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Temperature influence on the carbon isotopic composition of *Globigerina bulloides* and *Orbulina universa* (planktonic foraminifera)

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Abstract

Laboratory experiments with the planktonic foraminifera *Globigerina bulloides* (nonsymbiotic) and *Orbulina universa* (symbiotic) were carried out to examine the effects of temperature, irradiance (symbiont photosynthesis), $[CO_3^{2-}]$, and ontogeny on shell $\delta^{13}C$ values. In ambient seawater ($[CO_3^{2-}] = 171$ μmol kg^{-1}), the $\delta^{13}C$ of *G. bulloides* shells decreases 0.11‰ °C^{-1}, a pattern that likely results from the incorporation of more respired CO_2 into shell carbon at higher metabolic rates. The $\delta^{13}C$ of *O. universa* shells grown under low light (LL) levels is insensitive to temperature and records the $\delta^{13}C$ value of seawater ΣCO_2, whereas the $\delta^{13}C$ of high light (HL) shells increases slightly with temperature (0.05‰ °C^{-1}). HL *O. universa* grown in elevated $[CO_3^{2-}]$ seawater are isotopically depleted relative to those grown in ambient seawater, although it is uncertain from these experiments whether the $[CO_3^{2-}]$ influence on $\delta^{13}C$ is affected by temperature. When applied to deep-sea core material, these results demonstrate that differences in sea surface temperature and $[CO_3^{2-}]$ can bias how we interpret downcore shifts in foraminiferal $\delta^{13}C$.

Keywords: paleoclimatology; biogeochemistry; temperature; irradiance; ontogeny

1. Introduction

The carbon isotopic composition ($\delta^{13}C$ value) of foraminiferal shells tracks the $\delta^{13}C$ of total dissolved inorganic carbon $\left(\delta^{13}C_{\Sigma CO_2}\right)$ in the ocean (Berger et al., 1978; Grossman, 1984; Bouvier-Soumagnac and Duplessy, 1985; Spero, 1992). This proxy has been used extensively in paleoenvironmental studies to trace changes in the global carbon cycle. For instance, it has been proposed that down-core studies of the planktonic–benthic $\delta^{13}C$ difference in deep-sea sediments provide information about the surface to deep water $\delta^{13}C$ gradient and the strength of the biological pump over time (Shackleton et al., 1983, 1992; Curry and Crowley, 1987; Leuenberger et al., 1992).

Carbon isotopes are used routinely in paleoceanographic studies, despite evidence that shell $\delta^{13}C$ values of planktonic foraminifera are typically depleted relative to predicted thermodynamic equilibrium (Williams et al., 1977; Shackleton and Vincent, 1978; Kahn, 1979; Oppo and Fairbanks, 1989). Attempts to correlate the $\delta^{13}C$ of plankton tow-collected foraminifera with ambient temperature and

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$\delta^{13}C_{\Sigma CO_2}$ have demonstrated that physiological processes ('vital effects') often mask environmental signals (Williams et al., 1977; Berger et al., 1978; Fairbanks et al., 1982; Curry et al., 1983; Deuser, 1987). For example, planktonic foraminifera collected at similar temperatures and seawater $\delta^{13}C_{\Sigma CO_2}$ values can show $\delta^{13}C$ differences of >2‰ among species (Deuser, 1987; Deuser and Ross, 1989; Ravelo and Fairbanks, 1995; Ortiz et al., 1996). Furthermore, relationships between shell size and $\delta^{13}C$ exist for some species (Williams et al., 1977; Berger et al., 1978; Duplessy et al., 1981; Bouvier-Soumagnac and Duplessy, 1985; Ravelo and Fairbanks, 1995). The resulting $\delta^{13}C$ variability among species and size fractions limits our ability to understand carbon cycling in past oceans.

Laboratory experiments with living foraminifera have helped to identify many of the factors that affect carbon isotopic variability. For instance, symbiont photosynthetic activity enriches shells in ^{13}C through the preferential removal of ^{12}C from the foraminiferal microenvironment (Spero and DeNiro, 1987; Spero and Williams, 1988; Spero and Lea, 1993b). This effect is greatest at higher irradiances and minimized when ambient light levels approach the compensation point for symbiont photosynthesis (~50 μmol photons m^{-2} s^{-1}). In contrast, $\delta^{13}C$ values decrease when shell calcite incorporates ^{12}C-enriched respired carbon derived from the metabolism of organic compounds (Berger et al., 1978; Spero and Lea, 1996; Bijma et al., 1998). More recent studies have demonstrated that seawater pH can also affect shell $\delta^{13}C$. Planktonic foraminifera cultured under conditions of elevated seawater carbonate ion concentration (higher pH) calcify shells with lower $\delta^{13}C$ values relative to shells that grew in lower $[CO_3^{2-}]$ (lower pH) water (Spero et al., 1997).

Given the importance of biological processes on shell $\delta^{13}C$, environmental parameters that affect physiological rates probably also alter shell $\delta^{13}C$ values. The influence of temperature on physiology is well-documented: metabolic rates increase exponentially over small temperature ranges (Li, 1980; Bijma et al., 1990; Ortiz et al., 1996). This effect would likely increase the influence of respiration and photosynthesis on shell geochemistry at higher temperatures, which would further divert shell $\delta^{13}C$ values from predictions.

Although others have suggested the importance of temperature-dependent metabolic processes on foraminiferal shell $\delta^{13}C$ (e.g., Ortiz et al., 1996), shell $\delta^{13}C$–temperature relationships have not yet been quantified under controlled conditions. In this study, we explore the influence of temperature, $[CO_3^{2-}]$, and ontogeny on shell $\delta^{13}C$ for live foraminifera maintained in the laboratory. Experiments were conducted with the symbiont-bearing foraminifer *Orbulina universa* (15–25ºC) and nonsymbiotic *Globigerina bulloides* (15–24ºC).

2. Methodology

2.1. Experimental procedure

Approximately 100 *O. universa* and 230 *G. bulloides* were cultured using established procedures that have been discussed by Bemis et al. (1998). Briefly, live foraminifera were hand-collected from water depths of 2 to 6 m in the San Pedro Basin off the Southern California Bight (33º23′N, 118º26′W) and maintained in the laboratory at temperatures ranging from 15–25ºC (±0.2ºC). The foraminifera were fed one *Artemia* nauplius (San Francisco Bay strain, *Artemia* Reference Center #1157, $\delta^{13}C_{organic} = -20.4 \pm 0.2$‰) every other day. *O. universa* was grown under two irradiance levels: high light (HL, >386 μmol photons m^{-2} s^{-1}), which corresponds to maximum symbiont photosynthetic rates (P_{max}) (Spero and Parker, 1985; Rink et al., 1998), and low light (LL, 20–30 μmol photons m^{-2} s^{-1}), which is below the compensation light level (photosynthetic O_2 production < respired O_2 utilization) (Rink et al., 1998). The $[CO_3^{2-}]$ of the ambient filtered seawater in which *G. bulloides* and *O. universa* were grown was increased from 171 to 458 μmol kg^{-1} for additional experiments with HL *O. universa* at 17 and 24ºC. This 'high $[CO_3^{2-}]$' water was made by adding ~1.8 ml of 1 N NaOH to 4 l of filtered seawater, which increased the seawater pH from ~8.15 to ~8.64 (NBS scale).

2.2. Sample preparation and isotopic analysis

Carbon isotopic analyses were conducted on individual *O. universa* shells. For *G. bulloides*, labo-

ratory-grown chambers were severed from identical positions in the shell whorl and combined for each analysis (Spero and Lea, 1996). The experimental shell size–chamber total relationships for 11-, 12- and 13-chambered *G. bulloides* shells were 301 ± 25 μm, 369 ± 30 μm, and 414 ± 39 μm, respectively. An average of 12 *G. bulloides* chambers (average chamber weight ~1.5 μg) from identical positions in the shell whorl were combined for each analysis. All shells were roasted in vacuo for 30 minutes at 375ºC to remove volatile organic matter and adsorbed water prior to isotopic analysis on a Fisons Optima IRMS using a common acid bath autocarbonate device. Analytical precision of the $\delta^{13}C$ analyses was ±0.03‰ relative to the V-PDB standard (Craig, 1957). Culture water $\delta^{13}C_{\Sigma CO_2}$ was determined by acid-stripping CO_2 from 5 ml of seawater under vacuum (using 105% orthophosphoric acid) and purifying the CO_2 cryogenically prior to mass spectrometric analysis. Water $\delta^{13}C_{\Sigma CO_2}$ and $[CO_3^{2-}]$ changed little during the experiments (±0.10‰ and ±8 μmol kg^{-1}, respectively).

2.3. Calibration of $\delta^{13}C$–temperature relationships

Least squares regression was used to generate linear relationships between temperature and all individual $\delta^{13}C$ analyses for *O. universa* shells and *G. bulloides* chambers. Quoted errors on the slopes and *y*-intercepts are 95% confidence intervals. All statistical tests use the *F*-statistic at the 95% confidence level. The *G. bulloides* chamber data are combined using a mass balance relationship to produce $\delta^{13}C$–temperature relationships for whole shells consisting of a total of 11, 12, and 13 chambers (Bemis et al., 1998). For these calculations, $\Delta\delta^{13}C_f$ 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 16ºC (Spero and Lea, 1996) and 22ºC (this study).

3. Results and discussion

3.1. Experimental data

Because we are interested in how closely foraminiferal $\delta^{13}C$ records $\delta^{13}C_{\Sigma CO_2}$, we will discuss the experimental results in terms of the isotopic difference $\Delta\delta^{13}C_f$, where:

$$\Delta\delta^{13}C_f\,(‰) = \delta^{13}C_{foram} - \delta^{13}C_{\Sigma CO_2} \quad (1)$$

This term is positive when shells are enriched in ^{13}C relative to ΣCO_2 and negative when they are depleted. A value close to zero means that shell $\delta^{13}C$ records that of seawater.

For *O. universa*, $\Delta\delta^{13}C_f$ responds to temperature differently under HL and LL conditions (Table 1, Fig. 1). When the influence of symbiont photosynthetic activity is maximized due to high irradiance (HL), *O. universa* shells that grew in ambient seawater show average $\Delta\delta^{13}C_f$ values that increase from about 1.0‰ to 1.3‰ between 15 and 25ºC. This relationship is best expressed by the linear equation:

$$\Delta\delta^{13}C_f(‰) = 0.21(\pm 0.22) + 0.05(\pm 0.01) \times T\,(ºC)$$
$$r^2 = 0.24 \quad \text{HL, ambient } \left[CO_3^{2-}\right] \quad (2)$$

Although the relationship appears weak as demonstrated by the low r^2 value, the slope is significantly different from zero ($p < 0.01$). We therefore conclude that there is a significant relationship between $\Delta\delta^{13}C_f$ and temperature in HL *O. universa*. In contrast, the $\delta^{13}C$ of *O. universa* grown under LL (negligible photosynthetic influence) is insensitive to temperature across 15–25ºC, as shown by a $\Delta\delta^{13}C_f$–temperature slope that is indistinguishable from zero ($p = 0.75$). Coincidentally, the shell $\delta^{13}C$ of the LL specimens approximately records $\delta^{13}C_{\Sigma CO_2}$ ($\Delta\delta^{13}C_f = 0.13 \pm 0.28$‰). Because the slopes of the HL and LL relationships are significantly different from one another ($p < 0.01$), the $\Delta\delta^{13}C_f$ offset between HL and LL shells appears to increase at higher temperatures.

In the HL experiment where seawater $[CO_3^{2-}]$ was increased from 171 to 458 μmol kg^{-1}, *O. universa* shell $\Delta\delta^{13}C_f$ values decreased on average 2‰ relative to the ambient $[CO_3^{2-}]$ group (Fig. 1). This corresponds to a -0.007‰ μmol^{-1} kg^{-1} shift in $\delta^{13}C$, which is consistent with the slope of -0.0055 ± 0.0015‰ μmol^{-1} kg^{-1} found in a similar experiment using more data coverage (Spero et al., 1997). If temperature influences the magnitude of the $[CO_3^{2-}]$ effect on shell $\delta^{13}C$, then we would expect to see different $\Delta\delta^{13}C_f$–temperature slopes for the ambient and elevated $[CO_3^{2-}]$ shells. However, this is diffi-

Table 1
Experimental data for cultured *Orbulina universa* (symbiotic)

Temperature (ºC)	$[CO_3^{2-}]$ (μmol kg^{-1})	Irradiance	$\delta^{13}C$ (‰ VPDB)	$\delta^{18}O$ (‰ VPDB)	$\Delta\delta^{13}C_f$ (‰ VPDB)
15	171	HL	2.44	−0.64	0.71
15	171	HL	2.73	−0.46	0.96
15	171	HL	2.69	−0.48	0.94
15	171	HL	3.17	−0.41	1.42
15	171	HL	3.01	−0.48	1.26
15	171	HL	2.70	−0.57	0.95
15	171	HL	2.53	−0.51	0.81
15	171	HL	2.28	−0.64	0.47
15	171	HL	3.34	−0.66	1.53
15	171	HL	2.38	−0.67	0.57
15	171	LL	1.79	−0.26	0.04
15	171	LL	2.43	−0.19	0.84
15	171	LL	2.08	−0.26	0.44
15	171	LL	1.70	−0.31	−0.05
15	171	LL	1.94	−0.30	0.13
15	171	LL	1.61	−0.46	−0.16
17	171	HL	3.15	−0.98	1.33
17	171	HL	2.96	−1.02	0.88
17	171	HL	2.25	−0.85	0.19
17	171	HL	3.09	−0.98	1.15
17	171	HL	2.81	−0.91	0.97
17	171	HL	2.34	−1.02	0.40
17	171	HL	2.84	−0.98	0.90
17	171	HL	2.95	−0.80	1.01
17	171	HL	2.73	−1.07	0.81
17	171	LL	1.93	−0.71	0.00
17	171	LL	2.43	−0.47	0.54
17	171	LL	2.30	−0.44	0.39
17	171	LL	1.67	−0.82	0.46
17	458	HL	1.48	−1.28	−0.24
17	458	HL	0.28	−1.50	−1.58
17	458	HL	0.65	−1.46	−1.14
17	458	HL	1.10	−1.42	−0.69
18	171	HL	3.22	−1.17	1.38
18	171	HL	2.92	−1.23	1.08
18	171	HL	2.67	−1.09	0.83
18	171	LL	1.85	−0.98	0.01
18	171	LL	1.82	−0.79	−0.02
19	171	HL	3.00	−1.31	1.28
19	171	HL	2.83	−1.36	1.09
19	171	HL	2.89	−1.11	1.03
19	171	HL	2.84	−1.34	1.19
19	171	HL	2.53	−1.45	0.79
19	171	HL	2.71	−1.23	0.97
19	171	LL	1.90	−0.97	0.16
19	171	LL	1.88	−1.02	0.19
19	171	LL	1.75	−1.01	0.02
19	171	LL	1.62	−1.05	−0.10
19	171	LL	1.82	−1.00	0.10

Table 1 (continued)

Temperature (ºC)	$[CO_3^{2-}]$ (μmol kg^{-1})	Irradiance	$\delta^{13}C$ (‰ VPDB)	$\delta^{18}O$ (‰ VPDB)	$\Delta\delta^{13}C_f$ (‰ VPDB)
22	171	HL	2.99	−2.05	1.27
22	171	HL	2.80	−2.07	1.01
22	171	HL	3.11	−1.93	1.30
22	171	HL	3.03	−2.02	1.24
22	171	HL	2.69	−2.05	0.90
22	171	HL	2.41	−2.03	0.62
22	171	HL	2.67	−2.01	0.75
22	171	HL	3.23	−1.98	1.34
22	171	HL	2.85	−2.02	1.25
22	171	HL	3.40	−1.76	1.49
22	171	HL	3.21	−1.84	1.34
22	171	HL	3.20	−1.92	1.33
22	171	HL	2.80	−1.89	0.93
22	171	HL	3.46	−1.76	1.64
22	171	LL	1.69	−1.51	0.07
22	171	LL	1.53	−1.47	−0.09
22	171	LL	1.45	−1.59	−0.17
22	171	LL	1.70	−1.68	0.08
22	171	LL	1.40	−1.61	−0.22
22	171	LL	1.51	−1.77	−0.11
22	171	LL	1.67	−1.57	0.05
22	171	LL	1.51	−1.74	−0.11
22	171	LL	1.43	−1.67	−0.19
22	171	LL	1.67	−1.46	0.05
22	171	LL	1.38	−1.88	−0.24
22	171	LL	1.53	−1.75	−0.09
22	171	LL	1.64	−1.44	0.02
24	171	HL	3.02	−2.44	1.47
24	171	HL	2.82	−2.34	1.19
24	171	HL	2.85	−2.35	1.22
24	171	HL	3.09	−2.35	1.46
24	171	HL	2.80	−2.44	1.19
24	171	HL	3.20	−2.40	1.47
24	171	HL	3.14	−2.24	1.51
24	171	HL	1.77	−2.51	0.16 [a]
24	171	LL	2.16	−2.01	0.72
24	171	LL	1.76	−1.98	0.32
24	171	LL	1.94	−2.15	0.50
24	171	LL	1.74	−2.24	0.30
24	171	LL	1.92	−2.24	0.48
24	171	LL	2.10	−2.00	0.66
24	458	HL	0.58	−2.85	−1.04
24	458	HL	0.44	−2.97	−1.27
24	458	HL	1.27	−2.65	−0.46
24	458	HL	1.22	−2.83	−0.41
24	458	HL	0.92	−2.79	−0.54
24	458	HL	0.26	−2.83	−1.37
25	171	HL	2.88	−2.58	1.43
25	171	HL	3.07	−2.68	1.68
25	171	HL	2.64	−2.62	1.22

Table 1 (continued)

Temperature (ºC)	$[CO_3^{2-}]$ (μmol kg^{-1})	Irradiance	$\delta^{13}C$ (‰ VPDB)	$\delta^{18}O$ (‰ VPDB)	$\Delta\delta^{13}C_f$ (‰ VPDB)
25	171	HL	2.99	−2.72	1.57
25	171	HL	2.88	−2.61	1.46
25	171	HL	2.42	−2.55	1.00
25	171	HL	2.20	−2.74	0.78
25	171	HL	2.85	−2.50	1.43
25	171	LL	1.68	−2.23	0.26
25	171	LL	1.59	−2.25	0.17
25	171	LL	1.12	−2.50	−0.30

The carbon isotopic composition of foraminifera is expressed as $\Delta\delta^{13}C_f$, the $\delta^{13}C$ difference between the shells and seawater ΣCO_2 (i.e., $\delta^{13}C_{foram} - \delta^{13}C_{\Sigma CO_2}$). Ambient seawater $[CO_3^{2-}] = 171$ μmol kg^{-1}. Irradiance groups refer to high light (HL, >386 μmol photons m^{-2} s^{-1}) and low light (LL, 20–30 μmol photons m^{-2} s^{-1}), which correspond to maximum and sub-compensation point photosynthetic rates, respectively.

[a] Not included in calculated means or regression equations.

cult to resolve because we lack data at intermediate temperatures and the $\Delta\delta^{13}C_f$ variability is higher in the elevated $[CO_3^{2-}]$ groups. This higher $\Delta\delta^{13}C_f$ variability could reflect a more variable proportion of field-grown to lab-grown shell calcite in the elevated $[CO_3^{2-}]$ groups, which were terminated prior to gametogenesis. In contrast, most specimens in the experiments were terminated after gametogenesis, when field-grown juvenile chambers have typically been resorbed (Brummer et al., 1987; Spero, 1988).

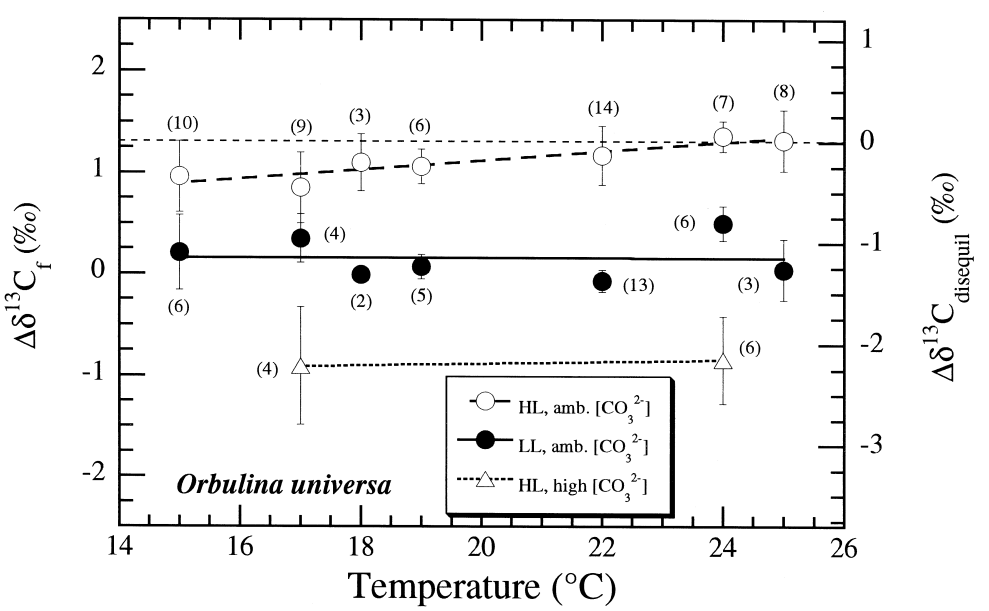

Fig. 1. Mean carbon isotopic values ($\pm 1\sigma$) versus temperature for *O. universa*, where $\Delta\delta^{13}C_f = \delta^{13}C_{foram} - \delta^{13}C_{\Sigma CO_2}$ and $\Delta\delta^{13}C_{disequil} = \Delta\delta^{13}C_f - \Delta\delta^{13}C_{EQ}$ (see text for definition of terms). Numbers within parentheses indicate the number of individual shell analyses represented by each point. The equilibrium $\delta^{13}C$ value is +1.3‰ for ambient seawater groups (dashed line) and +1.5‰ for the HL, high $[CO_3^{2-}]$ group (not shown). High light (HL) is >386 μmol photons m^{-2} s^{-1} (photosynthetic maximum, or P_{max}) and low light (LL) = 20–30 μmol photons m^{-2} s^{-1} (sub-compensation light level). Ambient $[CO_3^{2-}] = 171$ μmol kg^{-1} and high $[CO_3^{2-}] = 458$ μmol kg^{-1}. LL *O. universa* shells record $\delta^{13}C_{\Sigma CO_2}$ and HL shell $\Delta\delta^{13}C_{disequil}$ decreases with temperature.

Table 2
Experimental data for cultured *Globigerina bulloides* (nonsymbiotic)

Temperature (ºC)	Shell (chamber #)	$\delta^{13}C$ (‰ VPDP)	$\delta^{18}O$ (‰ VPDB)	$\Delta\delta^{13}C_f$ (‰ VPDB)
15	11	0.15	−1.13	−1.59 [a]
15	11	−0.92	−0.86	−2.66
15	12	0.04	−0.64	−1.70
15	12	−0.50	−0.81	−2.24
15	12	−0.45	−0.59	−2.19
15	13	−0.06	−0.52	−1.80
15	13	−0.27	−0.56	−2.01
17	11	−1.04	−1.46	−2.79
17	12	−0.52	−1.15	−2.27
17	13	−0.59	−1.14	−2.34 [a]
19	11	−0.88	−1.70	−2.76
19	12	−0.45	−1.41	−2.33
19	12	−0.48	−1.50	−2.36
19	13	−0.17	−1.36	−2.05
22	11	−1.20	−2.30	−3.05
22	11	−1.20	−2.00	−3.05
22	12	−0.66	−2.08	−2.51
22	12	−0.75	−2.21	−2.60
22	12	−0.74	−2.21	−2.59
22	12	−0.68	−2.24	−2.53
22	13	−0.26	−2.01	−2.11
22	13	−0.21	−2.19	−2.06
22	13	−0.24	−1.74	−2.09
22	13	0.05	−1.89	−1.80
24	11	−1.67	−2.72	−3.28
24	12	−0.97	−2.72	−2.58
24	12	−0.96	−2.64	−2.57
24	13	−0.69	−2.60	−2.30
16	1–10			−2.49 [b]
22	1–10			−3.56 [b]

The carbon isotopic composition of foraminifera is expressed as $\Delta\delta^{13}C_f$, the $\delta^{13}C$ difference between the shells and seawater ΣCO_2 (i.e., $\delta^{13}C_{foram} - \delta^{13}C_{\Sigma CO_2}$). Shell Chamber # refers to ontogenetic position within the shell whorl. Ambient seawater $[CO_3^{2-}] = 171\ \mu mol\ kg^{-1}$.
[a] Not included in calculated means or regression equations.
[b] Field-collected specimens. Temperatures represent ambient surface water during collection. 16ºC shell data calculated via mass balance using data from Spero and Lea (1996); 22ºC data from this study.

Isotopic data from the *G. bulloides* experiments demonstrate the influences of ambient temperature and specimen size (Table 2, Fig. 2). Individual *G. bulloides* chambers show mean $\Delta\delta^{13}C_f$ values that are significantly higher (more positive) in larger specimens ($p < 0.01$) (Fig. 2a), but the $\Delta\delta^{13}C_f$–temperature slopes are not significantly different (common slope = −0.05‰ ºC^{-1}; $p = 0.14$). The $\Delta\delta^{13}C_f$–temperature relationships for whole *G. bulloides* shells show a similar pattern of larger shells that are less depleted in ^{13}C relative to ΣCO_2 (Fig. 2b). The slopes of these linear equations appear to decrease slightly with increasing shell size:

$$\Delta\delta^{13}C_f\ (‰) = -0.47(\pm 0.15) - 0.13(\pm 0.01) \times T(ºC)$$
$$r^2 = 0.99 \quad 11 - \text{ch. shell} \tag{3}$$

$$\Delta\delta^{13}C_f\ (‰) = -0.77(\pm 0.08) - 0.11(\pm 0.00) \times T(ºC)$$
$$r^2 = 0.99 \quad 12 - \text{ch. shell} \tag{4}$$

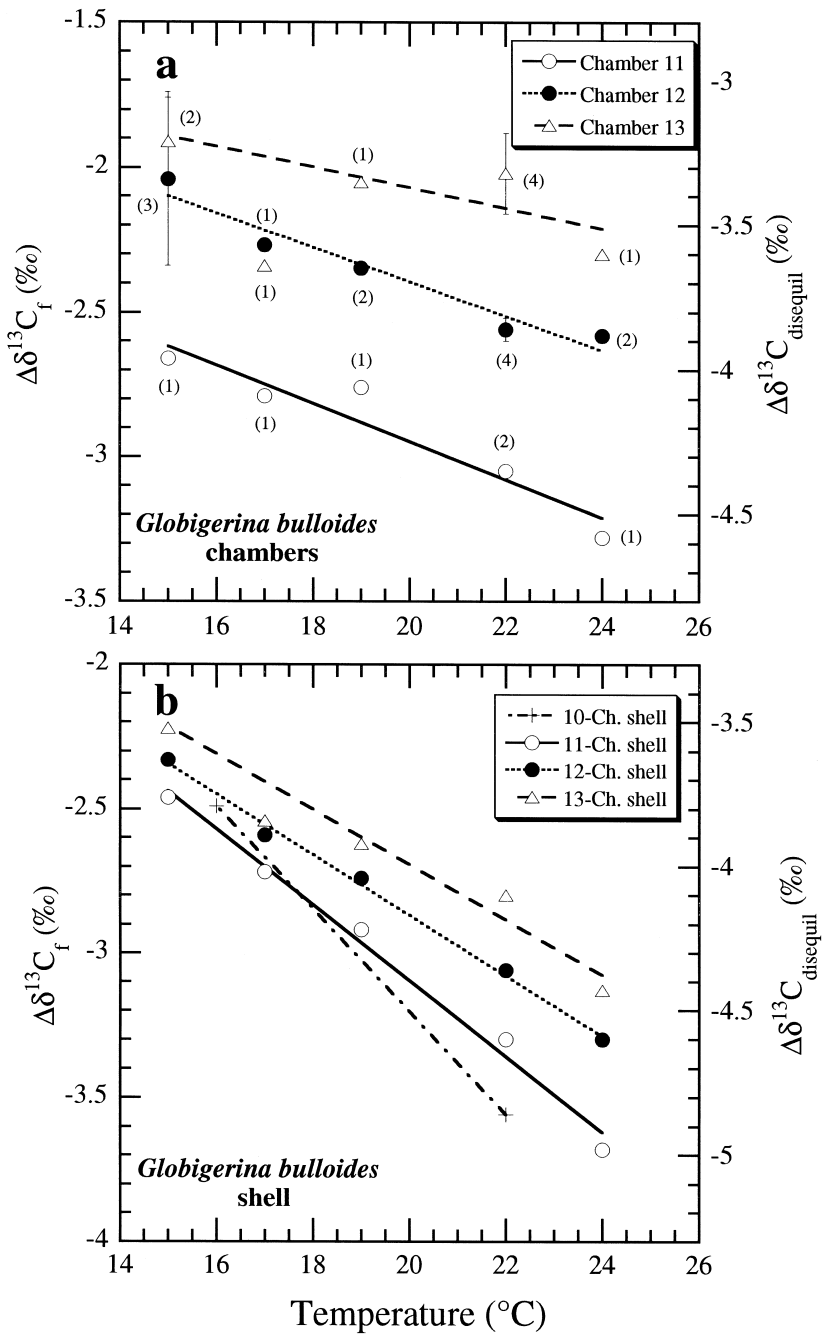

Fig. 2. Mean carbon isotopic values ($\pm 1\sigma$) versus temperature for *G. bulloides*, where $\Delta\delta^{13}C_f = \delta^{13}C_{foram} - \delta^{13}C_{\Sigma CO_2}$ and $\Delta\delta^{13}C_{disequil} = \Delta\delta^{13}C_f - \Delta\delta^{13}C_{EQ}$ (see text for definition of terms). The equilibrium $\delta^{13}C$ value is +1.3‰. (a) Chambers 11, 12, and 13. Numbers within parentheses indicate the number of individual shell analyses represented by each point. (b) Reconstructed whole shells consisting of 11, 12, and 13 chambers (common slope = −0.11‰ $^{o}C^{-1}$). Each point represents a single calculated value based on a mass balance. 10-chambered shell data are from field-collected specimens (this study and Spero and Lea, 1996). The magnitude of $\Delta\delta^{13}C_{disequil}$ increases with temperature.

$$\Delta\delta^{13}C_f\ (‰) = -0.78(\pm 0.22) - 0.10(\pm 0.01) \times T(^oC)$$
$$r^2 = 0.97 \quad 13 - \text{ch. shell} \qquad (5)$$

but the difference in slope between 12- and 13-chambered shells is not significant ($p = 0.42$). Therefore, we suggest using the common slope of $-0.11‰$ $^oC^{-1}$ ($p = 0.02$) when relating changes in temperature and *G. bulloides* $\Delta\delta^{13}C_f$. For comparison, the $\Delta\delta^{13}C_f$–temperature slope for 10-chambered shells collected in the field at temperatures of 16 and 22ºC is $-0.18‰$ $^oC^{-1}$.

3.2. Carbon isotopic equilibrium

Many studies have investigated whether or not foraminifera precipitate their shells in carbon isotopic equilibrium with seawater (e.g., Williams et al., 1977; Berger et al., 1978; Shackleton and Vincent, 1978; Oppo and Fairbanks, 1989; Ortiz et al., 1996). To test this question, researchers often use an isotopic enrichment factor, ε, to estimate the $\delta^{13}C$ value of calcite ($\delta^{13}C_{calcite}$) precipitated in isotopic equilibrium with dissolved bicarbonate (HCO_3^-):

$$\varepsilon_{calcite-HCO_3^-}\ (‰) = \left[\left(\frac{1000 + \delta^{13}C_{calcite}}{1000 + \delta^{13}C_{HCO_3^-}}\right) - 1\right] \times 1000 \qquad (6)$$

Within measurement error, this term is equal to $\delta^{13}C_{calcite}$ minus $\delta^{13}C_{HCO_3^-}$.

Laboratory determinations of $\varepsilon_{calcite-HCO_3^-}$ vary considerably, and therefore so do estimates of equilibrium $\delta^{13}C_{calcite}$. For example, Rubinson and Clayton (1969) determined a $\varepsilon_{calcite-HCO_3^-}$ value of $0.9 \pm 0.2‰$ at 25ºC for inorganically precipitated calcite, whereas Turner (1982) obtained an average value of $1.40 \pm 0.7‰$. Several researchers have combined the Rubinson and Clayton (1969) data with temperature–fractionation data from Emrich et al. (1970) to predict a $\delta^{13}C_{calcite}$ increase of ~0.5‰ relative to $\delta^{13}C_{HCO_3^-}$ over 15–25ºC (Grossman, 1984; Mook, 1986). However, the Emrich et al. (1970) data were for mixed calcite–aragonite precipitates that may have contained more isotopically enriched aragonite at higher temperatures (Romanek et al., 1992). Therefore, an increase in $\varepsilon_{calcite-HCO_3^-}$ at higher temperatures is probably not valid. In contrast to previous studies, Romanek et al. (1992) carefully constrained the mineralogy of precipitates and found no temperature dependence for inorganically precipitated calcite (10–40ºC). The $\varepsilon_{calcite-HCO_3^-}$ value they obtained appears to be the best estimate to date, so we will use it to calculate equilibrium $\delta^{13}C_{calcite}$ in this study:

$$\varepsilon_{calcite-HCO_3^-}\ (‰) \simeq \delta^{13}C_{calcite} - \delta^{13}C_{HCO_3^-}$$
$$= 1.0 \pm 0.2‰ \qquad (7)$$

In paleoceanographic studies, a relationship like Eq. 7 is used to estimate seawater $\delta^{13}C_{\Sigma CO_2}$ from shell $\delta^{13}C$ (or vice versa). It is common in this case to assume that $\delta^{13}C_{HCO_3^-}$ equals $\delta^{13}C_{\Sigma CO_2}$. Although this assumption is fairly good at typical oceanic pH values where HCO_3^- accounts for ~90% of ΣCO_2, it still overestimates $\delta^{13}C_{\Sigma CO_2}$ and underestimates shell $\delta^{13}C$ by about 0.3‰ (Zhang et al., 1997). This implies that studies that have relied on shell $\delta^{13}C$ as a $\delta^{13}C_{\Sigma CO_2}$ proxy (e.g., Stott, 1992) have underestimated the already large ^{13}C-depletion in some foraminifera.

Furthermore, because the difference between $\delta^{13}C_{HCO_3^-}$ and $\delta^{13}C_{\Sigma CO_2}$ increases in seawater of higher pH and $[CO_3^{2-}]$ (Zhang et al., 1997) (Fig. 3), $\delta^{13}C_{\Sigma CO_2}$ and $\delta^{13}C_{calcite}$ estimates can be even further apart. This change in offset occurs because $\delta^{13}C_{\Sigma CO_2}$ decreases when the proportion of relatively ^{13}C-depleted CO_3^{2-} ion increases at elevated pH. The influence of pH on estimating $\delta^{13}C_{\Sigma CO_2}$ could especially bias downcore studies and comparisons between regions, because surface water pH and $[CO_3^{2-}]$ vary seasonally (Bates et al., 1996) and latitudinally (Bainbridge, 1981; Broecker et al., 1982; Weiss et al., 1983) and the glacial ocean was more alkaline than at present (Sanyal et al., 1995).

To compare our foraminiferal data to predicted equilibrium, we calculate the $\delta^{13}C$ difference between calcite and ΣCO_2 at equilibrium:

$$\Delta\delta^{13}C_{EQ}\ (‰) = \delta^{13}C_{calcite} - \delta^{13}C_{\Sigma CO_2} \qquad (8)$$

To obtain $\Delta\delta^{13}C_{EQ}$, we correct Eq. 7 for the $\delta^{13}C$ difference between HCO_3^- and ΣCO_2 across the temperature and pH ranges of our experiments. Mass balance calculations using isotopic enrichment factors for the dissolved carbon species (Zhang et al., 1997) indicate that HCO_3^- is enriched in ^{13}C relative to ΣCO_2 by about 0.3‰ and 0.5‰ in our ambient

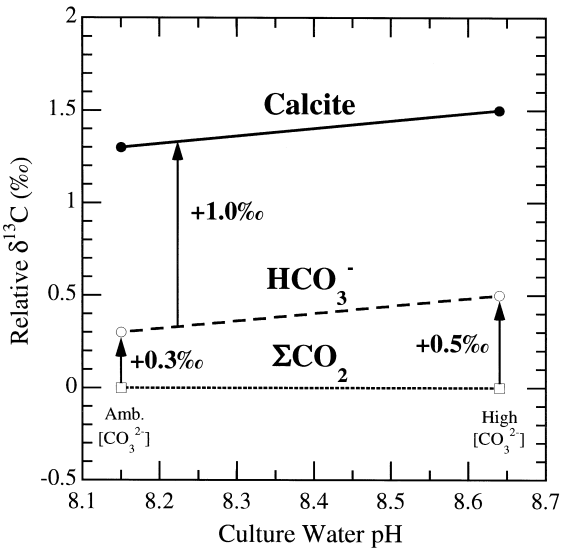

Fig. 3. Relative $\delta^{13}C$ differences among ΣCO_2, HCO_3^-, and precipitated calcite at equilibrium as a function of pH and $[CO_3^{2-}]$ in these experiments. These relationships are insensitive to temperature between 15 and 25ºC. Calcite-HCO_3^- $\delta^{13}C$ offset is from Romanek et al. (1992) and $HCO_3^- - \Sigma CO_2$ $\delta^{13}C$ offset is calculated via mass balance equations using the isotopic enrichment factors of Zhang et al. (1997).

and high $[CO_3^{2-}]$ groups, respectively. Therefore, if calcite is enriched by 1.0‰ relative to HCO_3^- according to Eq. 7, then carbon isotopic equilibrium values for calcite precipitated in our experiments are:

$$\Delta\delta^{13}C_{EQ}\,(‰) = 1.3 \pm 0.2‰ \quad \text{ambient}\left[CO_3^{2-}\right](171\ \mu\text{mol kg}^{-1}) \tag{9}$$

$$\Delta\delta^{13}C_{EQ}\,(‰) = 1.5 \pm 0.2‰ \quad \text{high}\left[CO_3^{2-}\right](458\ \mu\text{mol kg}^{-1}) \tag{10}$$

These values are insensitive to temperature between 15 and 25ºC (Romanek et al., 1992; Zhang et al., 1997). Throughout the remainder of this paper we will refer to foraminiferal $\Delta\delta^{13}C_f$ offsets from these equilibrium values as $\delta^{13}C$ 'disequilibrium', where:

$$\delta^{13}C_{disequil} = \Delta\delta^{13}C_f - \Delta\delta^{13}C_{EQ} \tag{11}$$

A larger $\delta^{13}C_{disequil}$ magnitude means a greater difference between the predicted and experimental data.

3.3. Comparison of experimental data to $\delta^{13}C$ disequilibrium

3.3.1. Orbulina universa

When symbiont photosynthesis is minimized in our LL experiment, *O. universa* shell $\delta^{13}C$ values are unaffected by temperature and depleted in ^{13}C by an average of ~1.2‰ relative to equilibrium (Eq. 9). That is, $\Delta\delta^{13}C_{disequil} = -1.2‰$ (Fig. 1). Several processes might explain this pattern. One possibility is that shell calcification is sufficiently rapid to cause incomplete (nonequilibrium) isotopic exchange between dissolved inorganic carbon and precipitated calcite (McConnaughey, 1989a,b). Turner (1982) found evidence for this kinetic fractionation when he determined that the isotopic enrichment factor $\varepsilon_{calcite-HCO_3^-}$ for inorganically precipitated calcite decreases with increasing precipitation rate. However, Romanek et al. (1992) found no effect for inorganically precipitated calcite over a much larger range of precipitation rates than that found in experimental studies with planktonic foraminifera (Lea et al., 1995). Furthermore, a recent reevaluation of the Turner (1982) data suggests no significant correlation between $\varepsilon_{calcite-HCO_3^-}$ and precipitation rate in those experiments (Romanek et al., 1992). Therefore, at this time calcification rate does not appear to be responsible for the depleted $\delta^{13}C$ values. This conclusion is in agreement with the recent results of Bijma et al. (1999).

A second possibility for the $\delta^{13}C$ disequilibrium is that LL *O. universa* incorporates ^{13}C-depleted respired carbon during calcification, which drives shell $\delta^{13}C$ toward lower values. If correct, then we would expect $\Delta\delta^{13}C_{disequil}$ to increase over 15–25ºC, because higher temperatures should increase respiration rate (Spero et al., 1991; Ortiz et al., 1996) and presumably the proportion of metabolic carbon contributed to the foraminiferal microenvironment and shell. To explore this process further, we attempt to illustrate the temperature influence on respiration and $\Delta\delta^{13}C_f$ by considering the term Q_{10}, which describes a metabolic rate increase over a 10ºC temperature change:

$$R_2 = R_1 \times Q_{10}^{(T_2-T_1)/10} \tag{12}$$

where R_1 and R_2 are metabolic rates (or some proxy) at temperatures T_1 and T_2 (e.g., Ortiz et al., 1996).

A typical Q_{10} of 2 would indicate a doubling of metabolic rate over 10ºC. If we assume that the change in the difference between our experimental data ($\Delta\delta^{13}C_f$) and some reference value is solely a function of a metabolic rate change between two temperatures, then we can relate $\Delta\delta^{13}C_f$ to Q_{10} (Ortiz et al., 1996). For example, we could relate the foraminiferal $\delta^{13}C$ difference from equilibrium (i.e., $\Delta\delta^{13}C_{disequil}$) to a respiration Q_{10} by replacing R_1 and R_2 in Eq. 12 with the appropriate $\Delta\delta^{13}C_{disequil}$ values at 15 and 25ºC. However, because the absolute values chosen for R_1 and R_2 influence the calculated Q_{10}, we proceed with the goal of merely illustrating the potential magnitude of effects.

Caron et al. (1987) used shell growth rates to determine a Q_{10} of 1.6 for *O. universa*. Based on this result and our average LL $\Delta\delta^{13}C_{disequil}$ value at 15ºC (i.e., $R_1 = -1.2‰$), Eq. 12 predicts a 0.7‰ decrease in shell $\delta^{13}C$ (greater $\Delta\delta^{13}C_{disequil}$) between 15 and 25ºC. This is inconsistent with the observed values of $\Delta\delta^{13}C_{disequil}$, which are not temperature dependent. However, it is possible that another metabolic process such as a symbiont photosynthetic rate increase at higher temperatures (Li, 1980) could balance this predicted $\delta^{13}C$ decrease. Such an effect should be insignificant for these foraminifera, though, because they were grown under light-limited conditions that allowed only minimal photosynthesis. Therefore, we conclude that respired CO_2 does not comprise a significant portion of shell carbon in *O. universa*. This is consistent with the results of studies that used prey $\delta^{13}C$ values as tracers of metabolic carbon incorporation (Spero and Lea, 1993a; Spero, 1998).

If calcification rate and metabolic CO_2 cannot account for the $\Delta\delta^{13}C_{disequil}$ of ~1‰ in LL *O. universa*, then we are left without the standard explanations for depleted shell $\delta^{13}C$ values. Alternatively, some fundamental difference between inorganic and biogenic calcification could explain isotopic disequilibrium. Unlike inorganic calcite precipitation, biogenic calcification is regulated by a template of organic molecules (Towe, 1972; Anderson and Bé, 1978; Mann, 1983; Simkiss and Wilbur, 1989; Robbins and Donachy, 1991) whose influence on $\delta^{13}C_{calcite}$ is poorly understood. These organic matrix proteins are thought to facilitate crystal nucleation by bonding with mineral ions, thereby inducing supersaturation and reducing the nucleation free energy barrier (Mann, 1983; Simkiss and Wilbur, 1989; Stumm and Morgan, 1996). If the organic matrix is kinetically selective during this process, then isotopic disequilibrium would be an inherent function of biogenic calcification. If correct, then comparison to inorganic equilibrium may be appropriate only to a certain point.

In contrast with LL *O. universa* shells, $\Delta\delta^{13}C_{disequil}$ for HL shells is slightly temperature-dependent, and shifts from approximately −0.3‰ to +0.0‰ between 15 and 25ºC (Fig. 1). Although $\Delta\delta^{13}C_{disequil}$ is zero at the highest temperatures, meaning that shell $\Delta\delta^{13}C_f$ values are the same as those expected at equilibrium, it does not mean that the shells were precipitated in isotopic equilibrium. Indeed, the similarity of isotopic values is probably coincidental, because the photosynthetic effect on HL shell $\delta^{13}C$ is superimposed over the LL shell disequilibrium discussed earlier. Furthermore, equilibrium should not be influenced by temperature in these experiments, yet the HL shell $\delta^{13}C$ values seem to be temperature-sensitive.

These results indicate that the influence of symbiont photosynthesis on *O. universa* $\delta^{13}C$ is temperature-dependent. Specifically, at higher temperatures the isotopic enrichment of inorganic carbon increases near the calcification site, so shells have higher $\delta^{13}C$ values. This pattern can be accomplished by: (i) an increase in the isotopic fractionation factor between inorganic and photosynthetically fixed carbon; or (ii) increased rate of photosynthetic removal of ^{12}C near the calcifying shell. Explanation (i) does not work here, because we know from phytoplankton studies that photosynthetic fractionation by the carbon-fixing enzyme rubisco (ribulose-1,5-biphosphate carboxylase/oxygenase) is smaller at higher temperatures, not larger (see review by Descolas-Gros and Fontugne, 1990). This would produce a pattern opposite to our observations: shell $\delta^{13}C$ would decrease between 15 and 25ºC.

Explanation (ii) finds support in studies showing that photosynthetic rate increases at higher temperatures in phytoplankton and hermatypic corals (Coles and Jokiel, 1977; Li, 1980; Jacques et al., 1983; Muthiga and Szmant, 1987). Like the influence of increased irradiance on symbiont photosynthetic rate, higher temperatures cause more rapid uptake of inorganic carbon and therefore a greater discrimination

against ^{13}C (Descolas-Gros and Fontugne, 1990). This would explain the shift toward higher $\Delta\delta^{13}C_f$ in HL *O. universa* shells as temperature increases. If we calculate the temperature-related increase in symbiont photosynthetic rate required to explain this shift, using the mean LL $\Delta\delta^{13}C_f$ as a reference (0.13‰), we obtain a photosynthetic $Q_{10} = 1.4$. This is similar to the Q_{10} estimated by Caron et al. (1987) for the foraminiferal host and slightly smaller than values estimated for symbiotic reef corals (Coles and Jokiel, 1977; Jacques et al., 1983; Muthiga and Szmant, 1987). In summary, respiration changes with temperature are not recorded in the isotopic signature of *O. universa* shells, but temperature does slightly affect the symbiont influence on shell $\delta^{13}C$ and $\Delta\delta^{13}C_{disequil}$.

3.3.2. *Globigerina bulloides*

Average $\Delta\delta^{13}C_{disequil}$ values in cultured *G. bulloides* range from approximately −3.2‰ to −4.0‰ in individual chambers at 15ºC and increase in magnitude ~0.5‰ across the temperature range (Fig. 2a). For whole shells, $\Delta\delta^{13}C_{disequil}$ is −3.5‰ to −3.8‰ at 15ºC and increases ~1‰ between 15 and 24ºC (Fig. 2b). This pattern is consistent with the incorporation of more metabolic carbon into shell calcite at higher respiration rates. The $\Delta\delta^{13}C_{disequil}$ increase can be explained by a respiration Q_{10} of 1.3–1.4 (for 13- and 11-chambered shells, respectively). These Q_{10} values are considerably smaller than an earlier Q_{10} estimate of 2.0 calculated by Ortiz et al. (1996) for *G. bulloides* laboratory data at 16 and 22ºC.

Other than temperature, additional factors that affect *G. bulloides* metabolic rate could influence shell $\delta^{13}C$ and $\Delta\delta^{13}C_{disequil}$. For example, Ortiz et al. (1996) argued that variations in feeding rate could reasonably explain $\Delta\delta^{13}C_{disequil}$ variations in nonsymbiotic foraminifera collected in north Pacific plankton tows. Based on our experimental results, we expect that feeding-enhanced metabolic rates will produce lower shell $\delta^{13}C$ values and increase $\Delta\delta^{13}C_{disequil}$ magnitude at all temperatures. Ontogenetic changes in metabolic rates have been used to explain correlations between shell size and $\delta^{13}C$ for *G. bulloides*, where smaller shells are relatively depleted in ^{13}C (Berger et al., 1978; Fairbanks et al., 1982; Oppo and Fairbanks, 1989; Spero and Lea, 1996). This pattern has been explained by higher respiration rates in younger (smaller) foraminifera, which results in the incorporation of more ^{13}C-depleted metabolic CO_2 during calcification (Berger et al., 1978; Ravelo and Fairbanks, 1995). Our results are in agreement with this explanation because smaller chambers and shells exhibit greater $\Delta\delta^{13}C_{disequil}$ values than larger specimens at all experimental temperatures.

3.4. *Paleoceanographic implications*

These experiments demonstrate that *G. bulloides* and *O. universa* shell $\delta^{13}C$ varies as a function of sea surface temperature (SST), and therefore, SST differences could bias how we interpret shell $\delta^{13}C$ differences between regions and deep-sea core intervals. For example, a downcore shift in shell $\delta^{13}C$ could be interpreted as a regional or whole ocean $\delta^{13}C$ change, perhaps due to a change in water mass (Pedersen et al., 1991) or transfer of carbon between the terrestrial and oceanic reservoirs (Shackleton, 1977). Because a SST shift could also produce an apparent $\delta^{13}C$ shift by changing the $\delta^{13}C$ of the calcifying microenvironment, it is worthwhile examining the potential magnitude of this effect on glacial–interglacial SST time scales.

For *O. universa*, cooler glacial SST will decrease $\delta^{13}C$ values slightly, with the greatest effect on HL shells (0.05‰ ºC^{-1}). If tropical SST was ~2–5ºC cooler during the LGM (Rind and Peteet, 1985; Broecker, 1986; Guilderson et al., 1994; Stott and Tang, 1996), then average $\delta^{13}C$ values for these shells should be at most 0.10–0.25‰ lower than today due to this effect. However, because *O. universa* grows across a range of depths and light levels (Fairbanks et al., 1982; Bouvier-Soumagnac and Duplessy, 1985; Ravelo and Fairbanks, 1992), not all shells will show the same $\delta^{13}C$ difference. The $\delta^{13}C$–temperature influence should decrease with light level and depth until the compensation light level, where temperature has no additional effect on shell $\delta^{13}C$. Thus, multiple-shell analyses should minimize SST-related $\delta^{13}C$ differences because they combine shells that grew across the photic zone. For instance, in MOCNESS plankton tows in the eastern equatorial Atlantic (Ravelo and Fairbanks, 1992), 23% of *O. universa* in the upper 100 m grew under light lev-

els equal to or exceeding our experimental HL group (>386 μmol photons m^{-2} s^{-1}). The remainder of the population grew at lower light levels, calculated by assuming a light extinction coefficient of 0.04 typical of oligotrophic waters (Raymont, 1980). We can estimate the $\delta^{13}C$ change at each depth for a given SST change if we assume the $\delta^{13}C$–temperature slope for *O. universa* decreases linearly between HL and LL. These changes, when weighted by shell abundances at each depth (Ravelo and Fairbanks, 1992), yield a mean $\delta^{13}C$ decrease of 0.07–0.19‰ for a 2–5ºC LGM cooling. If the $\delta^{13}C$–temperature influence is also common to other symbiotic foraminifera, then the $\delta^{13}C$ decrease would be greater for species that have an abundance maximum shallower than *O. universa* (e.g., *Globigerinoides sacculifer* and *G. ruber*) (Hemleben et al., 1989; Ravelo and Fairbanks, 1992).

Billups and Spero (1996) calculated an approximate 2ºC LGM cooling in the eastern and western equatorial Atlantic using individual *O. universa* $\delta^{18}O$ values. However, a recalculation of their G–I temperature change using new pore water-derived ice volume estimates (Schrag and DePaolo, 1993; Schrag et al., 1996) and the possible isotopic effect of a more alkaline ocean during the LGM (Spero et al., 1997) would produce a temperature drop of approximately 4ºC. The mean 0.15‰ shell $\delta^{13}C$ reduction we predict from this cooling at both sites would be enhanced by the effect of higher LGM $[CO_3^{2-}]$. Using a conservative estimate of 60 μmol kg^{-1} higher $[CO_3^{2-}]$, LGM *O. universa* $\delta^{13}C$ would be depleted 0.36‰, and therefore we predict the combined influences would decrease mean shell $\delta^{13}C$ by ~0.5‰. The core data from these sites show mean $\delta^{13}C$ decreases of 0.1‰ to 0.2‰ (Billups and Spero, 1996). Although these shifts initially suggest a $\delta^{13}C_{\Sigma CO_2}$ decrease, our predictions indicate that surface water $\delta^{13}C_{\Sigma CO_2}$ had to increase by 0.3‰ to 0.4‰ to offset the influence of G–I changes in SST and ocean alkalinity. Our interpretation is consistent with Broecker and Henderson (1998), who estimate that surface water $\delta^{13}C_{\Sigma CO_2}$ would have increased 0.35‰ if enhanced biological productivity produced the LGM drawdown of atmospheric CO_2.

The temperature influence on *G. bulloides* shell $\delta^{13}C$ should be 2–3 times that of *O. universa* and in the opposite direction. This means that LGM *G. bulloides* shells should have higher $\delta^{13}C$ values than specimens that grew in warmer Holocene surface waters. For a glacial cooling of only 2ºC, this means that shell $\delta^{13}C$ values would increase by about 0.2‰ (0.11‰ $ºC^{-1}$) due to decreased incorporation of metabolic CO_2. Interestingly, the temperature effect will offset the influence of higher LGM $[CO_3^{2-}]$ on *G. bulloides* $\delta^{13}C$ instead of increasing it like in *O. universa*. This is apparent in *G. bulloides* extracted from sediments in core SU81-18 from the northeastern Atlantic, off Portugal (Bard et al., 1989; L. Labeyrie, pers. comm.). We estimate that LGM surface waters cooled 12ºC at this site, using a new *G. bulloides* paleotemperature equation (Bemis et al., 1998) and correcting for the effects of higher LGM $\delta^{18}O_{water}$ (Schrag et al., 1996) and alkalinity (Spero et al., 1997). This temperature drop would increase *G. bulloides* $\delta^{13}C$ by 1.32‰, which, when combined with the 0.72‰ decrease from the $[CO_3^{2-}]$ influence, would predict a net glacial shell increase of 0.6‰. The core data show that *G. bulloides* $\delta^{13}C$ increased 0.4‰, so LGM surface water $\delta^{13}C_{\Sigma CO_2}$ must have decreased slightly (0.2‰) to produce what we observe. The influences of temperature and $[CO_3^{2-}]$ must both be taken into account when interpreting downcore shifts in foraminiferal $\delta^{13}C$.

4. Conclusions

We have developed a suite of new $\delta^{13}C$–temperature relationships for laboratory-grown *G. bulloides* and *O. universa*. *G. bulloides* shells show decreased $\delta^{13}C$ values at higher temperatures (−0.11‰ $ºC^{-1}$), which is probably a function of greater metabolic modification of $\delta^{13}C_{\Sigma CO_2}$ near the shell at higher temperatures. A pattern of smaller $\Delta\delta^{13}C_{disequil}$ in larger *G. bulloides* chambers and shells is consistent with an ontogenetic decrease in metabolic rate in this species. The relationships for *O. universa* respond to changes in irradiance (symbiont photosynthetic rate) and seawater $[CO_3^{2-}]$. Shells grown under LL in ambient seawater record $\delta^{13}C_{\Sigma CO_2}$ independently of temperature. Our results indicate that calcification rate and incorporation of respired CO_2 cannot explain the observed $\Delta\delta^{13}C_{disequil}$ in these LL shells. In contrast, HL shells are enriched in ^{13}C relative to ΣCO_2, with $\Delta\delta^{13}C_f$ values that may be influenced

by temperature-dependent enhancement of symbiont photosynthetic activity.

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