of CLIMAP, we applied (1) to both core-top sediments and to the CLIMAP LGM data set augmented by newer data on LGM foraminiferal assemblages in the tropical Pacific [Mix and Morey, 1996] and

Atlantic [Mix *et al.*, 1986]. Next we found the gridded core-top estimate (i.e., the average of core tops within a  $2^\circ$  latitude  $\times$   $5^\circ$  longitude box) associated with each glacial maximum sample. The difference between these two values defines the extent of change from LGM to modern (Plate 1b). We calculated the differences this way rather than gridding both the LGM and modern estimates and differencing the grids because the data density of the LGM samples is lower than that of the core tops. By calculating the differences between LGM estimates and core-top estimates rather than between LGM estimates and modern atlas values we minimize the effects of bias in the transfer functions noted above.

The resulting map of temperature anomalies (LGM minus modern) reveals major cooling of the tropics, up to  $6^\circ\text{C}$  on an annual average in the equatorial Atlantic and  $\sim 5^\circ\text{C}$  in the equatorial Pacific (Plate 1b). Significant cooling in our reconstruction extends into the Caribbean ( $3\text{--}4^\circ\text{C}$  change) and in the eastern boundary regions (up to  $6^\circ\text{C}$  change). In the equatorial zones our new reconstruction of LGM temperature anomalies is significantly different than that of CLIMAP [1981]. In the center of the subtropical gyres our findings are consistent with previous inferences of little or no change [CLIMAP, 1981; Prell 1985], although the spatial patterns of subtropical change are somewhat different.

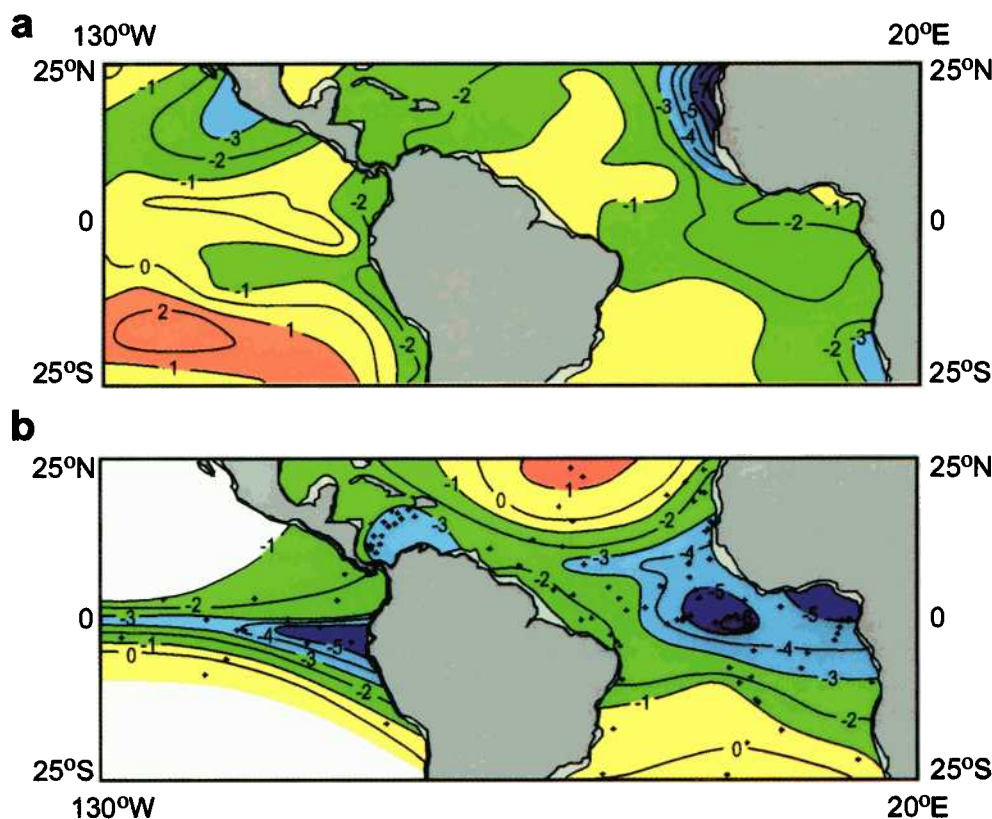
## 4. Discussion

Why are our estimates of tropical climate change so different from those of CLIMAP [1981] when they use basically similar transfer function methods? We see two reasons.

First, our downcore faunal factors, all generated from tropical locations, better represent the faunal variations that actually occurred in the tropics. Because the CLIMAP factors grouped some species that are not correlated in the geologic past, they effectively smoothed the downcore record of faunal variability. This smoothing resulted in underestimates of SST changes.

Second, because our calibration includes only low-latitude samples, it optimizes the temperature estimate equations to reconstruct the tropics. In contrast, the CLIMAP equations were heavily weighted to polar faunas. The cold end-member that dominated the CLIMAP temperature equations (including the sinistral-coiling morphotype of the species *N. pachyderma*) was not relevant to the oceanographic context of the tropics. Polar conditions never occurred there. Our present result suggests that the CLIMAP equations were desensitized to temperature variations at low latitudes.

How do our new estimates of LGM cooling of the tropical oceans compare to other estimates? Recent faunal estimates based on radiolaria from the eastern equatorial Pacific [Pisias and Mix, 1997] agree with the estimates made here based on foraminifera. Some geochemical data from the tropical ocean and from the continents suggest large changes in tropical SSTs, although the geochemical data are themselves in conflict with each other. For example, Sr/Ca ratios in Barbados corals suggest  $4^\circ$  to  $5^\circ\text{C}$  ice age cooling [Guilderson *et al.*, 1994], somewhat more than the  $3^\circ\text{C}$  change we estimate here near Barbados. Other studies of coral chemistry, however, question these results because the sensitivity of Sr/Ca to temperature changes is affected by coral growth rates and varies in different coral species [de Villiers *et al.*, 1994].



**Plate 1.** Annual average SST anomalies, LGM minus modern, based on (a) The *CLIMAP* [1981] reconstruction, averaging winter and summer estimates, (b) The Oregon State University (OSU) reconstruction (this paper, LGM core locations noted). The white area in Pacific indicates no data. Our new reconstruction suggests significantly greater ice age cooling in the equatorial band associated with the equatorial current systems. Although the spatial pattern of change within the subtropics is somewhat different, our reconstruction supports the inference of *CLIMAP* [1981] that the subtropical gyre centers remained relatively warm and stable during the LGM.

Another geochemical index, U/Ca, in the same Barbados corals suggests glacial maximum cooling of  $\sim 3^\circ\text{C}$  relative to modern conditions [Min *et al.*, 1995]. A temperature index based on Mg/Ca ratios in foraminifera suggests ice age cooling of  $2.6^\circ \pm 1.3^\circ\text{C}$  relative to modern in the Caribbean and in the North Equatorial Counter Current of the Atlantic [Hastings *et al.*, 1998]. Both the U/Ca and Mg/Ca estimates are consistent with our new faunal estimates in the region.

Oceanic data that support relatively little ice age cooling in the subtropics include organic geochemical thermometers  $U^{k_{37}}$  [Sikes and Keigwin, 1994; Roselle-Melé *et al.*, 1998]. Our estimates in these regions suggest little change or even slight warming during the LGM. Our calibration scheme, however, does not include downcore records from the subtropical gyres, and should be re-assessed with local data from those regions.

What about the continents? Rare gas content of ice age groundwater in tropical South America and the southern United States implies significant ice age cooling of  $3^\circ$  to  $5^\circ\text{C}$  in these regions [Stute *et al.*, 1995]. Because low-latitude land temperatures are relatively closely tied to regional SSTs [Rind and Peteet, 1985], these estimates would appear to constrain lower ocean temperatures at the glacial maximum. At high altitudes, oxygen isotope data from ice cores in Peru suggest ice age

cooling roughly consistent with those of the lowlands [Thompson *et al.*, 1995].

The continental data, however, do not necessarily require that oceanic cooling occurred in all areas of the tropics. The effect on the continents of our proposed geographically limited ice age cooling of the equatorial oceans is addressed by using our LGM SSTs as a boundary condition to an atmospheric circulation model (S.W. Hostetler and A.C. Mix, Ice age cooling of the tropics reassessed, submitted to *Nature*, 1999). This comparison reveals that most of the mismatches between the continental and oceanic data can be resolved by SSTs reconstructed here.

What oceanic processes could produce such cooling, concentrated in the cold “tongues” associated with the westward flowing equatorial currents? We suggest cooling of the ice age thermocline driven by faster upper ocean ventilation. Mode waters forming in subpolar regions, chilled by cold continental air masses displaced equatorward by polar glaciation, return to the surface through equatorial and eastern boundary upwelling. Such cold waters are then advected into the tropical oceans by strong westward flowing equatorial currents. Poleward return flow of tropical surface waters would complete the advective loop, resulting in enhanced net transport of heat out of the tropics.



This view of greater thermocline turnover, effectively a smaller version of the so-called conveyor belt advective heat transport, is consistent with benthic foraminiferal data from shallow sites suggesting cooler and better ventilated thermocline [Slowey and Curry, 1992], and with inferences of a stronger east-west gradient in pycnocline depth at the glacial maximum [Andreassen and Ravelo, 1997]. Such a change is also manifested directly in the foraminiferal species in the equatorial region. The largest change here is associated with the eastern boundary fauna (our factor 3 noted in Table 1) rather than with the upwelling fauna [Mix and Morey, 1996]. Thus, the species distributions support the idea that advection is the major source of cooling in the equatorial cold tongues. This inference based analysis of the foraminifera is supported by analysis of radiolarian faunas [Pisias and Mix, 1997].

## 5. Conclusions

Here we develop a new strategy for calibrating faunal transfer functions to estimate tropical SSTs in the past. Our key innovation is the use of Pleistocene samples from the tropics to define robust faunal assemblages that covary through time rather than core-top samples to define assemblages that covary geographically in the modern ocean. Our approach circumvents the problem of no-analog faunas in the ice age ocean, which plagues past faunal estimates using either transfer function or modern analog techniques.

We estimate LGM SSTs in the equatorial Atlantic and eastern Pacific significantly cooler than those of CLIMAP [1981]. Our faunal estimates are more in line with recent geochemical proxies of SST and continental temperature changes. The long-standing conflict between the CLIMAP reconstruction in the

tropics and other data and models may thus be at least partially resolved.

Our findings have implications for the sensitivity of the tropics to large-scale climate change and the processes that drive such changes. We suggest that the equatorial currents, especially where they interact with the eastern boundary current systems, are the most sensitive to change and that these systems are responsible for the bulk of the LGM cooling within the tropics. We support CLIMAP's original inference of stability of SSTs within the subtropical gyres.

With our new approach to calibrating faunal assemblages in transfer functions we have made progress, but uncertainties remain. Our reconstruction is focused on the eastern equatorial Atlantic and Pacific Oceans. Areas distant from our downcore calibration of faunas should be reanalyzed with local calibration using our downcore method to resolve robust faunal assemblages. We have noted potential biases in our temperature estimates, perhaps linked to the intensity (but not the depth) of the pycnocline. For example, SSTs in areas with a low-salinity surface layer may be difficult to reconstruct from foraminiferal faunas. It is possible that the addition of more downcore faunal data in such regions would better define the faunal assemblages and improve the SST estimates. Alternatively, tracers of total density contrast within the upper ocean could help to identify problem areas and improve future transfer function estimates of SST.

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S. W. Hostetler, U.S. Geological Survey, Corvallis, OR 97330.

A. C. Mix, A. E. Morey, and N. G. Pisias, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331-5503. (mix@oce.orst.edu)

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