

Reevaluation of the oxygen isotopic composition of planktonic foraminifera: Experimental results and revised paleotemperature equations

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Abstract. Cultured planktonic foraminifera, *Orbulina universa* (symbiotic) and *Globigerina bulloides* (nonsymbiotic), are used to reexamine temperature: $\delta^{18}\text{O}$ relationships at 15°-25°C. Relationships for both species can be described by linear equations. Equations for *O. universa* grown under low light (LL) and high light (HL) share a slope of -4.80 ($0.21\text{‰ } ^\circ\text{C}^{-1}$) with a HL-LL offset of -0.33‰ due to symbiont photosynthetic activity. The effect of $[\text{CO}_3^{2-}]$ on *O. universa* is $-0.002\text{‰ } \mu\text{mol}^{-1} \text{ kg}^{-1}$ and is insensitive to temperature. For *G. bulloides*, ontogenetic effects produce size-related trends in temperature: $\delta^{18}\text{O}$, whereby larger shells are enriched in ^{18}O relative to smaller specimens. The *O. universa* temperature: $\delta^{18}\text{O}$ relationships are more accurate than previously published equations for describing plankton tow data. Our equations do not explain planktonic core top data with the same precision but provide a good fit to benthic *Cibicides* data below 10°C. Temperature: $\delta^{18}\text{O}$ relationships for *G. bulloides* provide good agreement with field data for this species from the northeast Pacific.

1. Introduction

In 1947, Harold Urey proposed that the oxygen isotopic composition ($\delta^{18}\text{O}$ value) of carbonate fossils could be used to reconstruct environmental temperatures during the life of an organism [Urey, 1947]. His hypothesis was borne out in early experiments with inorganically precipitated calcite. The work of *McCrea* [1950] verified the theoretical magnitude of calcite-water oxygen isotopic fractionation at low temperatures and produced the first empirical temperature: $\delta^{18}\text{O}$ relationship.

During the past several decades many empirically derived "paleotemperature" equations have been published (Table 1). *Epstein et al.* [1953] generated a mollusk shell-based paleotemperature equation that agreed well with the results of *McCrea* [1950] and substantiated the potential of oxygen isotope paleothermometry for biogenically precipitated calcite. *Craig* [1965] later modified *Epstein et al.*'s relationship by correcting for slight errors in the original analytical measurements. Another temperature: $\delta^{18}\text{O}$ relationship was determined for mollusk shells cultured in Japan by *Horibe and Oba* [1972]. *O'Neil et*

al. [1969] generated a paleotemperature equation based on calcite precipitated inorganically at temperatures of 0°-500°C, and *Shackleton* [1974] proposed that a linearization of the low temperature portion of this relationship ($<16.9^\circ\text{C}$) was a good fit to field data of the benthic foraminifer *Uvigerina* spp. The first empirically derived temperature: $\delta^{18}\text{O}$ relationship based on planktonic foraminifera was generated by *Erez and Luz* [1983] for laboratory-grown specimens of the symbiotic species *Globigerinoides sacculifer* (14°-30°C). *Bouvier-Soumagnac and Duplessy* [1985] generated temperature: $\delta^{18}\text{O}$ relationships for planktonic foraminifera collected in oblique tows from 0 to 200 m depth and found good agreement with relationships they determined for cultured specimens. More recently, *Kim and O'Neil* [1997] reinvestigated temperature: $\delta^{18}\text{O}$ relationships for inorganically precipitated calcite at low temperatures (10°-40°C). Although most of these temperature: $\delta^{18}\text{O}$ relationships appear to be similar, temperature reconstructions can differ by as much as 2°C when ambient temperature varies from 15° to 25°C.

Efforts to calibrate these equations for use with planktonic foraminifera have produced ambiguous results. For instance, oxygen isotope values of shells collected from Bermuda plankton tows across several seasons were too low relative to predicted equilibrium [Williams *et al.*, 1981]. In this case the equation of *Epstein et al.* [1953] estimated temperatures that

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Table 1. Comparison of Commonly Used Calcite Temperature: $\delta^{18}\text{O}$ Relationships With Equations Developed in This Study

Reference	Source	$T(^{\circ}\text{C}) = a + b(\delta_{\text{c}} - \delta_{\text{w}}) + c(\delta_{\text{c}} - \delta_{\text{w}})^2$			δ_{w} Correction (VSMOW to VPDB)	$T(^{\circ}\text{C})$ Offset From LL Equation (1)			$T(^{\circ}\text{C})$ Offset From HL Equation (2)		
		<i>a</i>	<i>b</i>	<i>c</i>		0°C	15°C	25°C	0°C	15°C	25°C
<i>McCrea</i> [1950]	Inorganic	16.0	-5.17	0.09	-0.20‰	-0.2	-0.2	+0.7	+1.4	+1.5	+2.5
<i>Epstein et al.</i> [1953]	Mollusk	16.5	-4.3	0.14	-0.20‰	+3.6	+0.5	-0.1	+4.7	+1.9	+1.5
<i>Craig</i> [1965]	Mollusk (modified from <i>Epstein et al.</i> [1953])	16.9	-4.2	0.13	-0.20‰	+4.2	+0.9	+0.1	+5.3	+2.3	+1.6
<i>O'Neil et al.</i> [1969]	Inorganic*	16.9	-4.38	0.1	-0.20‰	+3.3	+0.8	+0.3	+4.5	+2.3	+1.9
<i>Horibe and Oba</i> [1972]	Mollusk	17	-4.34	0.16	-0.20‰	+4.2	+1.0	+0.6	+5.3	+2.4	+2.2
<i>Shackleton</i> [1974]	BF: (modified from <i>O'Neil et al.</i> [1969]; calibrated with <i>Uvigerina</i>)	16.9	-4.0		-0.20‰	+3.4	+0.9		+4.8	+2.3	
<i>Erez and Luz</i> [1983]	PF: <i>Globigerinoides sacculifer</i> (laboratory)	17.0	-4.52	0.03	-0.22‰	+2.0	+0.8	+0.3	+3.5	+2.3	+1.9
<i>Bouvier-Soumagnac and Duplessy</i> [1985]	PF: <i>Orbulina universa</i> (laboratory)	16.4	-4.67		-0.20‰	+0.7	+0.3	+0.0	+2.2	+1.8	+1.6
<i>Bouvier-Soumagnac and Duplessy</i> [1985]	PF: <i>O. universa</i> (Indian Ocean)	15.4	-4.81		-0.20‰	-0.8	-0.8	-0.7	+0.8	+0.8	+0.9
<i>Kim and O'Neil</i> [1997]	Inorganic*	16.1	-4.64	0.09	-0.27‰	+1.2	-0.3	-0.4	+2.6	+1.2	+1.3
This study, (1)	PF: <i>O. universa</i> (LL)	16.5	-4.80		-0.27‰						
This study, (2)	PF: <i>O. universa</i> (HL)	14.9	-4.80		-0.27‰						
This study, (3)	PF: <i>Globigerina bulloides</i> (11-chambered shell)	12.6	-5.07		-0.27‰						
This study, (4)	PF: <i>G. bulloides</i> (12-chambered shell)	13.2	-4.89		-0.27‰						
This study, (5)	PF: <i>G. bulloides</i> (13-chambered shell)	13.6	-4.77		-0.27‰						

The abbreviations are defined as follows: BF, benthic foraminifera; PF, planktonic foraminifera; LL, low light (20-30 $\mu\text{Einst m}^{-2} \text{s}^{-1}$); HL, (>380 $\mu\text{Einst m}^{-2} \text{s}^{-1}$); and VSMOW, Vienna SMOW; and VPDB, Vienna Peedee belemnite. Temperature offsets of published equations from (1) and (2) are calculated for 0°, 15°, and 25°C. Asterisks denote a conversion from “10³In‰” notation using a quadratic approximation (see text).

were $\sim 1^{\circ}\text{--}2^{\circ}\text{C}$ above the actual seasonal sea surface temperatures (SST). Other calibration efforts have produced similar results [Deuser and Ross, 1989; Erez and Honjo, 1981; Fairbanks et al., 1982; Sautter and Thunell, 1991; Shackleton et al., 1973]. Nonequilibrium $\delta^{18}\text{O}$ values in planktonic foraminifera have never been adequately explained.

Recently, laboratory experiments with live foraminifera have demonstrated that the photosynthetic activity of algal symbionts and the carbonate ion concentration ($[\text{CO}_3^{2-}]$) of seawater also affect shell $\delta^{18}\text{O}$ values [Spero, 1992; Spero et al., 1997; Spero and Lea, 1993; J. Bijma, submitted manuscript, 1997]. In these cases an increase in symbiont photosynthetic activity or $[\text{CO}_3^{2-}]$ results in a decrease in shell $\delta^{18}\text{O}$ values. Given the inconsistent SST reconstructions obtained using existing paleotemperature equations and the recently identified parameters controlling shell $\delta^{18}\text{O}$ values, there is a clear need to reexamine the temperature: $\delta^{18}\text{O}$ relationships for planktonic foraminifera.

In this paper we present the results of laboratory experiments that examine the relationships between temperature, $\delta^{18}\text{O}_{\text{water}}$, irradiance (symbiont photosynthesis), $[\text{CO}_3^{2-}]$, and shell $\delta^{18}\text{O}$. Experiments were conducted with the symbiont-bearing foraminifer *Orbulina universa* and nonsymbiotic *Globigerina bulloides* at temperatures of $15^{\circ}\text{--}25^{\circ}\text{C}$. Temperature: $\delta^{18}\text{O}$ relationships developed for these species predict more accurate $\delta^{18}\text{O}$ values for planktonic foraminifera data and produce SST estimates that are $\sim 1^{\circ}\text{--}5^{\circ}\text{C}$ cooler than those predicted by existing equations across the calibration.

2. Materials and Methods

2.1. Experimental Procedure

Approximately 100 *O. universa* and 230 *G. bulloides* specimens were cultured in these experiments using established procedures [Spero and Lea, 1993]. During 1994–1996, scuba divers hand collected live foraminifera from water depths of 2–6 m in the San Pedro Basin (“SPB”) within the Southern California Bight ($33^{\circ}23' \text{N}$, $118^{\circ}26' \text{W}$). Specimens were brought to the Wrigley Marine Science Center on Santa Catalina Island, where they were identified, measured with an inverted microscope, and transferred to $0.8 \mu\text{m}$ filtered seawater in 115 mL glass jars. The jars were sealed without an air space and placed into thermostated water tanks maintained at temperatures of 15°C , 17°C , 19°C , 22°C , and 24°C ($\pm 0.2^{\circ}\text{C}$); *O. universa* was also grown at 18°C and 25°C . Illumination was provided by F24T12/CW/HO fluorescent bulbs on a 12:12 hour light:dark cycle. *O. universa* was maintained under high light (HL, $>380 \mu\text{Einst m}^{-2} \text{s}^{-1}$), which corresponds to maximum symbiont photosynthetic rates (P_{max}) [Spero and Parker, 1985], and low light (LL, $20\text{--}30 \mu\text{Einst m}^{-2} \text{s}^{-1}$), which is below the compensation light level [Rink, 1996]. For comparison, ambient field light levels were $>2000 \mu\text{Einst m}^{-2} \text{s}^{-1}$ at the surface.

The foraminifera were fed one *Artemia* nauplius (San Francisco Bay strain, Artemia Reference Center #1157, $\delta^{13}\text{C}_{\text{organic}} = -20.4 \pm 0.2\text{‰}$) every other day until gametogenesis. Empty shells were then rinsed in purified water and archived in covered slides for later analysis. Water displaced during feeding was replaced with additional water from the same preparation. Culture water samples were collected at the start and end of experiments

for the determination of $\delta^{18}\text{O}_{\text{water}}$ and seawater $[\text{CO}_3^{2-}]$. We determined the $[\text{CO}_3^{2-}]$ of culture waters via equilibrium calculations after measuring pH and titrating to determine total alkalinity. The $[\text{CO}_3^{2-}]$ of ambient filtered seawater ($171 \mu\text{mol kg}^{-1}$) was increased to $458 \mu\text{mol kg}^{-1}$ to obtain a “high $[\text{CO}_3^{2-}]$ ” group by addition of $\sim 1.8 \text{ mL}$ of 1 N NaOH to 4 L of filtered seawater. This treatment increased the seawater pH from ~ 8.15 to ~ 8.64 (free hydrogen scale).

2.2. Sample Preparation and Analysis

Oxygen isotopic analyses were conducted on individual *O. universa* shells and pooled *G. bulloides* chambers. The isotopic data are available from the World Data Center A for Paleoclimatology, 325 Broadway, Boulder, Colorado; <http://www.ngdc.noaa.gov/paleo/paleo.html>; email: paleo@ngdc.noaa.gov (data contribution series 98-003). Archived *G. bulloides* shells were remeasured across the maximum dimension of each growth stage (i.e., chamber addition) and a previously established relationship between shell size (length) and total number of chambers [Spero and Lea, 1996] allowed us to assign positions to individual chambers (11–13). In our study the experimental shell size:chamber total relationships for 11- 12- and 13-chambered shells are $301 \pm 25 \mu\text{m}$, $369 \pm 30 \mu\text{m}$, and $414 \pm 39 \mu\text{m}$, respectively. Laboratory-grown chambers were amputated from the test and pooled according to their relative position in the shell whorl. An average of 12 *G. bulloides* chambers (average chamber weight $\sim 1.5 \mu\text{g}$) from identical ontogenetic positions was combined for each analysis. All shells were roasted in vacuo for 30 min at 375°C to remove adsorbed water prior to isotopic analysis on a Fisons Optima isotope ratio mass spectrometer (IRMS) using a common acid bath autocarbonate device. Analytical precision of the $\delta^{18}\text{O}$ analyses was $\pm 0.05\text{‰}$ relative to the Vienna Pee Dee belemnite (VPDB) standard. Culture water $\delta^{18}\text{O}$ values were determined via CO_2 equilibration with an automated water equilibrator attached to a Finnigan MAT 251 IRMS. The precision of replicates was $\pm 0.03\text{‰}$ versus Vienna standard mean ocean water (VSMOW). Water $\delta^{18}\text{O}$ and $[\text{CO}_3^{2-}]$ remained constant during the experiments ($\pm 0.09\text{‰}$ and $\pm 8 \mu\text{mol kg}^{-1}$, respectively).

2.3. Calibration of Temperature: $\delta^{18}\text{O}$ Relationships

Least squares regression was used to generate relationships between temperature and all individual shell $\delta^{18}\text{O}$ analyses (not group means, as plotted). We express shell $\delta^{18}\text{O}$ in these equations as the isotopic difference between calcite and water ($\delta^{18}\text{O}_{\text{c}} - \delta^{18}\text{O}_{\text{w}}$ or $\delta_{\text{c}} - \delta_{\text{w}}$), where both values are expressed in the conventional δ notation relative to VPDB. Quoted errors on the slope and intercept are 95% confidence intervals; the r^2 value and standard error of estimate are also presented for each equation. We found no statistical basis for excluding any data points prior to our generation of the temperature: $\delta^{18}\text{O}$ relationships. Furthermore, there were no consistent isotopic differences between the shells of gametogenic individuals and those terminated prior to gametogenesis, so we include data from some pregametogenic individuals. It was not necessary to apply a correction for field-grown chambers in *O. universa* shells because the juvenile shell is generally absent or negligible in gametogenic shells of this species [Brunner et al., 1987; Spero,

1988]. We combine the *G. bulloides* chamber data using a mass balance relationship to produce temperature: $\delta^{18}\text{O}$ relationships for whole shells consisting of a total of 11, 12, and 13 chambers. For these calculations, $\delta^{18}\text{O}$ values of chambers 1-10 are estimated at our experimental temperatures using interpolation of 10-chamber data from *G. bulloides* shells collected at ambient temperatures of 16°C [Spero and Lea, 1996] and 22°C (this study).

A small difference between published paleotemperature equations and those presented here is the correction value applied to convert $\delta^{18}\text{O}_w$ values from the VSMOW to VPDB scales. This correction is necessary to compare measured $\delta^{18}\text{O}$ values of CO_2 produced by the reaction of calcite with H_3PO_4 and CO_2 equilibrated with water (see discussions of Friedman and O'Neil [1977] and O'Neil [1986a]). Our temperature: $\delta^{18}\text{O}$ relationships are generated using the most recent $\delta^{18}\text{O}_w$ correction of -0.27‰ [Hut, 1987], whereas earlier empirical relationships were determined using values of -0.20‰ or -0.22‰ (Table 1). The choice of conversion factor would account for a 0.2°-0.3°C difference in temperature estimates. For published equations we apply the VSMOW to VPDB correction most current at publication if we could not identify the conversion value from the original text (i.e., -0.20‰ [Craig, 1965] or -0.22‰ [Friedman and O'Neil, 1977]).

For comparison with the relationships derived here, two published paleotemperature equations were modified from the form $10^3 \ln \alpha = A(10^6 T^{-2}) + B$ or $10^3 \ln \alpha = A(10^3 T^{-1}) + B$, where α is the oxygen isotopic fractionation factor between calcite and water, T is temperature in kelvins, and A and B are constants. These equations were approximated by the quadratic equation $T(^{\circ}\text{C}) = a + b(\delta_c - \delta_w) + c(\delta_c - \delta_w)^2$, which is the standard form used in paleoceanographic studies. Coefficients a , b , and c were obtained for the O'Neil et al. [1969] equation from Wefer and Berger [1991]. The equation of Kim and O'Neil [1997] was approximated by least squares regression of their data, following conversion of the data to the VPDB scale.

3. Results and Discussion

3.1. Experimental Data

Isotopic data for *O. universa* experiments show that temperature: $\delta^{18}\text{O}$ relationships from different irradiance groups at 15°-25°C are best described by linear equations with a slope of -4.80 (0.21‰ °C⁻¹) (Figure 1a):

$$T(^{\circ}\text{C}) = 16.5(\pm 0.2) - 4.80(\pm 0.16) * (\delta_c - \delta_w) \quad r^2 = 0.96$$

LL, ambient $[\text{CO}_3^{2-}]$ (1)

$$T(^{\circ}\text{C}) = 14.9(\pm 0.1) - 4.80(\pm 0.08) * (\delta_c - \delta_w) \quad r^2 = 0.98$$

HL, ambient $[\text{CO}_3^{2-}]$ (2)

The standard errors for (1) and (2) are $\pm 0.7^{\circ}\text{C}$ and $\pm 0.5^{\circ}\text{C}$, respectively. In seawater with ambient $[\text{CO}_3^{2-}]$, *O. universa* shells grown under HL levels are depleted in ^{18}O by an average of 0.33‰ relative to specimens grown under LL levels. This observation is consistent with results from previous experiments [Spero, 1992; Spero and Lea, 1993]. *O. universa* groups grown under HL in seawater with elevated $[\text{CO}_3^{2-}]$ (458 versus 171 $\mu\text{mol kg}^{-1}$) are depleted in ^{18}O by an additional 0.5‰ relative to

the HL ambient groups. The $\delta^{18}\text{O}/[\text{CO}_3^{2-}]$ slope of -0.002‰ $\mu\text{mol}^{-1} \text{kg}^{-1}$ is also consistent with results from other experiments with *O. universa* [Spero et al., 1997] and shows that the effect of $[\text{CO}_3^{2-}]$ on $\delta^{18}\text{O}$ is insensitive to temperature. We plot a linear regression through these data merely to illustrate that they are offset from the ambient group by the same amount at 17°C and 24°C.

The mechanisms driving the effects of symbiont photosynthesis and $[\text{CO}_3^{2-}]$ on shell $\delta^{18}\text{O}$ in *O. universa* are not well understood but appear to be linked. During photosynthetic activity, CO_2 uptake by the symbionts increases pH in the microenvironment around the shell [Jørgensen et al., 1985; Rink, 1996]. Therefore, more alkaline conditions correspond to locally elevated $[\text{CO}_3^{2-}]$ and relatively ^{18}O -depleted shells. The ^{18}O depletion of shells due to higher symbiont photosynthetic activity is consistent with the effect of higher ambient $[\text{CO}_3^{2-}]$.

Isotopic data for *G. bulloides* experiments show that among individual chambers the slopes of the temperature: $\delta^{18}\text{O}$ relationships differ through ontogeny, from -5.36(± 0.56) in chamber 11 to -4.58(± 0.40) in chamber 13 (Figure 1b). Successive chambers are progressively enriched in ^{18}O relative to earlier ones, although the $\delta^{18}\text{O}$ values appear to converge at higher temperatures. For example, the increase in mean $\delta^{18}\text{O}$ between chambers 11 and 13 is 0.46‰ at 15°C and 0.12‰ at 24°C.

Not surprisingly, size-related trends in the slopes and $\delta^{18}\text{O}$ values of whole shells parallel ontogenetic trends for individual chambers because larger shells contain more ^{18}O -enriched chambers (Figure 1c):

$$T(^{\circ}\text{C}) = 12.6(\pm 0.3) - 5.07(\pm 0.22) * (\delta_c - \delta_w) \quad r^2 = 0.99$$

11-chambered shell (3)

$$T(^{\circ}\text{C}) = 13.2(\pm 0.3) - 4.89(\pm 0.21) * (\delta_c - \delta_w) \quad r^2 = 0.99$$

12-chambered shell (4)

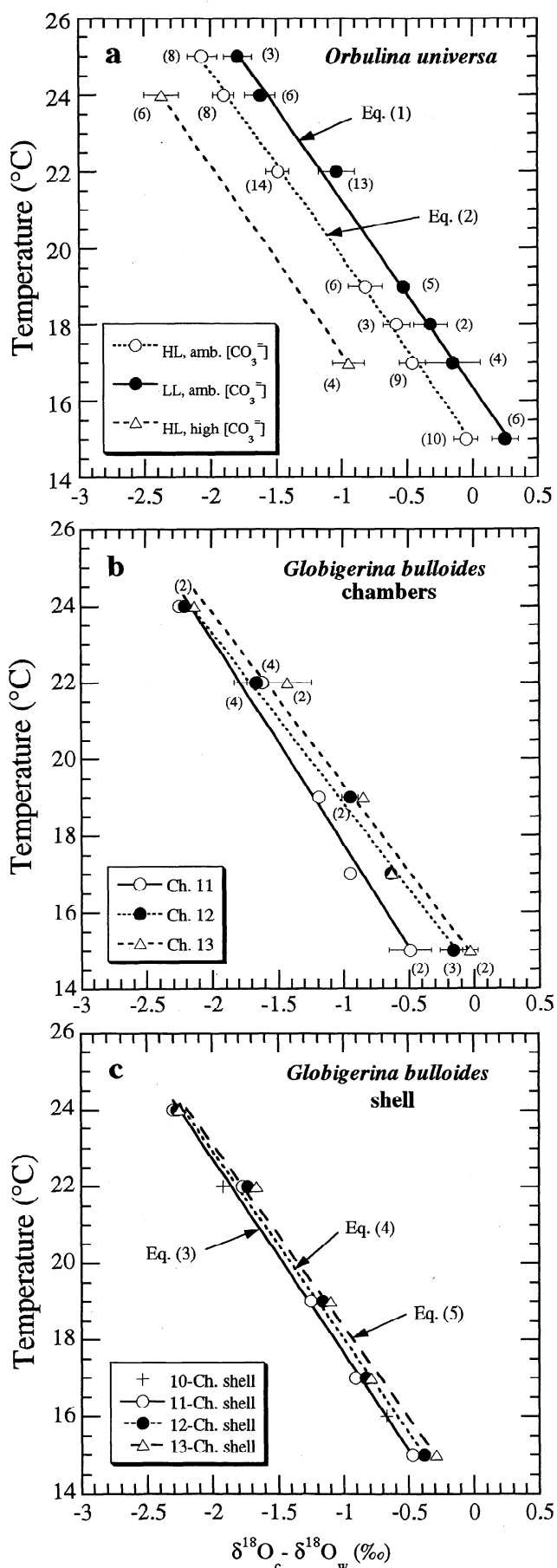
$$T(^{\circ}\text{C}) = 13.6(\pm 0.4) - 4.77(\pm 0.27) * (\delta_c - \delta_w) \quad r^2 = 0.99$$

13-chambered shell (5)

Standard errors for these equations are $\pm 0.3^{\circ}$ - 0.4°C . The slopes of the temperature: $\delta^{18}\text{O}$ relationships for whole *G. bulloides* shells decrease with increasing shell size. Larger shells are progressively enriched in ^{18}O relative to smaller shells and less depleted in ^{18}O relative to seawater. Average $\delta^{18}\text{O}$ differences between 11- and 13-chambered shells decrease from 0.18‰ to 0.05‰ across the temperature increase of 15°-24°C.

3.2. Linear Versus Quadratic Temperature: $\delta^{18}\text{O}$ Relationships

Traditionally, temperature: $\delta^{18}\text{O}$ relationships used in paleoceanographic applications have been expressed as quadratic equations. This practice is based on theoretical predictions that the oxygen isotopic fractionation factor between a mineral and water, α , varies such that $\ln \alpha$ is a function of T^{-1} or T^{-2} at low and very high temperatures, respectively [Bigeleisen and Mayer, 1947; O'Neil, 1986b; Urey, 1947]. Over the limited oceanic temperature range this relationship is commonly approximated by a quadratic equation with terms of temperature ($^{\circ}\text{C}$), $\delta^{18}\text{O}_{\text{calcite}}$, and $\delta^{18}\text{O}_{\text{water}}$. However, a detailed examination of the data sets that generated published paleotemperature equa-



tions demonstrates that linear and quadratic equations provide equally good fits at warm oceanic temperatures. For instance, linear regression of the *Erez and Luz* [1983] data yields the equation

$$T(^{\circ}\text{C}) = 17.0 - 4.59(\delta_c - \delta_w) \quad (6)$$

with an $r^2 = 0.90$, which is identical to that of the quadratic fit. Similarly, the experimental data of *Epstein et al.* [1953] can be expressed by the linear equation

$$T(^{\circ}\text{C}) = 16.6 - 4.30(\delta_c - \delta_w) \quad r^2 = 0.97 \quad (7)$$

In both of these instances the data sets produce linear equations that yield temperatures within 0.2°C of the published quadratic equations across the temperature range 9°–24°C. This variation is equivalent to a calcite $\delta^{18}\text{O}$ measurement precision of $\pm 0.05\%$.

Several possibilities may explain the similarity of quadratic and linear temperature: $\delta^{18}\text{O}$ relationships at warm oceanic temperatures. First, the inflection of the expected thermodynamic relationship may not be apparent across the relatively small temperature range tolerated by an organism. This could arise because either the $\delta^{18}\text{O}$ measurement precision of $\pm 0.05\%$ may be insufficient or the organism's intraspecific isotopic variability may be too great to define a quadratic relationship. Second, an organism's physiological control of calcification and shell $\delta^{18}\text{O}$ may mask thermodynamic equilibrium.

The appropriateness of a linear versus a quadratic temperature: $\delta^{18}\text{O}$ relationship becomes more important at lower temperatures. Extrapolation of paleotemperature equations below their original calibration temperatures is a common but dangerous practice that has required the establishment of correction factors to adjust foraminiferal data to an equation's predicted " $\delta^{18}\text{O}$ equilibrium." At the lower end of the oceanic temperature range, discrepancies between other equations and estimates based on (1) and (2) are most pronounced, with differences of up to 5°C (Table 1).

3.3. Comparison With Other Paleotemperature Equations

O. universa temperature: $\delta^{18}\text{O}$ relationships predict lower temperatures, in general, relative to estimates from commonly used equations (Figure 2 and Table 1). Equation (1), which reflects minimal influence of symbiont photosynthesis under LL, is most similar to other equations from the literature. However, most published relationships still overestimate temperature by up to 1°C relative to (1) and by $\sim 1.0^{\circ}$ – 2.5°C relative to (2) across the temperature range 15°–25°C (Table 1). The tem-

Figure 1. Mean experimental $\delta^{18}\text{O}_c - \delta^{18}\text{O}_w$ values ($\pm 1\sigma$) versus temperature for cultured foraminifera, where $\delta^{18}\text{O}_w$ (VPDB) = $\delta^{18}\text{O}_w$ (VSMOW) - 0.27‰. Numbers within parentheses indicate the number of individual shell analyses within each experimental group: (a) *Orbulina universa* shells, where high light (HL) > 380 $\mu\text{Ein} \text{ m}^{-2} \text{ s}^{-1}$ and low light (LL) = 20–30 $\mu\text{Ein} \text{ m}^{-2} \text{ s}^{-1}$; ambient $[\text{CO}_3^{2-}] = 171 \mu\text{mol kg}^{-1}$ and high $[\text{CO}_3^{2-}] = 458 \mu\text{mol kg}^{-1}$; and the slopes of the regressions are -4.8 ($0.21\% \text{ } ^{\circ}\text{C}^{-1}$); (b) *Globigerina bulloides* chambers 11, 12, and 13; and (c) reconstructed whole *G. bulloides* shells consisting of 11, 12, and 13 chambers. 10-chambered shell data are from this study (22°C) and *Spero and Lea* [1996] (16°C).

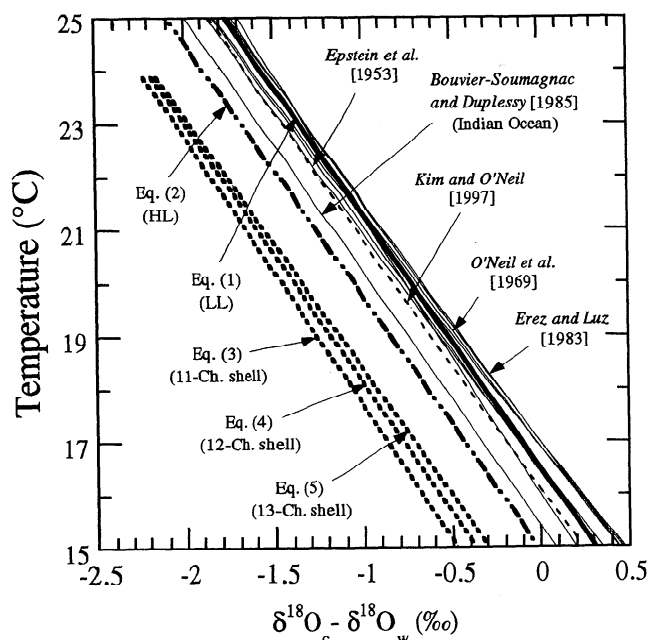


Figure 2. Comparison of temperature predictions using new *O. universa* and *G. bulloides* temperature: $\delta^{18}\text{O}$ relationships and published paleotemperature equations. Several published equations are identified for reference. Equations presented in this study predict lower temperatures than most other equations. Temperatures were calculated using the VSMOW to VPDB corrections listed in Table 1 for $\delta^{18}\text{O}_w$ values.

perature: $\delta^{18}\text{O}$ relationship of Kim and O'Neil [1997] falls between (1) and (2) in our calibration range and is closest to (1) when extrapolated to low temperatures. Although this equation was calibrated for inorganic calcite, its similarity to (1) and (2) across the oceanic temperature range suggests that the *O. universa* relationships may be applicable beyond their calibration range.

G. bulloides (whole shell) equations produce the lowest temperature estimates (for a given $\delta_c - \delta_w$ value) among published equations (Figure 2). For example, at a $\delta_c - \delta_w$ value of -1‰ , (3)-(5) estimate temperatures between $\sim 17.5^\circ$ and 18.5°C , whereas most other equations from the literature predict temperatures of $\sim 21^\circ$ – 22°C . This difference has been well documented and has limited the use of *G. bulloides* for paleotemperature reconstructions [Curry and Matthews, 1981; Kahn and Williams, 1981; Sautter and Thunell, 1991]. The accuracy of the new relationships for *O. universa* and *G. bulloides* can be tested by calibration with field data.

3.4. Field Calibration of *O. universa* Equations

Some of the best published isotope data currently available for cross-species calibration of (1) and (2) are from plankton tows in the Indian Ocean and near Bermuda [Bouvier-Soumagnac and Duplessy, 1985; Duplessy et al., 1981a; Williams et al., 1981]. These studies contain concurrent hydrographic data and $\delta^{18}\text{O}$ analyses of the symbiont-bearing species *Globigerinoides ruber* (white and pink), *G. sacculifer*, *Globigerinoides conglobatus*, and *O. universa*. Given the influence of $[\text{CO}_3^{2-}]$ on *O. universa* $\delta^{18}\text{O}$ and the higher mixed layer $[\text{CO}_3^{2-}]$

in the Indian Ocean site relative to the Southern California Bight (~ 250 versus $171 \mu\text{mol kg}^{-1}$) [Weiss et al., 1983], a $\delta^{18}\text{O}$ correction of $+0.16\text{‰}$ is needed to account for the $[\text{CO}_3^{2-}]$ difference ($-0.002\text{‰} \mu\text{mol}^{-1} \text{kg}^{-1}$). Because $[\text{CO}_3^{2-}]$ effects on shell $\delta^{18}\text{O}$ appear to be species-specific [Spero et al., 1997], we correct only *O. universa* in this data compilation. We also include mean isotopic data ($\pm 1\sigma$) for *O. universa* and *G. sacculifer* collected in a drift tow (10 m depth) off southwestern Puerto Rico during the summer of 1997. The drift-tow *O. universa* data are corrected by $+0.21\text{‰}$ to account for the $\sim 100 \mu\text{mol kg}^{-1}$ higher $[\text{CO}_3^{2-}]$ at that site.

The $\delta_c - \delta_w$ values of the foraminiferal field data are in good agreement with values predicted by (1) and (2) from 19° – 30°C (Figure 3a). Isotope values of *G. ruber*, *O. universa*, and *G. conglobatus* generally fall between LL equation (1) and HL equation (2), whereas *G. sacculifer* values are lower than those estimated by (2). The good fit of *O. universa* with (1) and (2) serves as a direct field test of our experimentally derived temperature: $\delta^{18}\text{O}$ relationships. Except for the Puerto Rico drift tow values, the *O. universa* data are from a series of oblique plankton tows in the Indian Ocean [Bouvier-Soumagnac and Duplessy, 1985]. In that study, linear regression of the hydrographic and isotopic data produced an *O. universa* temperature: $\delta^{18}\text{O}$ relationship with a slope identical to (1) and (2) (Table 1), although the y intercepts are different. If we correct for the $[\text{CO}_3^{2-}]$ influence as discussed above and account for the different VSMOW to VPDB correction used by Bouvier-Soumagnac and Duplessy [1985] (Table 1), the modified equation for their plankton-tow *O. universa* becomes

$$T(^{\circ}\text{C}) = 16.5 - 4.81(\delta_c - \delta_w) \quad (8)$$

with a y intercept identical to LL equation (1). Because the Indian Ocean study obtained *O. universa* from oblique tows across 0–200 m depth and this species is most abundant in the lower mixed layer [Bouvier-Soumagnac and Duplessy, 1985; Fairbanks et al., 1982; Ravelo and Fairbanks, 1992], a y intercept similar to that of (1) would be expected. The similarity of (1) and (8) indicates that the experimental equations for *O. universa* can provide accurate temperature estimates using field data.

Given the good agreement between most of the foraminiferal field data and the $\delta^{18}\text{O}$ predictions of (1) and (2), it is interesting that 85% of the plankton tow data have values lower than those predicted by the equation of Erez and Luz [1983] (Figure 3a). This equation was derived from experiments with another symbiotic foraminifer, *G. sacculifer*. Irradiance levels in the Erez and Luz [1983] study are somewhat ambiguous, making direct comparison with (1) and (2) difficult. However, on the basis of the results of other laboratory experiments with *O. universa* and *G. sacculifer* [Spero and Lea, 1993] the differences between the Erez and Luz [1983] relationship and (1) and (2) could be a function of species-specific symbiont effects on shell $\delta^{18}\text{O}$. For example, Spero and Lea [1993] demonstrated that *G. sacculifer* displays a symbiont photosynthesis: $\delta^{18}\text{O}$ response that is approximately double that of *O. universa* at 29°C ($\sim 0.6\text{‰}$ versus $\sim 0.3\text{‰}$). Consequently, if the Erez and Luz [1983] equation was generated for *G. sacculifer* under conditions that simulated a medium-low light environment, then a temperature: $\delta^{18}\text{O}$ relationship for high light specimens would be expected to be shifted nearly -0.6‰ and would fall on the *G. sacculifer* field

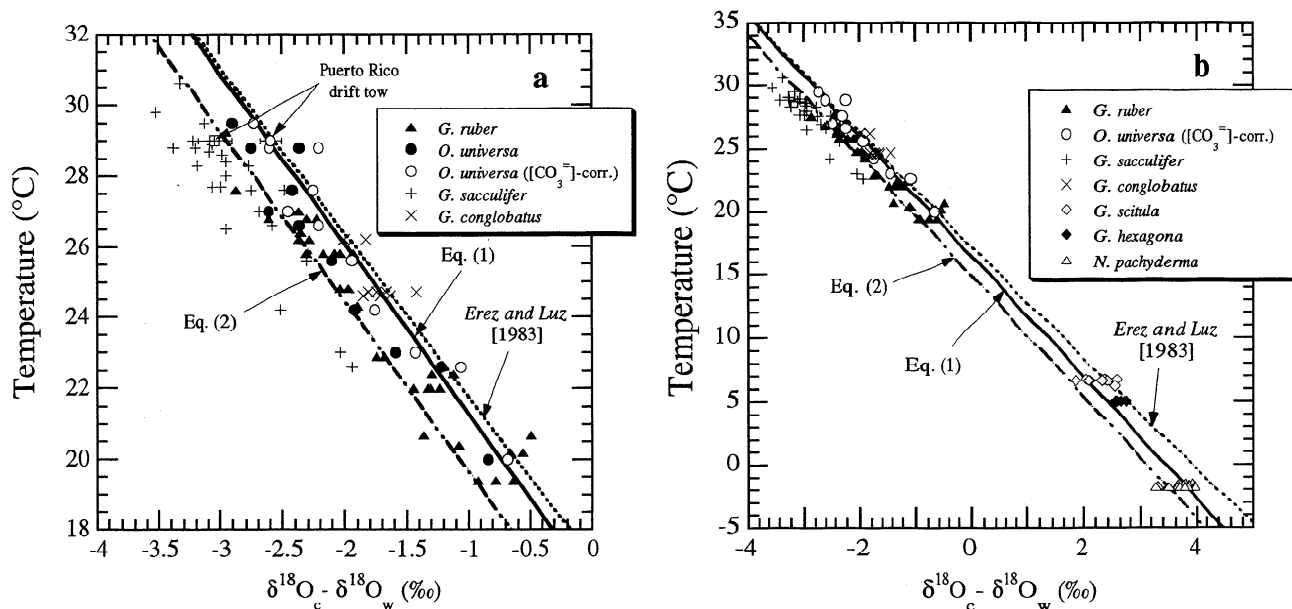


Figure 3. Published plankton tow data for symbiont-bearing foraminifera with predicted shell $\delta^{18}\text{O}$ values. (a) Warm water calibration data from the Sargasso Sea and Indian Ocean [Bouvier-Soumagnac and Duplessy, 1985; Duplessy et al., 1981a; Williams et al., 1981]. Unpublished drift-tow *O. universa* and *Globigerinoides sacculifer* data from Puerto Rico are shown as mean values $\pm 1\sigma$; (b) additional cold water calibration data from the northeast Pacific and Arctic Oceans [Bauch et al., 1997; Ortiz et al., 1996]. *O. universa* data are presented as published and also CO_3^{2-} -corrected with the experimentally determined $\delta^{18}\text{O}/[\text{CO}_3^{2-}]$ slope of $-0.002\text{‰}\mu\text{mol}^{-1}\text{kg}^{-1}$. The Erez and Luz [1983] equation is shifted by $+0.05\text{‰}$ to adjust for the difference in VSMOW to VPDB corrections to $\delta^{18}\text{O}_w$.

data (Figure 3a). The greater effect of symbiont photosynthesis on *G. sacculifer* $\delta^{18}\text{O}$ values could also explain why that species is depleted in ^{18}O relative to (1) and (2).

We would like to clear up an inconsistency between the experimental study of Spero and Lea [1993] and the data set presented here. In the earlier study it was reported that *O. universa* and *G. sacculifer* growing under HL produced shells in oxygen isotopic equilibrium according to the equation of Erez and Luz [1983]. In contrast, individuals maintained under LL had shell $\delta^{18}\text{O}$ values that were enriched relative to equilibrium. Although the HL-LL $\delta^{18}\text{O}$ offset is consistent in both direction and magnitude with the data presented here, the values were higher than would be expected. We hypothesize that the earlier experiments were affected by the $[\text{CO}_3^{2-}]$ effect. Spero and Lea stated that the foraminifera were maintained in seawater in containers that had a small air space and loosely fitting tops. Their observation that the $\delta^{13}\text{C}$ of seawater ΣCO_2 decreased up to 2‰ over a 48 hour period suggests that the $p\text{CO}_2$ of the recirculating laboratory air was very high and atmospheric CO_2 was invading the culture water. The net effect of such a CO_2 invasion would be to decrease seawater $p\text{H}$ and $[\text{CO}_3^{2-}]$, which would produce elevated shell $\delta^{18}\text{O}$ values and explain the experimental offset.

Because our experiments are calibrated down to 15°C, cold water calibration of these equations must rely on published field data from polar and subpolar environments. A suite of stable isotope data is available for the planktonic species *Globorotalia scitula*, *Globoquadrina hexagona*, and left-coiling *Neoglobobulimina pachyderma* at temperatures of -2° to 7°C [Bauch et al., 1997; Ortiz et al., 1996]. We use data for *G. scitula* and *G. hexagona* collected in depth-stratified tows from 200-600 m depth in the northeast Pacific Ocean [Ortiz et al., 1996] and *N.*

pachyderma collected from 0-50 m depth in the Arctic Ocean [Bauch et al., 1997]. The $\delta_c - \delta_w$ values for *G. scitula* and *G. hexagona* fall between the values predicted by (2) and the equation of Erez and Luz [1983] (Figure 3b). The *N. pachyderma* data also show scatter but fall primarily between (1) and (2).

Given the agreement between field (plankton tow) and predicted isotope values, (1) and (2) are more accurate than published relationships for estimating temperature at tropical and subtropical temperatures. Although extrapolation of (1) and (2) to colder temperatures appears to work reasonably well, further calibration of these equations is needed at lower temperatures. Because downcore variations in light level (calcification depth) affect temperature predictions, we recommend using (1) and (2) together to bracket a range of potential temperatures for symbiotic foraminifera. The $\delta^{18}\text{O}/[\text{CO}_3^{2-}]$ relationship for *O. universa* can be used to correct for downcore $[\text{CO}_3^{2-}]$ variations that must have accompanied glacial-interglacial changes in atmospheric $p\text{CO}_2$ and surface water $p\text{H}$ [Sanyal et al., 1995; Spero et al., 1997]. However, the carbonate ion effect must be quantified for other species before correcting their data [Spero et al., 1997].

3.5. Field Calibration of *Globigerina bulloides* Equations

Spero and Lea [1996] developed empirical correction factors for *G. bulloides* from laboratory experiments to adjust $\delta^{18}\text{O}$ values to equilibrium. *G. bulloides* from a sediment trap time series in the SPB [Sautter and Thunell, 1991] were used to test these corrections, significantly improving the original interpretation that was based on the Epstein et al. [1953] paleotemperature equation. However, correction factors do not describe the

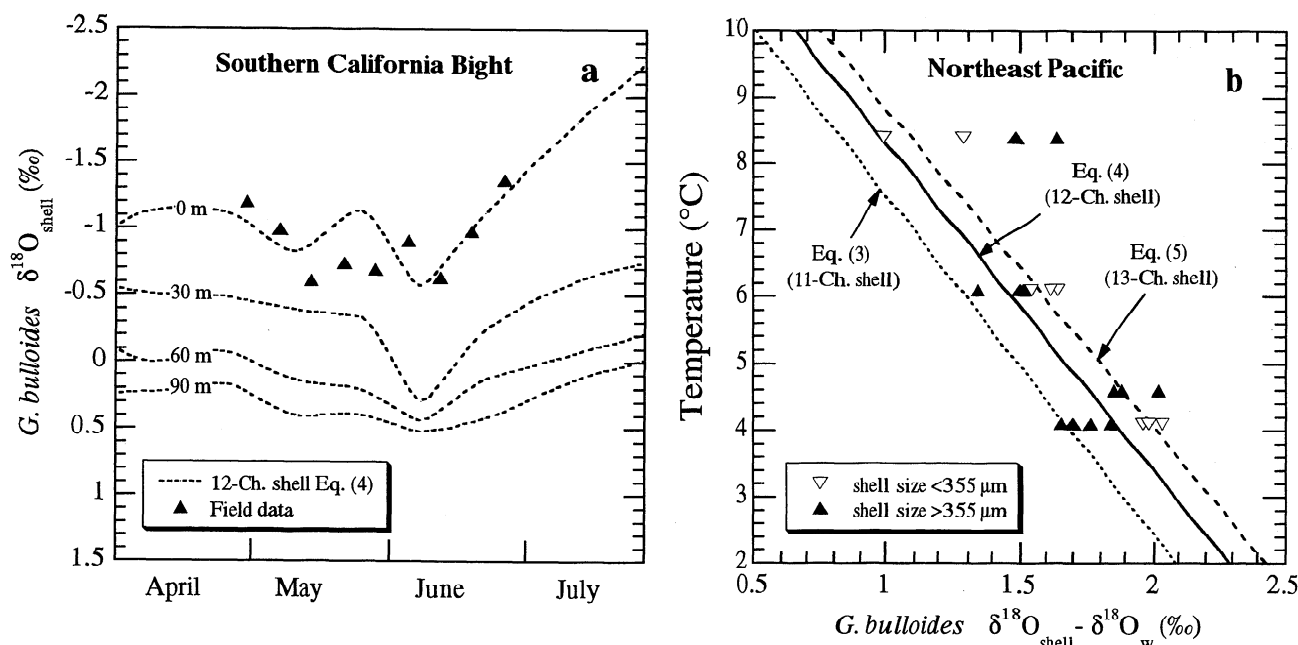


Figure 4. Comparison of *G. bulloides* field data with predicted $\delta^{18}\text{O}$ values. (a) Time series sediment trap data of Sautter and Thunell [1991] plotted with predicted shell $\delta^{18}\text{O}$ values using 12-chambered *G. bulloides* equation (4). This equation provides realistic calcification depths for this species, in contrast with the original interpretation with the equation of Epstein *et al.* [1953]. (b) Plankton-tow data of cold water *G. bulloides* [Kahn and Williams, 1981] compared with values predicted with new equations. The equations account for 85% of the data, but the relative size: $\delta^{18}\text{O}$ pattern is reversed from our observations.

unique temperature: $\delta^{18}\text{O}$ relationship for *G. bulloides* (Figure 2). We reinterpret the calcification depth of *G. bulloides* in the SPB study by applying the 12-chambered shell equation (4) to the concurrent hydrographic data to predict shell $\delta^{18}\text{O}$ values at depths of 0-90 m (Figure 4a). Because mixed-layer [CO_3^{2-}] in this study is the same as in our calibration experiments, no correction of the *G. bulloides* data is required [Spero *et al.*, 1997]. The reconstructed calcification depth of *G. bulloides* is 0-30 m throughout the seasonal sampling period of spring through early summer, which is consistent with Spero and Lea [1996] and other observations [Hemleben *et al.*, 1989; Kahn and Williams, 1981; Schiebel *et al.*, 1998]. Equation (4) does not help to resolve the $\delta^{18}\text{O}$ values of several specimens collected during April in the original study (not shown in Figure 4a). These shells have anomalously high $\delta^{18}\text{O}$ values and are more massive than other specimens. The significance of these shells is unclear, but it is apparent that calcification conditions are different from the majority of the population.

We attempted to calibrate (3)-(5) below 15°C with a set of plankton-tow-collected *G. bulloides* that grew at ~4°-9°C in the northeastern Pacific Ocean [Kahn and Williams, 1981]. Geochemical Ocean Sections Study (GEOSECS) data indicate that [CO_3^{2-}] values for 0-100 m depth in this region are 170-173 $\mu\text{mol kg}^{-1}$ [Broecker *et al.*, 1982], which is the same as the San Pedro Basin and therefore requires no $\delta^{18}\text{O}$ correction of the data [Spero *et al.*, 1997]. Surprisingly, although 85% ($n=20$) of the $\delta_c - \delta_w$ values can be accounted for by (3)-(5), the two size classes of field data (<355 and >355 μm) do not coincide with laboratory data (Figure 4b). Rather, the relative ^{18}O enrichments are reversed (i.e., larger shells should be enriched in ^{18}O relative to smaller shells) [Berger *et al.*, 1978; Duplessy *et al.*, 1981a]. This pattern is puzzling because our results indicate that $\delta^{18}\text{O}$ trends among different size fractions of *G. bulloides*

can be accounted for by ontogenetic effects alone. Because application of the *G. bulloides* temperature: $\delta^{18}\text{O}$ relationships requires the assumption that all chambers of a shell calcified in the same environment, vertical migration of the foraminifera could complicate interpretation [Hemleben and Bijma, 1994]. The reversal of size: $\delta^{18}\text{O}$ trends would be consistent with juvenile *G. bulloides* living below or within the thermocline and vertically migrating to shallower depths during later growth stages, thereby masking the underlying ontogenetic signal. Shell values that are not explained by our equations are enriched in ^{18}O by up to ~0.5‰ relative to 13-chambered shell (5). It is possible that these *G. bulloides* shells are the massive variety discussed earlier.

Although further calibration of *G. bulloides* $\delta^{18}\text{O}$ values in other regions and at lower temperatures is required before these equations can be confidently applied to all field and deep-sea core data, our results show that the equations are more accurate than published relationships for describing *G. bulloides* $\delta^{18}\text{O}$ data in the northeast Pacific Ocean. Of the three size-related temperature: $\delta^{18}\text{O}$ relationships for *G. bulloides* shells, it is probably sufficient to use the 12-chambered shell equation (4) for paleoenvironmental reconstructions (Figure 4b). Temperature estimates using (4) are within $\pm 0.5^\circ\text{C}$ of (3) (11-chambered shell) and (5) (13-chambered shell) at 15°C, and differences are negligible at 24°C (Figure 1c). We caution that the *G. bulloides* equations are only appropriate for that species.

3.6. Comparison With Core Top Data

3.6.1. Planktonic foraminifera. We can test the applicability of *O. universa* equations (1) and (2) to deep-sea core material by comparing core top planktonic foraminifera and hydrographic data for the overlying water column (Figure 5a). Pub-

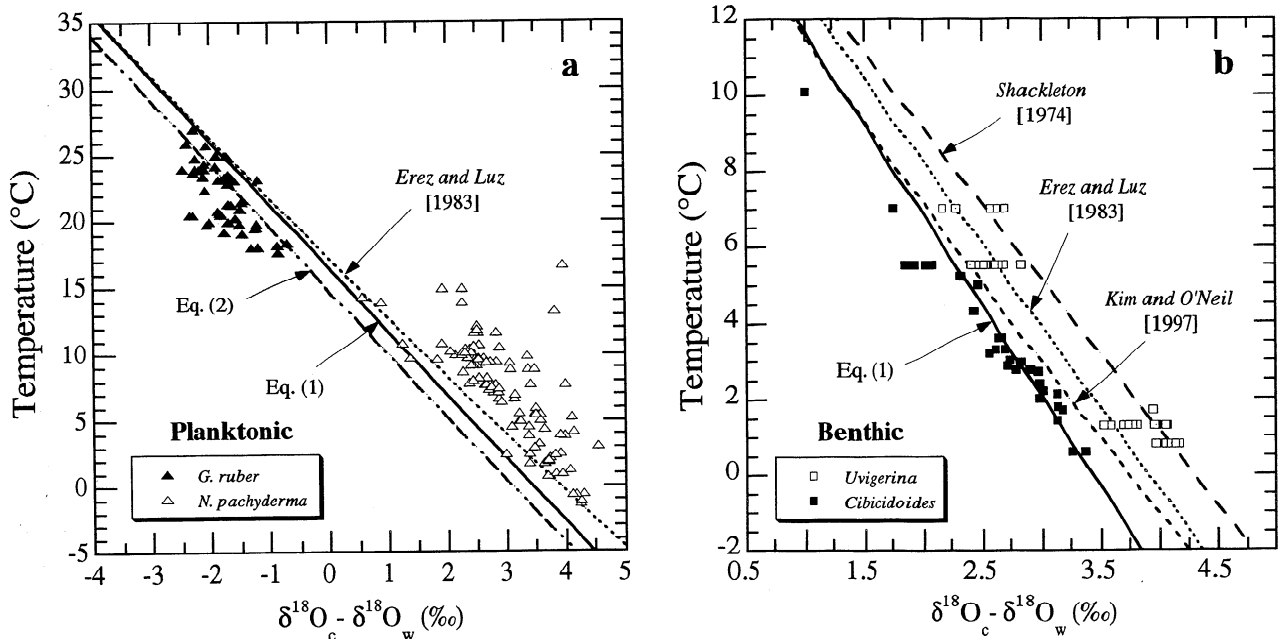


Figure 5. Published and predicted $\delta^{18}\text{O}$ values for (a) planktonic foraminifera from core tops in the equatorial to North Atlantic and the Southern Ocean [Duplessy *et al.*, 1991; Wang *et al.*, 1995; Wu and Hillaire-Marcel, 1994], and (b) benthic foraminifera from core tops in the Atlantic, Pacific, and Indian Oceans and the Arabian Sea and Gulf of Mexico [Kallel, 1988, and references therein; Loubere *et al.*, 1995; Shackleton, 1974]. Equation (1) provides a good fit to the *Cibicidoides* data.

lished data sets of Duplessy *et al.* [1991], Wang *et al.* [1995], and Wu and Hillaire-Marcel [1994] provide isotope data for *N. pachyderma* (left-coiling) from the Southern Ocean and *G. ruber* from the equatorial to North Atlantic with summer hydrographic data. The equation of Erez and Luz [1983] is shown for reference.

A portion of the *G. ruber* data can be accounted for by (1) and (2), although most of the shell values are depleted in ^{18}O by nearly 1‰ relative to prediction. In contrast, most of the *N. pachyderma* data are enriched in ^{18}O relative to both (1) and the equation of Erez and Luz [1983]. At this time we are unable to adequately explain such discrepancies, although there are several possibilities. First, the hydrographic data used to predict the shell $\delta^{18}\text{O}$ values may be incorrect or may not coincide with the season of foraminiferal growth. For example, if the *G. ruber* specimens actually grew during warmer conditions or in water with a lower $\delta^{18}\text{O}_w$ value, then the data would fall on or above (1) as we observe. However, the errors in estimating temperature and $\delta^{18}\text{O}_w$ in the overlying water column would have to be large to explain the magnitude of these offsets.

A second possibility for the discrepancy in predicted and observed $\delta^{18}\text{O}$ values is that postgametogenic processes affect the shell $\delta^{18}\text{O}$ values. After gametogenesis some planktonic foraminifera continue to calcify as they sink into the thermocline [Bé, 1980; Brummer *et al.*, 1987; Duplessy *et al.*, 1981b; Hamilton, 1996; Lohmann, 1995]. Gametogenic calcite is relatively enriched in ^{18}O because it precipitates from cooler waters. In our experiments, where temperature was held constant, calcite added before and after gametogenesis has the same $\delta^{18}\text{O}$ value and therefore does not modify shell $\delta^{18}\text{O}$. Because isotopically enriched gametogenic calcite is typically more resistant than primary calcite, selective dissolution of shells could further modify shell $\delta^{18}\text{O}$ toward more positive values [Lohmann, 1995,

and references therein]. Although the addition of gametogenic calcite and dissolution of shells might explain the high $\delta^{18}\text{O}$ values of the core top *N. pachyderma* relative to predictions, these processes do not explain why *G. ruber* shells are relatively depleted in ^{18}O . Future work must address the issue of why (1) and (2) work well for plankton tow data but are less accurate for core top data.

3.6.2. Benthic foraminifera. Shackleton [1974] used core top data to calibrate a temperature: $\delta^{18}\text{O}$ relationship for the benthic foraminifer *Uvigerina* spp. (Table 1). Alternatively, Zahn and Mix [1991] proposed that $\delta^{18}\text{O}$ data for *Uvigerina peregrina* at depths of >2 km could be described best by the equation of Erez and Luz [1983]. Both of these studies assumed that *Uvigerina* precipitates its shell in oxygen isotopic equilibrium with seawater. We attempt to calibrate (1) with a compilation of published $\delta^{18}\text{O}$ data for the benthic foraminifera *Uvigerina* and *Cibicidoides* from core tops in the Atlantic, Pacific, and Indian Oceans and in the Arabian Sea and Gulf of Mexico [Kallel, 1988, and references therein; Loubere *et al.*, 1995; Shackleton, 1974]. The *Cibicidoides* data of Table I-3 by Kallel [1988] reflect a correction of +0.64‰, which we remove for this comparison.

The scattered *Uvigerina* data fall primarily on or between the equations of Shackleton [1974] and Erez and Luz [1983] (Figure 5b). In contrast, the *Cibicidoides* data are in excellent agreement with (1). On the basis of this comparison and the similarity of (1) to the new inorganic calcite equation of Kim and O'Neil [1997], we conclude that *Cibicidoides* precipitates its shell close to oxygen isotopic equilibrium with seawater, whereas *Uvigerina* shells are relatively enriched in ^{18}O . The enrichment of *Uvigerina* shells relative to *Cibicidoides* would be consistent with the habitat differences of the genera if a $[\text{CO}_3^{2-}]$ effect were operating. For instance, *Uvigerina* is infaunal and

experiences low pH and decreased $[\text{CO}_3^{2-}]$ in pore waters, whereas *Cibicidoides* inhabits the sediment surface where bottom water pH and $[\text{CO}_3^{2-}]$ are higher [Corliss and Emerson, 1990; Hales and Emerson, 1996; Jahnke et al., 1994; Martin and Sayles, 1996; McCorkle and Keigwin, 1990]. In such a scenario the isotopic offset between the foraminifera should partially reflect the $[\text{CO}_3^{2-}]$ gradient in the sediments. However, a $[\text{CO}_3^{2-}]$ effect has not yet been demonstrated for benthic foraminifera and must be addressed by ongoing culture experiments.

4. Conclusions

We have developed a suite of new temperature: $\delta^{18}\text{O}$ relationships for laboratory-grown *O. universa* and *G. bulloides*. The relationships for *O. universa* respond predictably to changes in irradiance (symbiotic photosynthesis) and seawater $[\text{CO}_3^{2-}]$. *G. bulloides* chamber $\delta^{18}\text{O}$ values vary during ontogeny, which requires the establishment of different temperature: $\delta^{18}\text{O}$ relationships for specific shell sizes.

After correcting for regional differences in $[\text{CO}_3^{2-}]$ between studies a published temperature: $\delta^{18}\text{O}$ relationship based on field-collected *O. universa* coincides with an equation determined experimentally in this study. Other species-specific $\delta^{18}\text{O}/[\text{CO}_3^{2-}]$ slopes must be determined experimentally in order to compare more accurately $\delta^{18}\text{O}$ values among foraminiferal groups and geographic regions.

Given the agreement between foraminiferal field data and predicted isotope values, the linear *O. universa* equations pre-

sented here are more accurate than published paleotemperature equations for estimating SST. We recommend using (1) and (2) together to bracket a potential range of temperature for symbiotic planktonic foraminifera from deep-sea cores. Although the equations explain $\delta^{18}\text{O}$ variations in plankton tow data well, they do not explain cold water ($<15^\circ\text{C}$) and core top data with the same precision. The agreement between (1) and *Cibicidoides* data suggests that this genus precipitates its shell near oxygen isotopic equilibrium, whereas *Uvigerina* shells are relatively enriched in ^{18}O .

The new temperature: $\delta^{18}\text{O}$ relationships for *G. bulloides* are more accurate than published equations for field data of this species from the northeast Pacific Ocean. The *G. bulloides* equations should be used with that species only. Most existing paleotemperature equations overestimate temperatures by $1.0^\circ\text{--}2.5^\circ\text{C}$ relative to *O. universa* equations and by $3^\circ\text{--}5^\circ\text{C}$ relative to *G. bulloides* equations when ambient temperature varies from $15^\circ\text{--}25^\circ\text{C}$. The temperature: $\delta^{18}\text{O}$ relationships presented here have the potential to improve paleoceanographic interpretations from deep-sea foraminiferal $\delta^{18}\text{O}$ values.

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