Temperature effect on respiration and photosynthesis of the symbiont-bearing planktonic foraminifera *Globigerinoides ruber* , *Orbulina universa* , and *Globigerinella siphonifera*

F. Lombard, J. Erez, Elisabeth Michel, L. Labeyrie

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F. Lombard[1]
Laboratoire des Sciences du Climat et de l'Environnement/Institut Pierre-Simon Laplace, laboratoire Commissariat à l'Energie Atomique/Centre National de la Recherche Scientifique/Université de Versailles Saint-Quentin, avenue de la Terrasse, F-91198 Gif-sur-Yvette CEDEX, France

J. Erez
Institute of Earth Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

E. Michel and L. Labeyrie
Laboratoire des Sciences du Climat et de l'Environnement/Institut Pierre-Simon Laplace, laboratoire Commissariat à l'Energie Atomique/Centre National de la Recherche Scientifique/Université de Versailles Saint-Quentin, avenue de la Terrasse, F-91198 Gif-sur-Yvette CEDEX, France

Abstract

Respiration and photosynthesis of the planktonic foraminifera *Globigerinoides ruber*, *Orbulina universa*, and *Globigerinella siphonifera* and their symbiotic algae were calculated from measured dissolved oxygen gradients using microelectrodes, using different temperatures in dark and light (250 μmol photon m^{-2} s^{-1}) conditions. At one temperature (24°C) the respiration rate increased as a power function of the foraminiferan organic carbon mass with a 0.57 ± 0.18 exponent. The effect of temperature on respiration was quantified in two ways: by normalizing the rates to the organic carbon mass and by normalizing the observed rates to a constant temperature (24°C). This latter normalization was also used for photosynthesis. The respiration rates increase as a function of temperature for all species and can be described either with a Q_{10} = 3.18 (±0.27) or with an Arrhenius temperature of T_A = 10,293°K (±768°K). Similar calculations for net photosynthesis yielded a Q_{10} = 2.68 (±0.36) and a T_A = 8766°K (±1203°K), and calculations for gross photosynthesis yielded a Q_{10} = 2.76 (±0.29) and a T_A = 9026°K (±926°K). For the species studied, the photosynthesis : respiration ratio varied from moderate for *G. siphonifera* (0.58) to very high (13) for *O. universa*. The high ratios indicate that photosynthesis is much higher than the carbon requirements for both foraminifera and symbiont growth. This excess carbon might be the source of organic exudates.

Planktonic foraminifera are calcifying protozoa widely distributed in the oceans. Although classically described as both herbivores and carnivores, a number of tropical to subtropical surface-dwelling, spinose species are associated with actively photosynthesizing symbiotic algae (Hemleben et al. 1989). Despite their relatively low abundance in the plankton (mean of 20–50 individuals [ind.] m^{-3} in oligotrophic to mesotrophic ocean; Schiebel and Hemleben 2005), foraminiferal calcite is responsible for 32–80% of the global $CaCO_3$ flux to the sediments (Schiebel 2002). Thus, foraminifera are an important contributor to the global oceanic carbon cycle. Their tests are well preserved above the carbonate compensation depth and accumulate in the oceanic sediments for periods of millions of years. These fossilized foraminifera are widely used for paleoclimatic reconstructions based on their elemental and isotopic compositions or according to their species abundance (Duplessy et al. 1991). Despite this relative importance in the oceanic $CaCO_3$ budget and for paleoclimatic reconstructions, the biology and especially the growth ability as a function of various environmental conditions are mainly reconstructed from their abundance patterns in the ocean (Žarić et al. 2005) and are only partially known from direct experimental studies. To understand and clearly determine both the effect of foraminifera on the oceanic carbon cycle and the influence of environmental parameters on paleoclimatic indicators, it is important to study the influence of environmental conditions (e.g., temperature) on their physiological processes.

For foraminifera, as for other organisms, growth can be defined as the difference between matter uptake (nutrition,

[1] Corresponding author (lombard@lsce.ipsl.fr).

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symbiont photosynthesis) and output (respiration, excretion). Several studies have focused on the growth of foraminifera (Bijma et al. 1990), but few observations were conducted on the physiological processes underlying their growth. Foraminifera respiration and symbiont photosynthesis were studied only for *Orbulina universa* (Spero and Parker 1985; Rink et al. 1998; Köhler-Rink and Kühl 2005), *Globigerinoides sacculifer* (Erez 1982; Jørgensen et al. 1985), and, for photosynthesis only, for *Globigerinoides ruber* (Gastrich and Bartha 1988). Despite the strong influence of temperature on foraminiferal growth (Bijma et al. 1990) and shell isotopic composition (Erez and Luz 1982, 1983), none of these studies has focused on the temperature influence on respiration and photosynthesis using direct observations.

The purpose of the present study is to examine the influence of temperature on the respiration and photosynthetic rates of three symbiont-bearing foraminifera species: *G. ruber*, *O. universa*, and *Globigerinella siphonifera*. The oxygen gradient surrounding the foraminifer was studied with oxygen microelectrodes under dark (respiration) and light (photosynthesis) conditions for different temperatures. Based on these measurements we discuss the possible influence of photosynthesis and respiration on foraminiferal physiology and nutrition.

Methods

Sampling of materials—Specimens of several foraminiferal species were collected during November–December 2006 from the surface water of the Gulf of Aqaba, northern Red Sea. Sampling was performed using 200-μm plankton net hauls about 1 km off the shore at the IUI (H. Steinitz Marine Biology Laboratory), Eilat, Israel. At the time of collection the water temperature was around 23°C and the salinity was 40.7. Immediately after the hauls, each plankton sample was separated into three subsamples and transferred to 1 liter of seawater. Fresh seawater from the sea surface was also sampled simultaneously for the culture.

In the laboratory, live foraminifera were sorted from the plankton sample using a wide-mouth pipette under a dissection microscope, transferred into 250-mL Pyrex precipitation dishes with fresh seawater, and maintained under metal–halide illumination of ~250 μmol photon m^{-2} s^{-1} for recovery. Three different species, *G. ruber*, *O. universa*, and *G. siphonifera*, were identified. *G. siphonifera* specimens had a large and very dark cytoplasm, with symbionts located along the spines and therefore probably belonging to Type II of this species, as defined by Bijma et al. (1998). According to this definition the symbionts of this species are probably Prymnesiophyte or Chrysophycophyte algae (Gast and Caron 2001). The symbionts of *G. ruber* and *O. universa* are dinoflagellates, probably *Gymnodinium béii* (Spero 1987; Gast and Caron 2001). Within 1 d after collection, foraminifera were carefully transferred to the Institute of Earth Sciences at The Hebrew University of Jerusalem. Here the foraminifera were kept in fresh seawater and placed under a strong metal–halide light (250 μmol photon m^{-2} s^{-1}) with a 12 : 12-h light : dark cycle at 24°C. Foraminifera were allowed to recover for 2–5 d before experiments, and all experiments were performed within 6 d after collection. Although many of the organisms lost their spines and some of their symbionts during the sampling, the spines had regenerated within 1 d or 2 d, and the foraminifera spread out their symbionts along the spines during daylight. The foraminifera were fed every 2–3 d with freshly hatched *Artemia nauplii* (brine shrimp). In order to keep the conditions as uniform as possible between individuals, only those specimens starved for 2 d were used for oxygen flux measurements.

Experimental setup and oxygen measurement—Each day, healthy foraminifera (long spines, abundant symbionts spreading out along the spines) were sorted from the culture and placed in a small Petri dish (20 mL) with a thin glass bottom; the Petri dish was filled with seawater. The Petri dish was placed under an inverted microscope (Nikon Eclipse TE2000-S) in a temperature-regulated holder under a 250–μmol photon m^{-2} s^{-1} light (for photosynthesis rate measurements) or dark (for respiration). The light was measured using a LI-COR model LI-1000 with a Quantum sensor for photosynthetically active radiation. The temperature was controlled by a cryothermostat, which allows water circulation inside an aluminum plate on which the observation dish was held. The temperature was measured regularly inside the observation dish with a digital thermometer and was constant at a level of ±0.1°C. For each specimen, the measurements were performed in stagnant conditions (avoiding turbulence due to movements or water convection), initially at 24°C, and in the light after 1-h acclimation. The light was then turned off and the dark measurements were performed when the oxygen gradient surrounding the foraminifer became stable. The temperature was then progressively changed and the foraminifera were allowed to acclimate to the new temperature for 1 h before new measurements were taken.

Oxygen was measured with a fast-response microelectrode with a sensing diameter of 10 μm (OX-10, UNISENSE, precision 0.3 μmol O_2 L^{-1}; Revsbech and Jørgensen 1986). This electrode was calibrated in seawater flushed to equilibrium with N_2, air, and O_2. The microelectrode was attached to a micromanipulator that could be manually moved in three dimensions and with which the electrodes could be advanced with a precision of ±5 μm. A second micromanipulator is used to move a long and fine glass micropipette with an external diameter of 2 μm. This extremely flexible needle was used to gently maintain the foraminifera immobile without stressing it while it continued to spread out its symbionts. The two micromanipulators were directly fixed on the inverted microscope with a 14° angle from the vertical.

For each measurement, the electrode was first progressively advanced to its position near the foraminiferan shell, along its radial axis. This step is the most delicate, because the foraminifera often stick to the electrode with their pseudopods. Once the electrode was placed next to the foraminiferan's shell, its position was recorded with a digital camera. The image was analyzed afterward (University of Texas, Health Science Center at San Antonio;

Table 1. Size, calculated organic carbon weight, and experimental temperature for the different specimens in this study.*

Species	Shell diameter (μm)	Calculated organic mass (μg C)	Temperatures tested (°C)			
G. ruber	189	0.31	17.3	21.6	24.1	
G. ruber	241	0.65	24.1	29.6		
G. ruber	249	0.72	19.4	24.2	29.5	
G. siphonifera	347	1.95	18.7	24.3	27.8	
O. universa	521	1.41	15.3	19.9	24.3	29.3

**G. ruber*, *Globigerinoides ruber*; *G. siphonifera*, *Globigerinella siphonifera*; *O. universa*, *Orbulina universa*.

UTHSCSA Image Tool, http://ddsdx.uthscsa.edu/dig/itdesc.html) to measure the foraminiferan diameter and the electrode tip position with a 3-μm precision. The organic carbon weight of the foraminiferan was estimated using two different shell volume–carbon weight relationships (Michaels et al. 1995), one corresponding to the normal globular foraminifera and the other to spherical specimens of *O. universa*. The oxygen gradient around the animal was then recorded by manually moving the sensor away in 50-μm steps. Each oxygen profile was repeated two to three times with a slightly different location around the foraminifer both in light and dark conditions in order to observe net photosynthesis and dark respiration.

Photosynthesis and respiration flux calculation—The total net photosynthesis or dark respiration fluxes of each specimen can be calculated from the oxygen gradient surrounding the individual (Jørgensen et al. 1985), if we consider that the foraminiferan symbionts are distributed in a spherical halo and that, because of the small dimensions between spines, the viscosity prevents convective water transport around the individuals. Thus, the oxygen and other dissolved substances are transported only through molecular diffusion. The oxygen flux can therefore be calculated from the radial gradient, dC/dr (nmol O_2 mm^{-4}), and from the molecular diffusion coefficient, D (mm^2 h^{-1}), of oxygen at the considered temperature (Li and Gregory 1974).

The calculation is based on the approximate spherical symmetry of the system. The radial flux, F (nmol O_2 h^{-1}), through a sphere of radius r and surface area $4\pi r^2$, which concentrically surrounds the foraminiferan, is (Jørgensen et al. 1985)

$$F = D\frac{dC}{dr}4\pi r^2 \quad (1)$$

Then the oxygen concentration, $C(x)$ (μmol O_2 L^{-1}) at the radius x (mm), compared to a reference point at the radius a with an oxygen concentration $C(a)$, is

$$C(x) = C(a) + \frac{F}{4\pi D}\left(\frac{1}{a} - \frac{1}{x}\right) \quad (2)$$

The oxygen flux is then identified on the radial gradient using Eq. 2 with a reference point a, chosen in the part of the profile that is closer to the individual outside of the symbiont halo and inside the spines (first third of the profile). Data points inside the symbiont halo were not considered. For all the different oxygen profiles the R^2 correlation coefficients between measured and calculated profiles (Eq. 2) ranged from 0.959 to 0.999.

Respiration is quantified by the flux in dark condition and net photosynthesis from the experiments under saturating light (250 μmol photon m^{-2} s^{-1}; Jørgensen et al. 1985; Rink et al. 1998). The gross photosynthesis is assumed to be the sum of net photosynthesis and respiration rates, as our experiment does not allow the direct measurement of the gross photosynthesis or the quantification of additional effects, such as enhanced respiration in light due to photorespiration.

Temperature effect on respiration and photosynthesis rates—One common way to estimate the influence of the temperature on a physiological rate is the use of the Q_{10} value that quantifies the rate increase for a 10°C increase. The rate, R, for a given temperature, T (°C), is defined as follows:

$$R(T) = R_0 Q_{10}^{T/10} \quad (3)$$

where R_0 (nmol O_2 ind.$^{-1}$ h^{-1}) is the rate measured at 0°C. The use of Q_{10} is convenient but presents the disadvantage of varying as a function of the temperature range considered. The Arrhenius relationship (T_A), on the other hand, is more stable over a wider temperature range (Kooijman 2000). This relationship uses temperatures in Kelvin scale and has the following form:

$$R(T) = R(T_1)\exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) \quad (4)$$

where $R(T_1)$ (nmol O_2 ind.$^{-1}$ h^{-1}) is the rate measured for a chosen reference temperature, T_1, and where T_A (°K) is the Arrhenius temperature.

In this study we use both Q_{10} and T_A to quantify the influence of temperature on respiration and photosynthesis rates.

Results

During our study we carried out several oxygen gradient measurements both in dark and light conditions for different temperatures for five individuals, including three *G. ruber*, one *G. siphonifera*, and one *O. universa* (Table 1). These specimens had shell diameters ranging from 189 μm to 521 μm, which correspond to individuals with cytoplasm carbon mass from 0.3 μg C to 2 μg C (calculated using the conversion factors of Michaels et al. [1995]). Different temperatures were tested for each specimen; temperatures

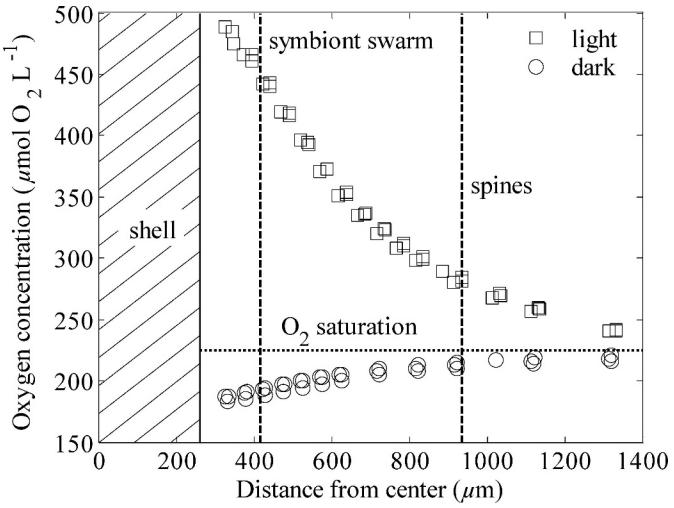

Fig. 1. Oxygen gradients observed in triplicates for *O. universa* at 29.3°C in light and dark conditions. Vertical dashed line indicates the outer periphery of the symbionts swarm and of the spines. Horizontal dashed line indicates the 100% O_2 saturation.

ranged from 15.3°C to 29.6°C. Figure 1 shows one example of the profiles measured on *O. universa* in light and dark condition at 29°C. In light conditions we always observe strong oxygen supersaturation (485 μmol O_2 L^{-1}; 197% of air saturation) in proximity to the specimen's shell. The oxygen depletion in the dark condition is lower (185 μmol O_2 L^{-1}; 77% of air saturation). Each measurement was repeated several times, and the measurements were reproducible even when the location of the profile was changed (Fig. 1).

For each specimen, the respiration rate increased with temperature (Fig. 2A), although a large variability between specimens (as a result of their size) was observed. At 24°C, specimens of *G. ruber* with lower weight respired less than did larger *O. universa* or *G. siphonifera* individuals (Fig. 2B). The respiration rates increased as a power function (with a 0.57 ± 0.18 exponent) of the individual organic carbon mass. When normalized for individual carbon mass, the changes in respiration with temperature became comparable among individuals (Fig. 2C). The increase in respiration rate could then be parameterized with $R_0 = 0.058$ (±0.02) nmol O_2 ind.$^{-1}$ $h^{-1}$and $Q_{10} = 2.70$

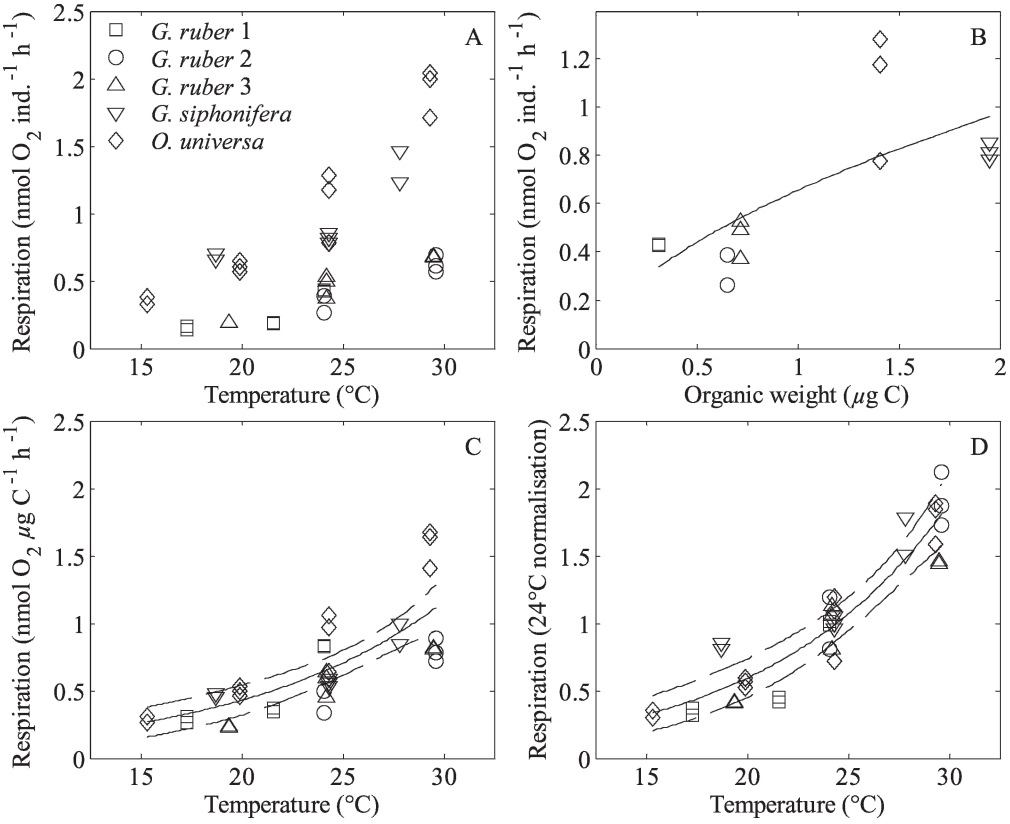

Fig. 2. Respiration rate of *G. ruber*, *G. siphonifera*, and *O. universa*. (A) Respiration rate (nmol O_2 ind.$^{-1}$ h^{-1}) in relation to temperature. (B) Respiration rate at 24°C in relation to the organic weight (μg C) calculated from shell size and a conversion factor from Michaels et al. (1995). Continuous line: least-squares regression for data fitted with a power model with a 0.57 ± 0.18 exponent. (C) Respiration rate in relation to temperature of the different specimens calculated for a 1 μg C individual using the precedent relationship (panel B). (D) Respiration rate in relation to temperature of the different specimens normalized by the mean observed value at 24°C. Solid line: least-squares regression for data fitted with the Arrhenius relationship (Table 2); dashed lines: 95% confidence intervals for the regression.

Table 2. Respiration rate and net and gross photosynthesis rate parameters (Eq. 3 and 4) obtained by least-squares regression on the 24°C normalized data (Figs. 2D, 3B,C) and on respiration rate calculated for a 1 μg C foraminifera (Fig. 2C).*

	T_A	SD	R^2	Q_{10}	SD	R^2
Net photosynthesis (24°C normalized)	8766	1203	0.65	2.69	0.36	0.65
Gross photosynthesis (24°C normalized)	9026	926	0.77	2.76	0.29	0.77
Respiration (weight normalized)	8811	1442	0.58	2.70	0.44	0.58
Respiration (24°C normalized)	10,293	768	0.88	3.18	0.27	0.88

*T_A, Arrhenius temperature; SD, standard deviation.

($\pm$0.43) or with T_1 = 283°K (20°C), $R(T_1)$ = 0.42 ($\pm$0.05) nmol O_2 ind.$^{-1}$ h^{-1}, and T_A = 8811°K ($\pm$1442°K) (Table 2). However, the scatter between specimens remains high (R^2 = 0.58 for the two regressions) as a result of the fact that the shell can be less or more filled with the cytoplasm, leading to a slightly biased organic mass estimate as a function of shell size. A better temperature regression (Fig. 2D; R^2 = 0.87 for the regressions) is obtained by normalizing the rates observed at different temperatures for each specimen (Fig. 2A) to its mean observed rate at 24°C, defined as a reference point. With this new normalization the increase of respiration rate as a function of temperature can be described by a Q_{10} = 3.18 ($\pm$0.27) or by T_A = 10,293°K ($\pm$768°K) (Table 2).

The gross photosynthesis was calculated as the sum of the observed net photosynthesis (light conditions) and respiration (dark conditions). The gross photosynthesis increased also as a function of temperature, although the variability between individuals was larger than that observed for respiration (Fig. 3A). This larger variability is mainly due to the difference in size among specimens but is also due to the different number of symbionts carried by the foraminifer. For *G. siphonifera* we also observe a slight decrease of the gross photosynthesis rate for the higher temperature tested (27.8°C), when compared to the lower temperature tested (24.3°C). When the different photosynthesis rates are normalized to the mean value obtained for a temperature of $\approx$24°C, the scatter among individuals decreases significantly (R^2 = 0.77; Fig. 3B,C), and the increase in gross photosynthesis can be described with Q_{10} = 2.76 ($\pm$0.29) or with T_A = 9026°K ($\pm$926°K). The influence of temperature on net photosynthesis (Q_{10} = 2.69 [$\pm$0.36]; T_A = 8766°K [$\pm$1203°K]; Fig. 3C; Table 2) is slightly lower than for gross photosynthesis because of the large influence of temperature on respiration (Q_{10} = 3.18) used when calculating gross photosynthesis from respiration and net photosynthesis.

Discussion

The present microelectrode study of oxygen gradients around foraminifera shows that both respiration and photosynthesis are enhanced by temperature. However, some biases could have occurred. First, the collection technique involving use of a plankton net may have caused a loss of cytoplasm and symbionts, resulting in a possible reduction in the respiration and photosynthesis recorded. Second, in order to keep the conditions as stable as possible among individuals, the foraminifera were fed 2 d before the measurement. Therefore, our results probably represent low values for respiration, because digestion generally increases the respiration rate of organisms (Conover 1978) and foraminifers were in a starved condition. However, these uncertainties should not influence the effect of temperature on respiration and photosynthesis. Moreover, our estimate of the gross photosynthesis as the sum of net photosynthesis and dark respiration should be only considered as a minimum estimate. Effectively it has been showed that the respiration rate in light conditions is generally higher than in dark conditions (Rink et al. 1998). The gross photosynthesis rate may be directly quantified by using the light–dark shift technique (Jørgensen et al. 1985), but this method was not applicable in our case, because photosynthesis in foraminifera displays a diurnal cycle (Spero and Parker 1985), and the experimental setting did not allow sufficient equilibration time for each treatment to perform all these measurements during the daytime to avoid the daily cycle bias. However, our results are generally coherent with the few comparable data, taking into account the very different experimental conditions (Table 3). At 20–22°C and for *O. universa* specimens with shell diameters between 554 and 464 μm, Rink et al. (1998) observed net respiration rates between 4.57 and 8.72 nmol O_2 ind.$^{-1}$ h^{-1}, which is close to our observation for *O. universa* (521 μm, 19.9°C, 7.07–8.36 nmol O_2 ind.$^{-1}$ h^{-1}). The difference is larger for dark respiration rate, 1.7 $\pm$ 0.7 nmol O_2 ind.$^{-1}$ h^{-1}, whereas our measurement ranges from 0.56 to 0.63 nmol O_2 ind.$^{-1}$ h^{-1}. For *G. ruber*, the observed net respiration rate for a 249-μm–sized individual at 29.4°C is about 5.32 nmol O_2 ind.$^{-1}$ h^{-1}, a much higher value compared to previous measurements (0.63 nmol O_2 ind.$^{-1}$ h^{-1} at 28°C; Gastrich and Bartha 1988). This difference could originate from the low light intensity (170 μmol photon m^{-2} s^{-1}) used in the latter study. Other studies on foraminiferal photosynthesis and respiration (Jørgensen et al. 1985; Spero and Parker 1985) are hardly comparable to our study since they use different growth stages or different species. The measurements on juvenile *O. universa* seem to be coherent with our measurement, whereas those on *G. sacculifer* photosynthesis and respiration rates are higher than those measured in our study.

To our knowledge, this study is the first one to observe directly the influence of temperature on the respiration and photosynthesis rates of foraminifera. This offers new perspective on understanding foraminifera physiology. It is one of the necessary steps to reach an integrated view of the environmental factors that control foraminifera growth. The Q_{10} values observed in our study, $\sim$2.68, or

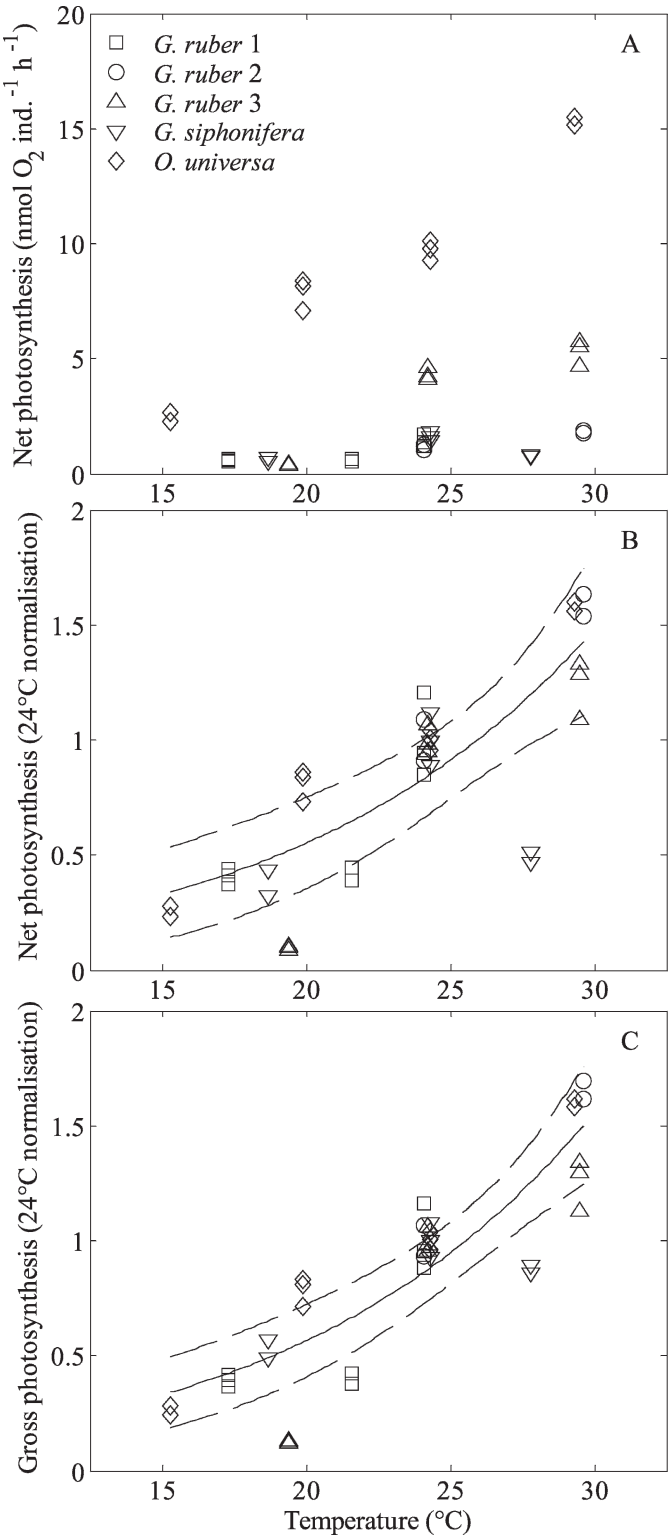

Fig. 3. Photosynthesis rate of *G. ruber*, *G. siphonifera*, and *O. universa*. (A) Net photosynthesis rate (nmol O_2 ind.$^{-1}$ h^{-1}) in relation to temperature. (B) Net photosynthesis rate in relation to temperature of the different specimens normalized by the mean observed value at 24°C. (C) Gross photosynthesis rate in relation to temperature of the different specimens normalized by the mean observed value at 24°C. Solid lines: least-squares regression for data fitted with the Arrhenius relationships (Table 2); dashed lines: 95% confidence intervals for the regression.

a T_A of ~8766°K for net photosynthesis corresponds to what is observed for cyanobacteria (Robarts and Zohary 1987). The observed Q_{10} for respiration, 3.18, and the T_A of 10,293°K are slightly higher than for tintinids (Verity 1985), microflagellates (Caron et al. 1986), copepods (Vidal 1980), appendicularians (Lombard et al. 2005), or euphausiids (Ross 1982); the Q_{10} for these typically ranges between 1.5 and 2.8 in this temperature range. Our direct Q_{10} estimates are also higher than previous ones calculated for foraminifera from indirect methods (based on the δ^{13}C of the shells), which give a Q_{10} for respiration of between 2 and 2.75 (Ortiz et al. 1996) and a Q_{10} of ~1.6 for photosynthesis (Bemis et al. 2000). Growth observations on foraminifera also give estimates of Q_{10} of about 1.75 for *O. universa* (Caron et al. 1987), and these estimates range from 2 to 9 for *G. ruber*, *G. sacculifer*, and *O. universa* (Bijma et al. 1990). However, growth is influenced by nutrition, respiration, and photosynthesis, and a strong temperature influence on respiration (e.g., a high Q_{10} value) could counteract the temperature influence on photosynthesis and nutrition, which would result in a lower Q_{10} for growth. Therefore, the Q_{10} arising from growth measurements are not directly comparable to our specific measurements. High Q_{10} values generally characterize species that have higher sensitivity for temperature changes and therefore indicate a stronger influence of the environmental temperature on the species metabolism. This high sensitivity to environmental temperature could possibly explain the strong species clustering observed as a function of latitude (Bé and Tolderlund 1971) that is used for paleoclimatic reconstructions (Climap 1981; Waelbroeck et al. 2005).

It should be mentioned that our experimental protocol does not allow long-term acclimation of the foraminifera to temperature. If some acclimation would occur, it would potentially result in a slightly lower Q_{10} value. Longer acclimation was not possible without introducing large biases due to biological processes (i.e., growth, gametogenesis, change in symbiont number, and feeding) that would have modified the metabolic rates significantly.

Whereas not significantly different (Student's t-test = 0.92; df = 73; p = 0.005), the respiration Q_{10} is slightly higher than for photosynthesis (i.e., the respiration seems to increase slightly more as a function of temperature than does the net or gross photosynthesis). This differential temperature dependence of heterotrophic processes and autotrophic processes could originate from the fact that interactions of photons with RuBisCO are less affected by temperature than biochemical oxygen interactions during mitochondrial respiration (Kooijman 2000; López-Urrutia et al. 2006). However, the difference between these processes and their different responses to temperature may play a role in the incorporation of stable isotopes and trace elements in the shell and their associated "vital effects" (Erez 1978; Spero et al. 1991; Erez 2003). A second possibility could be that the Q_{10} values for respiration and photosynthesis are essentially the same, and the variability associated with measurements and rate calculations is largely responsible for the observed differences.

The net photosynthesis:respiration (P : R) ratio quantifies by how much net photosynthesis exceeds respiration. It

Table 3. Net and gross photosynthesis and respiration rates of some planktonic foraminifera. SD, standard deviation.

Reference	Species	Specimen size (μm)	Light (μmol photon m^{-2} s^{-1})	T (°C)	Photosynthesis (nmol O_2 ind.$^{-1}$ h^{-1})				Respiration rate (nmol O_2 ind.$^{-1}$ h^{-1})	
					Net	SD	Gross	SD	Mean	SD
Spero and Parker 1985	*O. universa* (juv)	300*	250	20	4.79					
Jørgensen et al. 1985	*G. sacculifer*	400	400	25	14.90		18.10		3.00	
Gastrich and Bartha 1988	*G. ruber*	250	170	28	0.63					
Rink et al. 1998	*O. universa*	554	782	20–22	8.72		13.89		5.17	
	O. universa	554	782	20–22	5.06		11.00		5.94	
	O. universa	463	288	20–22	4.57		9.26		4.69	
	O. universa	473	446	20–22	6.45		8.16		1.71	
	O. universa	297	750	20–22	0.57		2.29		1.72	
Present study	*O. universa*	521	250	29.30	15.39	0.17	17.31	0.17	1.91	0.14
		521	250	24.30	9.70	0.35	10.78	0.35	1.08	0.22
		521	250	19.90	7.86	0.56	8.47	0.56	0.60	0.03
		521	250	15.30	2.48	0.20	2.83	0.20	0.35	0.03
	G. ruber 1	189	250	24.10	1.43	0.22	1.86	0.22	0.43	0.00
		189	250	17.30	0.58	0.04	0.73	0.04	0.15	0.01
		189	250	21.60	0.59	0.04	0.78	0.04	0.19	0.01
	G. ruber 2	241	250	29.60	1.84	0.06	2.46	0.06	0.62	0.05
		241	250	24.10	1.16	0.10	1.49	0.10	0.33	0.06
	G. ruber 3	249	250	19.40	0.41	0.02	0.60	0.02	0.19	0.00
		249	250	24.20	4.31	0.21	4.77	0.21	0.47	0.07
		249	250	29.50	5.32	0.45	6.00	0.45	0.67	0.00
	G. siphonifera	347	250	24.30	1.61	0.15	2.43	0.15	0.82	0.03
		347	250	27.80	0.79	0.04	2.13	0.04	1.34	0.11
		347	250	18.70	0.61	0.09	1.28	0.09	0.68	0.02

*Calculated from the observed photosynthesis per symbionts and the symbionts number of a 300-μm shell diameter individual (Spero and Parker 1985). *O. universa*, *Orbulina universa*; *G. sacculifer*, *Globigerinoides sacculifer*; *G. ruber*, *Globigerinoides ruber*; *G. siphonifera*, *Globigerinella siphonifera*.

is used to estimate the physiological efficiency of marine microalgae and to scale the relationship of consumption and production of organic material. This ratio varied between 1.3 and 5.7 for dinoflagellates (Humphrey 1975; Daneri et al. 1992) and between 2.7 and 9.1 for various planktonic algae, including diatoms and *Gymnodinium* species (Humphrey 1975); a mean P : R ratio of 2.4 for coral zooxanthellae have also been observed (Battey 1992). In our study, the P : R ratio is 0.58–1.97 for *G. siphonifera* (the least efficient photosynthesis), 2–9 for *G. ruber*, and 7–13 for *O. universa* (the most efficient). In our experiments, *G. siphonifera* symbiont photosynthesis produces enough carbon to supply the respiration needs only at 24.3°C (P : R = 1.97), whereas in the two other conditions tested (18.7°C and 27.8°C), the symbiont–foraminifer complex consumes more oxygen than it produces in a 12 : 12-h day : night basis. For *G. ruber* and *O. universa*, the required carbon for the foraminiferan respiration is always supplied by the symbionts on the temperature range tested. If compared to P : R ratio derived from other works, our *G. ruber* P : R is comparable to those of *G. sacculifer* at 25°C (4.96; Jørgensen et al. 1985) or *O. universa* at 20–22°C (≈3; Rink et al. 1998), whereas our range of estimated P : R ratio for *O. universa* is higher than all previous observations. This difference cannot be derived from our experimental protocol, which was the same for all these experiments, but probably arises from differences in the symbiont number hosted by *O. universa*, which is probably higher in our study than in that of Rink et al. (1998). This also shows that our sampling method does not lead to a significant loss of symbionts compared to scuba collections.

The lower P : R ratio for *G. siphonifera* at 27.8°C is due to a decrease of photosynthesis rate. This probably indicates that the symbiont photosynthetic enzymes are partially inactivated for this high temperature range and, consequently, photosynthesis is less efficient. This means that 27.8°C is probably above the photosynthesis optimum temperature for *G. siphonifera*, whereas its respiration rate continues to increase in this temperature range. Similar decreases in photosynthesis rates at high temperature have been already observed for cyanobacteria (Robarts and Zohary 1987) or coral symbiotic algae (Iglesias-Prieto et al. 1992).

One striking point already emphasized for foraminifera (Jørgensen et al. 1985) is the large observed photosynthesis rate, compared to respiration. For example, *O. universa* at 29.3°C have a respiration rate of 1.91 (±0.03) nmol O_2 h^{-1} and a net photosynthesis rate of ~15.39 (±0.04) nmol O_2 h^{-1}, but this is also true for *G. ruber*. If we assume that both the respiratory ratio (CO_2 produced : O_2 consumed) and the photosynthetic ratio (O_2 produced : CO_2 consumed) are equal to 1 on a 12 : 12-h day : night basis, the *O. universa* specimen of organic carbon mass of about 1.33 μg C (calculated following Michaels et al. [1995]) will increase its mass daily by 1.94 μg C and will then reach an

exponential growth rate of up to 0.89 d^{-1}. This appears unrealistic since the growth of *O. universa* in laboratory conditions is relatively low (growth rates calculated on organic carbon–increase basis; 0.22–0.24 d^{-1} at 25°C and 28°C [Caron et al. 1987]; 0.22 and 0.16 d^{-1} at 25.8°C and 30.7°C, respectively [Bijma et al. 1990]), and the symbionts show division rates of 0.65 d^{-1} at 25°C in cultures (Spero 1987). Thus, the organic matter produced by symbionts largely exceeds the amount needed for the growth of both the symbionts and foraminifera. One part of this organic carbon may effectively be used for growth, since symbiont nutrient uptake and prey capture would provide a substantial amount of nitrogen and phosphorus to the foraminifer (Uhle et al. 1997). However, Jørgensen et al. (1985) have shown that nutrient uptake may be insufficient to complement organic carbon. Thus, carbon is produced in excess compared to what is needed for growth of the foraminifera and its symbionts.

For phytoplankton, nutrient-starved cells continue to produce carbon compounds by photosynthesis while biomass synthesis is limited. This cellular carbon overflow in phytoplankton generally triggers polysaccharide exudation (Myklestad 1995). It is probable that the carbon excess production by the foraminiferan and symbiont complex leads to the exudation of a certain part of the photosynthetic products. This should not be considered as a net loss. Effectively, when phytoplankton exudates organic matter, a certain proportion of these exudates is composed of amino acids (Myklestad 1995), and numerous organisms, including bacteria and copepods, use these chemical compounds to follow the trails of their prey (Poulet and Ouellet 1982; Blakburn et al. 1998). Knowing that symbiotic foraminifera fed mostly on ciliates and copepods (Hemleben et al. 1989), it is thus not impossible that the strong carbon overproduction of symbionts can be used by the foraminifera as a chemical trail to attract planktonic organisms that can be potential sources of prey. This possible adaptation could be particularly important in symbiotic foraminifera, which often occur in oligotrophic oceans, where potential prey organisms are rare and where chemical trails have better chance to be detected as a result of the low concentration of organic matter in the water. This may also explain the abundance of free-swimming dinoflagellates observed around foraminifers collected by scuba diving (Spero and Angel 1991; Spero and Lea 1996) that could be attracted by chemical trails. However, more experiments have to be done to test this hypothesis.

References

Battey, J. F. 1992. Carbon metabolism in zooxanthellae-coelenterate symbiosis, p. 153–187. *In* W. Reiser [ed.], Algae and symbioses. Biopress.

Bé, A. W. H., and D. S. Tolderlund. 1971. VI. Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans, p. 105–149. *In* B. M. Funnell and W. R. Riedel [eds.], Micropaleontology of oceans. Cambridge Univ. Press.

Bemis, B. E., H. J. Spero, D. W. Lea, and J. Bijma. 2000. Temperature influence on the carbon isotopic composition of *Globigerina bulloides* and *Orbulina universa* (planktonic foraminifera). Mar. Micropaleontol. **38:** 213–228.

Bijma, J., W. W. J. Faber, and C. Hemleben. 1990. Temperature and salinity limits for growth and survival of some planktonic foraminifers in laboratory cultures. J. Foraminifer Res. **20:** 95–116.

———, C. Hemleben, B. T. Huber, H. Erlenkeuser, and D. Kroon. 1998. Experimental determination of the ontogenetic stable isotope variability in two morphotypes of *Globigerinella siphonifera* (d'Orbigny). Mar. Micropaleontol. **35:** 141–160.

Blakburn, N., T. Fenchel, and J. Mitchell. 1998. Microscale nutrient patches in planktonic habitats shown by chemotactic bacteria. Science **282:** 2254–2256.

Caron, D. A., W. W. J. Faber, and A. W. H. Bé. 1987. Growth of the spinose planktonic foraminifer *Orbulina universa* in laboratory culture and the effect of temperature on life processes. J. Mar. Biol. Assoc. UK **67:** 343–358.

———, J. C. Goldman, and M. R. Dennett. 1986. Effect of temperature on growth, respiration, and nutrient regeneration by an omnivorous microflagellate. Appl. Environ. Microbiol. **52:** 1340–1347.

Climap, 1981. Seasonal reconstructions of the Earth's surface at the last glacial maximum in Map Series, Technical report MC-26. Geological Society of America.

Conover, R. J. 1978. Transformation of organic matter, p. 221–499. *In* O. Kinne [ed.], Marine ecology: A comparative, integral treatise on life in oceans and coastal waters. V. 4. Dynamics. Wiley.

Daneri, G., A. Iriarte, V. M. Garcia, D. A. Purdie, and D. W. Crawford. 1992. Growth irradiance as a factor controlling the dark respiration rates of marine-phytoplankton. J. Mar. Biol. Assoc. UK **72:** 723–726.

Duplessy, J-C., L. Labeyrie, A. Juillet-Leclerc, F. Maitre, J. Duprat, and M. Sarnthein. 1991. Surface salinity reconstruction of the north Atlantic Ocean during the last glacial maximum. Oceanologica Acta **14:** 311–324.

Erez, J. 1978. Vital effect on the stable-isotope composition seen in foraminifera and coral skeletons. Nature **273:** 199–202.

———. 1982. Calcification rates, photosynthesis and light in planktonic foraminifera, p. 307–312. *In* P. Westbroek and E. D. Jong [eds.], Biomineralization and biological metal accumulation. D. Reidel Publishing Company.

———. 2003. The source of ions for biomineralization in foraminifera and their implications for paleoceanographic proxies. Rev. Mineral. Geochem. **54:** 115–149.

———, and B. Luz. 1982. Temperature control of oxygen isotope fractionation of cultured planktonic foraminifera. Nature **297:** 220–222.

———, and ———. 1983. Experimental paleotemperature equation for planktonic foraminifera. Geochim. Cosmochim. Acta **47:** 1025–1031.

Gast, R. J., and D. A. Caron. 2001. Photosymbiotic associations in planktonic foraminifera and radiolaria. Hydrobiologia **461:** 1–7.

Gastrich, M. D., and R. Bartha. 1988. Primary productivity in the planktonic foraminifer *Globigerinoides ruber* (D'Orbigny). J. Foraminifer Res. **18:** 137–142.

Hemleben, C., M. Spindler, and O. R. Anderson. 1989. Modern planktonic foraminifera. Springer-Verlag.

Humphrey, G. F. 1975. The photosynthesis : respiration ratio of some unicellular marine algae. J. Exp. Mar. Biol. Ecol. **18:** 111–119.

Iglesias-Prieto, R., J. Matta, W. Robins, and R. Trench. 1992. Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. Proc. Natl. Acad. Sci. USA **89:** 10302–10305.

Jørgensen, B. B., J. Erez, N. P. Revsbech, and Y. Cohen. 1985. Symbiotic photosynthesis in a planktonic foraminiferan, *Globigerinoides sacculifer* (Brady), studied with microelectrodes. Limnol. Oceanogr. **30:** 1253–1267.

Köhler-Rink, S., and M. Kühl. 2005. The chemical microenvironment of the symbiotic planktonic foraminifer *Orbulina universa*. Mar. Biol. Res. **1:** 68–78.

Kooijman, S. A. L. M. 2000. Dynamic energy and mass budgets in biological systems, 2nd ed. Cambridge Univ. Press.

Li, Y-H., and S. Gregory. 1974. Diffusion of ions in sea water and in deep-sea sediments. Geochim. Cosmochim. Acta **38:** 703–714.

Lombard, F., A. Sciandra, and G. Gorsky. 2005. Influence of body mass, food concentration, temperature and filtering activity on the oxygen uptake of the appendicularian *Oikopleura dioica*. Mar. Ecol. Prog. Ser. **301:** 149–158.

López-Urrutia, Á., E. San Martin, R. P. Harris, and I. Xabier. 2006. Scaling the metabolic balance of the oceans. Proc. Natl. Acad. Sci. USA **103:** 8739–8744.

Michaels, A. F., D. A. Caron, N. R. Swanberg, F. A. Howse, and C. M. Michaels. 1995. Planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda: Abundance, biomass and vertical flux. J. Plankton Res. **17:** 131–163.

Myklestad, S. M. 1995. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. Sci. Total Environ. **165:** 155–164.

Ortiz, J. D., A. C. Mix, W. Rugh, J. M. Watkins, and R. W. Collier. 1996. Deep-dwelling planktonic foraminifera of the northeastern Pacific Ocean reveal environmental control of oxygen and carbon isotopic disequilibria. Geochim. Cosmochim. Acta **60:** 4509–4523.

Poulet, S. A., and G. Ouellet. 1982. The role of amino acids in the chemosensory swarming and feeding of marine copepods. J. Plankton Res. **4:** 341–361.

Revsbech, N. P., and B. B. Jørgensen. 1986. Microelectrodes: Their use in microbial ecology. Adv. Microb. Ecol. **9:** 293–352.

Rink, S., M. Kühl, J. Bijma, and H. J. Spero. 1998. Microsensor studies of photosynthesis and respiration in the symbiotic foraminifer *Orbulina universa*. Mar. Biol. **131:** 583–595.

Robarts, R. D., and T. Zohary. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. NZ J. Mar. Freshw. Res. **21:** 391–399.

Ross, R. M. 1982. Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar. Biol. **68:** 1–13.

Schiebel, R. 2002. Planktic foraminiferal sedimentation and the marine calcite budget. Glob. Biogeochem. Cycles **16:** 1065, doi:10.1029/2001GB001459.

———, and C. Hemleben. 2005. Modern planktic foraminifera. Paläontol. Z. **79:** 135–148.

Spero, H. J. 1987. Symbiosis in the foraminifer *O. universa* and the isolation of its symbiotic dinoflagelates *Gymnodinium beei*. J. Phycol. **23:** 307–317.

———, and D. L. Angel. 1991. Planktonic sarcodines: Microhabitat for oceanic dinoflagellates. J. Phycol. **27:** 187–195.

———, and D. W. Lea. 1996. Experimental determination of stable isotope variability in *Globigerina bulloides*: Implications for paleoceanographic reconstruction. Mar. Micropaleontol. **28:** 231–246.

———, I. Lerche, and D. F. Williams. 1991. Opening the carbon isotope "vital effect" black box. 2. Quantitative model for interpreting foraminiferal carbon isotope data. Paleoceanography **6:** 639–655.

———, and S. L. Parker. 1985. Photosynthesis in the symbiotic planktonic foraminifer *Orbulina universa* and its potential contribution to oceanic productivity. J. Foraminifer Res. **15:** 273–281.

Uhle, M. E., S. A. Macko, H. J. Spero, M. H. Engel, and D. W. Lea. 1997. Sources of carbon and nitrogen in modern planktonic foraminifera: The role of algal symbionts as determined by bulk and compound specific stable isotopic analyses. Org. Geochem. **27:** 103–113.

Verity, P. G. 1985. Grazing, respiration, excretion and growth rates of tintinids. Limnol. Oceanogr. **30:** 1268–1282.

Vidal, J. 1980. Physioecology of zooplankton. III. Effects of phytoplankton concentration, temperature, and body size on the metabolic rate of *Calanus pacificus*. Mar. Biol. **56:** 195–202.

Waelbroeck, C., S. Mulitza, H. J. Spero, T. Dokken, T. Kiefer, and E. Cortijo. 2005. A global compilation of late Holocene planktonic foraminiferal $\delta^{18}O$: Relationship between surface water temperature and $\delta^{18}O$. Quat. Sci. Rev. **24:** 853–868.

Žarić, S., B. Donner, G. Fischer, S. Mulitza, and G. Wefer. 2005. Sensitivity of planktic foraminifera to sea surface temperature and export production as derived from sediment trap data. Mar. Micropaleontol. **55:** 75–105.

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