The Influence of Symbiont Photosynthesis on the δ^{18}O and δ^{13}C Values of Planktonic Foraminiferal Shell Calcite

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Abstract

The planktonic foraminifer, *Orbulina universa*, has been grown in the laboratory to measure the effect of symbiont photosynthetic activity on the incorporation of oxygen and carbon isotopes into shell calcite. Specimens were grown at $20\pm0.15°$C under four different light regimes and in darkness. Mass spectrometer analysis of gametogenic specimens showed that the δ^{18}O values of the various groups were similar: $\bar{x}\delta^{18}$O = -1.27$\pm$0.14°/oo. Thus, the photosynthetic activity of symbiotic algae does not affect the δ^{18}O value of calcite precipitated by *O. universa*.

The carbon isotope ratios of the shells were dependent on symbiont photosynthetic activity. δ^{13}C values ranged from +2.77°/oo at the brightest intensity to +2.05°/oo in low light and +0.45°/oo in total darkness. The mean diameter and shell weight were also correlated with light intensity. Comparisons of pre- and post-gametogenic specimens suggest that the δ^{13}C value of the shell is strongly influenced by physiological processes occurring during the final stage of calcification.

Keywords: carbon isotopes, foraminifera, *Orbulina universa*, oxygen isotopes, photosynthesis, symbiosis

1. Introduction

Planktonic foraminifera are an abundant group of marine protozoans whose fossil shells have provided an important link in the interpretation of the paleoecological and geological history of the oceans. Utilizing stable isotope analysis, researchers have produced reconstructions of paleoceanographic and paleoclimatic events from the $^{18}O/^{16}O$ and $^{13}C/^{12}C$ isotope ratios in the calcite of foraminiferal shells (Duplessy, 1978 for review). The interpretation of foraminiferal isotope data is based on the assumption that shell calcium carbonate is deposited in isotopic equilibrium with seawater, or is fractionated by constant amounts. However, studies of cultured benthic foraminifera and planktonic foraminifera from plankton tows have demonstrated that these assumptions are not valid for many species (van Donk, 1970; Shackleton et al., 1973; Fairbanks et al., 1980, 1982; Kahn, 1979; Vergnaud-Grazzini, 1976; Erez and Honjo, 1981; Williams et al., 1979). At present, the environmental parameters responsible for isotope disequilibrium are not completely understood.

A number of investigators have suggested that nonequilibrium isotope fractionation is caused by changes in the isotopic composition of the CO_2 available for calcification as a result of foraminiferal metabolism and photosynthetic activity of algae present in symbiont-bearing species (Shackleton et al., 1973; Williams et al., 1977; Shackleton and Vincent, 1978; Curry and Mathews, 1981; Erez and Honjo, 1981; Kahn and Williams, 1981; Fairbanks et al., 1982; Dunbar, 1983). Although the isotopic effect of symbiont photosynthetic activity has been examined in cultured benthic foraminifera (Williams et al., 1981; Zimmerman et al., 1983), the effect of symbiotic algae on the isotopic composition of planktonic foraminiferal shell calcite has not been assessed.

The present study examines the effect of symbiont photosynthetic activity on the isotopic composition of the shell of the planktonic foraminifer, *Orbulina universa*. This species is an ideal organism for such a study because its trochospiral stage can be collected in the field and be brought back to the laboratory where it secretes a final spherical chamber under controlled conditions. The final chamber makes up the majority of the total shell weight (Bé et al., 1973; Spero, 1986).

Calcification of the *O. universa* spherical chamber occurs in two stages. 'Pre-gametogenic' (pre-gam) calcification is characterized by the slow addition of calcite during the majority of the shell thickening period (Spero, 1986). Several hours prior to gametogenesis, however, a thick veneer of cal-

cite is added to the surface of the shell. This process, called 'gametogenic calcification', produces 13–28% of the shell mass over a period of several hours (Bé, 1980; Bé et al., 1983; Spero, 1986). Following gametogenic calcification and gametogenesis, the post-gametogenic (post-gam) shell is empty of cytoplasm. A detailed description of the life cycle and symbiotic association of *O. universa* has been described previously (Bé et al., 1983; Spero and Parker, 1985; Spero, 1987).

2. Materials and Methods

The techniques for collecting and maintaining *O. universa* in the laboratory were described by Spero and Parker (1985). Spherical and trochospiral *O. universa* were hand-collected by scuba divers from the surface waters of the Pacific Ocean, 2 km NNE of the Catalina Marine Science Center, Santa Catalina Island, CA. For the laboratory isotope experiments, trochospiral *O. universa* were transferred to acid-washed glass jars containing 100 ml of freshly filtered seawater, and then placed in a temperature bath at $20.00\pm0.15°$C. Illumination was provided by either GE F48 PG17 CW or GE F24 T12 CW-HO fluorescent bulbs, and each foraminifer was fed one one-day-old *Artemia* nauplius every other day. A number of *O. universa*, both trochospiral and spherical forms, were collected from seawater of ambient temperature, $20\pm1°$C, and were immediately washed and dried for later isotopic analysis.

Pre- and post-gametogenic *O. universa* shells for isotopic analysis were collected from culture jars, rinsed with distilled water and air dried. Pooled foraminifera (0.15–0.35 mg) were heated *in vacuo* for 1 hr at 425°C, then reacted *in vacuo* with concentrated phosphoric acid at 50°C. The isotopic difference between the derived sample CO_2 and the Pee Dee belemnite (PDB) standard was determined with a Finnegan MAT 250 mass spectrometer. The isotopic ratios are reported as δ values where

$$\delta = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] \times 10^3 \;\;°/_{oo}$$

and R is the isotope ratio $^{18}O/^{16}O$ or $^{13}C/^{12}C$. All isotopic values are presented relative to PDB.

All specimens grown in the laboratory had formed a spherical chamber and had undergone gametogenesis (post-gam) except one high-light group which was collected prior to gametogenesis (pre-gam). The $\delta^{18}O$ and $\delta^{13}C$

values presented reflect the isotopic composition of spherical chamber calcite secreted in the laboratory. These values have been calculated using a mass-balance equation that took into account the presence of the internal trochospiral shell which formed in the field.

Equilibrium values for calcite at 20°C were calculated (Epstein et al., 1953; Emrich et al., 1970) using measured $\delta^{18}O$ values of culture water collected randomly during the experiments ($\delta^{18}O_{H_2O} = -0.88 \pm 0.08°/oo$, $n = 8$), and $\delta^{13}C$ values for surface waters from the Southern California Borderland ($+2.08 \pm 0.12°/oo$, $n = 6$) (Grossman, 1984). $\delta^{13}C$ values for the culture water are not available. Therefore, during data analysis it was assumed that the $\delta^{13}C$ value of the total CO_2 in the culture vessels did not change significanlty during the 6–7 days (Spero, 1986) of each experiment. The following equation was used to calculate the $\delta^{13}C$ value of the culture water under different light intensities to test this assumption:

$$(\delta^{13}C \text{ final}) \ ([CO_2] + K) = (\delta^{13}C \text{ initial})([CO_2]) + (\delta^{13}C \text{ Foraminifer respiration})(R_1) + (\delta^{13}C \text{ Artemia respiration})(R_2) - (\delta^{13}C \text{ Symbiont photosynthesis})(R_3) - (\delta^{13}C \text{ Calcite removed})(R_4)$$

where $[CO_2]$ is the initial CO_2 concentration in 100 ml water, R_i is the amount of CO_2 added or removed from the system and $K = \sum_{4}^{i=1} R_i$. The values used in the solution of this equation are presented in Table 1. The results of these calculations indicate that in the extreme case, such as maximum photosynthetic rates or respiration only (dark group), the $\delta^{13}C$ value of the culture water only decreased $0.2°/oo$. The validity of this assumption is also supported by the observation that the $\delta^{13}C$ value for calcite secreted in the laboratory by the pre-gam high light group is identical to that precipitated by specimens in the field (Table 2).

3. Results

The $\delta^{18}O$ values of calcite in post-gametogenic shells grown at the same temperature, but under four different light intensities and in the dark, are similar, averaging $-1.27 \pm 0.14°/oo$ (Table 2). These light groups represent different levels of symbiont photosynthetic activity (Spero and Parker, 1985). The lack of a correlation between $\delta^{18}O$ values and light intensity strongly suggests that the photosynthetic activity of the symbiotic algae does not affect the $\delta^{18}O$ value of calcite precipitated by O. universa. The mean $\delta^{18}O$ value

Table 1. Equation values used to calculate the final $\delta^{13}C$ value of the experimental culture water. For the purpose of this calculation, a value of $-20°/°°$ is used to represent the $\delta^{13}C$ value of respired CO_2 and HCO_3^- removed by photosynthesis.

Equation term	$\delta^{13}C$ value $°/°°$	$[CO_2]$ or rate (R_1)	Time	Reference
$\delta^{13}C$ initial	+2.08	196 μMol CO_2/100 ml, $[CO_2]$		Grossman (1984) Spero (unpub. data)
Foraminiferal respiration	−20	2.7×10^{-3} μMol CO_2/hr, (R_1)	72 hr[a]	Jørgensen et al. (1985) Spero (1986)
Artemia respiration	−20	0.150 μMol CO_2/hr, (R_2)	9 hr[b]	Gilchrist (1956) Spindler et al. (1984)
Symbiont photosynthesis	−20	5.6×10^{-4} μMol C/hr[c], (R_3)	72 hr[d]	Spero and Parker (1985) Spero (1986)
Calcite removed	+0.45 +2.77	0.138 μMol C (Dark), (R_4) 0.295 μMol C (350 μE m^{-2} s^{-1})		Present study Present study

a — 6–12 hr dark periods

b — 3 feedings, digestion requires 3 hr

c — photosynthetic rate for 3,300 symbionts

d — 6–12 hr light periods

Table 2. Oxygen and carbon isotope values of post- and pre-gametogenic *Orbulina universa* from the laboratory and plankton. See text for equilibrium calculations.

	Light intensity (μE m^{-2} s^{-1})	Specimens Analyzed	δ^{18}O (per mil)	δ^{13}C (per mil)
A.	Laboratory:			
	Dark (post-gam)	11	−0.97	+0.51
		8	−1.29	+0.39
	65 (post-gam)	14	−1.14	+2.05
	130 (post-gam)	10	−1.39	+2.35
		12	−1.34	+2.54
	240 (post-gam)	9	−1.25	+2.65
		11	−1.13	+2.18
	350 (post-gam)	7	−1.40	+2.73
		14	−1.32	+2.67
		5	−1.42	+2.91
	350 (pre-gam)	12	−1.84	+2.00
B.	Plankton:			
	Spherical form	17	−2.29	+1.99
	Trochospiral form	27	−1.93	+1.94
C.	Equilibrium values at 20°C		−1.69	+3.93

is 0.42°/oo more positive than the calculated equilibrium value of −1.69°/oo. In contrast the δ^{18}O values of pre-gametogenic shells collected in the field, −2.11±0.25°/oo and grown in the laboratory at 350 μE m^{-2} s^{-1}, −1.84°/oo, were both more negative than the equilibrium value and significantly depleted in ^{18}O relative to the post-gam shells (Table 2).

In contrast to the oxygen isotope ratios, the carbon isotope ratios of post-gam *O. universa* were dependent on the photosynthetic activity of the symbiotic algae (Table 2, Fig. 1). The mean δ^{13}C values of illuminated specimens increased 0.72°/oo, from +2.05 to +2.77°/oo, in specimens grown between the lowest and highest light intensities. Specimens grown in darkness secreted calcite with a mean δ^{13}C value of +0.45±0.08°/oo, which was 1.60°/oo more negative than the value for specimens grown under the lowest light intensity. The δ^{13}C value of calcite from pre-gam *O. universa* grown under the highest light intensity, +2.00°/oo, was equal to that of *O. universa* collected from the
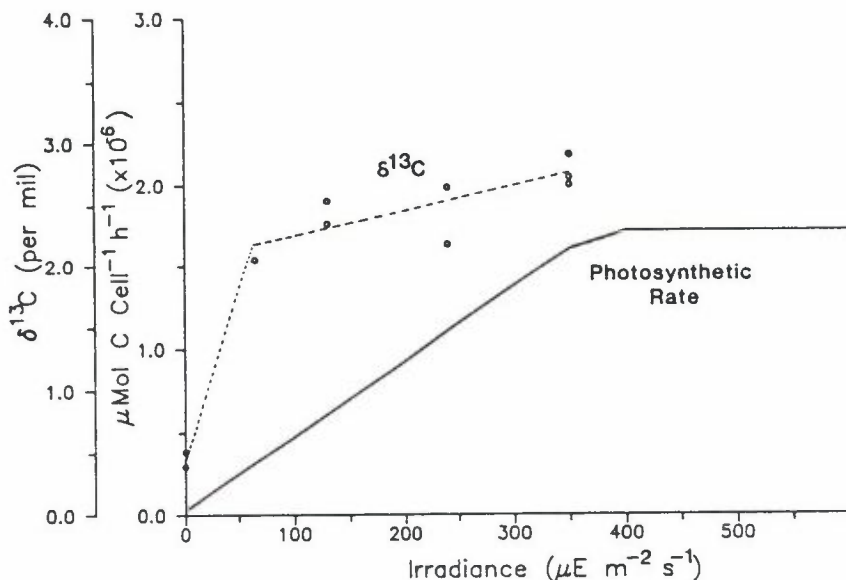
Figure 1. δ^{13}C value vs. irradiance level for *Orbulina universa* maintained in the laboratory. These data are plotted with a photosynthesis/irradiance curve previously determined for the *O. universa* symbiotic association (Spero and Parker, 1985).

plankton, $+1.97 \pm 0.04°/\infty$. However, these values are $0.77°/\infty$ more negative than the mean value of post-gam shells grown under the same high-light conditions. Both pre- and post-gametogenic shells were depleted in ^{13}C relative to the calculated equilibrium δ^{13}C value of $+3.93°/\infty$.

The final sphere diameter and weight of laboratory-grown *O. universa* are also correlated with irradiance levels. Spherical chamber diameters increased from a mean of 437 μm for specimens grown in the dark, to a mean of 520 μm for specimens maintained at light intensities greater than 130 μE m^{-2} s^{-1}. Specimens grown at 65 μE m^{-2} s^{-1} had an intermediate sphere diameter (Fig. 2a).

The foraminiferal shell weight followed the same trend as the sphere diameter (Fig. 2b). In both cases, maximum shell size and weight were attained at light intensities significantly below photosynthetic rate saturation levels (Spero and Parker, 1985).
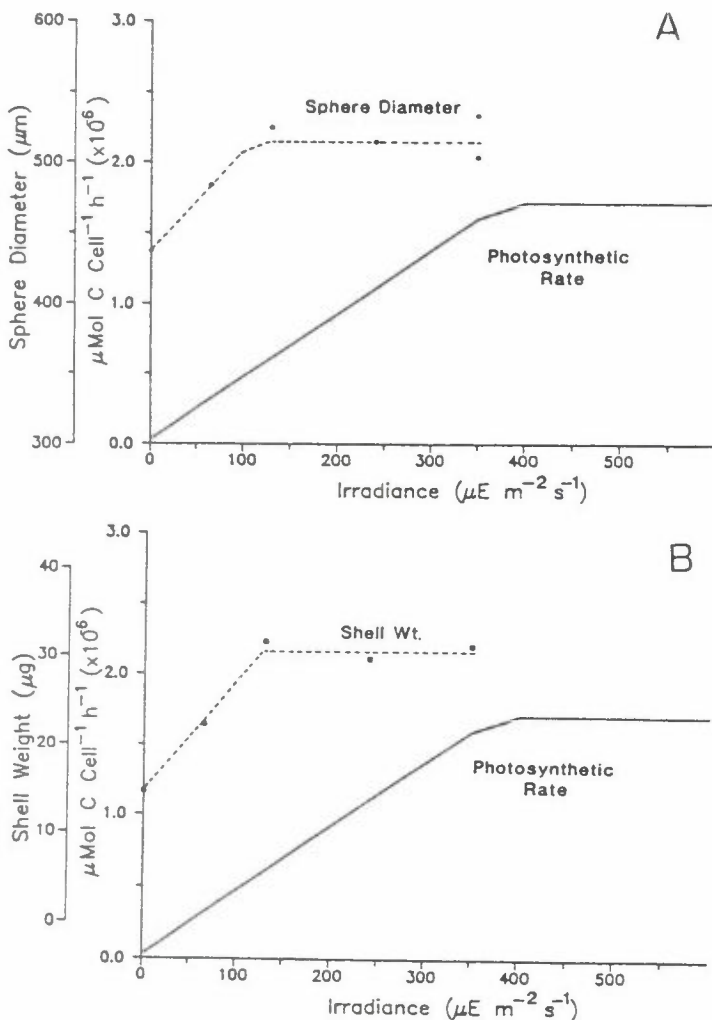
Figure 2. (a) *O. universa* sphere diameter and (b) shell weight as a function of irradiance
for specimens grown in the laboratory. The P/I curve is the same as Fig. 1.

4.   Discussion

Pioneering studies by Urey (1947) and Epstein et al. (1951, 1953) initially
demonstrated that oxygen isotope fractionation during calcium carbonate
precipitation could be used as a paleothermometer. These researchers rec-
ognized that the oxygen isotope ratio may be affected by the metabolic ac-
tivity of the organisms secreting the calcium carbonate. The results of this
study demonstrate that symbiont photosynthetic activity does not affect the
$^{18}O/^{16}O$ ratio of the *Orbulina universa* post-gametogenic shell, since the

$\delta^{18}O$ values of the shells do not vary systematically with changing symbiont photosynthetic rate. Thus, these experiments remove this metabolic process as a potential explanation for oxygen isotope disequilibrium in *O. universa*.

However, the observation that post-gametogenic specimens from the high-light (350 μE m^{-2} s^{-1}) group were significantly enriched in ^{18}O relative to high-light pre-gam and field plankton specimens is intriguing since all were growing at the same temperature. A similar ^{18}O enrichment has been reported in post-gam foraminiferal shells collected from sediment traps and cores relative to living pre-gametogenic specimens in surface waters (Erez and Honjo, 1981; Bé, 1980; Duplessy et al., 1981). This ^{18}O enrichment was attributed to the addition of gametogenic calcite at cold water temperatures (i.e. depths of 300–500 m). However, Bé et al. (1985) recently suggested that gamete release in foraminifera occurs before the shells sink below the euphotic zone, in which case gametogenic calcification would occur in shallow warmer water. Although the mechanism is not understood, the laboratory results presented here suggest that much of the difference in oxygen isotope ratios between pre- and post-gametogenic *O. universal* shell carbonate can be explained without invoking depth-related temperature effects as the cause.

The effect of symbiont photosynthetic activity on the $\delta^{13}C$ values of biogenically produced $CaCO_3$ has been studied in corals as well as benthic foraminifera. The results of these studies indicate that photosynthetic activity may either deplete (Erez, 1978; Land et al., 1977; Williams et al., 1981b; Zimmerman et al., 1983) or enrich (Cummings and McCarty, 1982; Goreau, 1977; Weber, 1974; Weber and Woodhead, 1970) the carbonate in ^{13}C, depending on the symbiotic association. In *Orbulina universa*, increased symbiont photosynthetic activity resulted in a ^{13}C enrichment in post-gam shell calcite. However, this enrichment was not observed in the high-light pre-gam group or specimens from the plankton, whose $\delta^{13}C$ values were close to the value for ambient total CO_2 (Grossman, 1984). (The pre-gam high-light group and plankton specimens are considered together because both grew at light levels that were close to or greater than symbiont photosynthetic rate saturation intensities (Spero and Parker, 1985)). These observations can be explained by the following model.

One important difference between the pre- and post-gametogenic groups is that the former lacks a gametogenic calcite layer. Thus, their isotopic differences should result from processes occurring during the gametogenic calcification stage. Important factors in this regard are symbiont location and chamber thickening rate during pre-gametogenic and gametogenic cal-
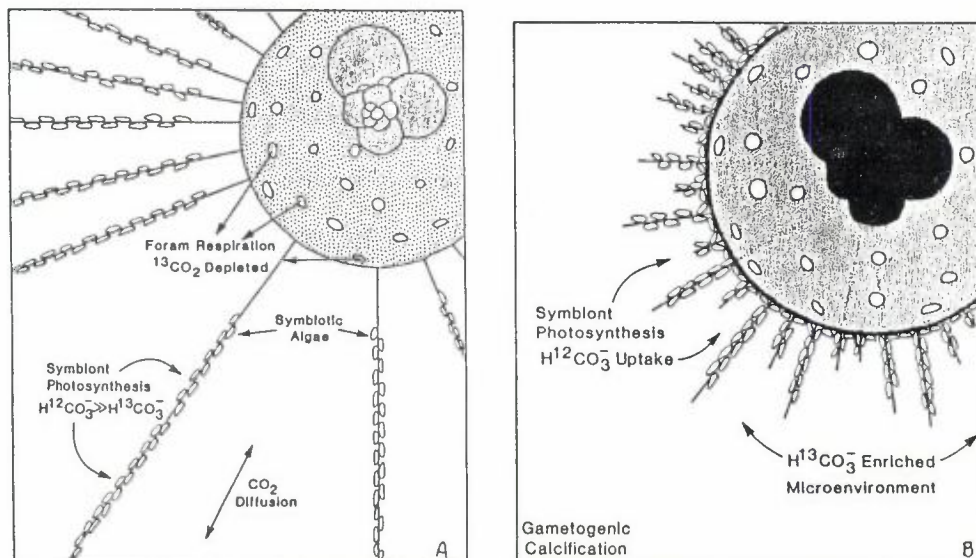
Figure 3a. Pre-gametogenic *Orbulina universa* with symbionts dispersed on spines. ^{13}C-depleted CO_2 is respired by the foraminifera while $^{12}CO_2$ is taken up by the symbiotic algae during photosynthesis. Diffusion during this period of slow calcite addition results in shell calcite with isotope values close to ambient CO_2.

Figure 3b. During gametogenic calcification, the isotopic composition of CO_2 available for calcification is controlled by photosynthesis and respiration. High photosynthetic rates result in ^{13}C enriched shells, low photosynthetic rates or dark conditions result in ^{13}C depleted shells.

cification. In pre-gam specimens, shell thickening occurs during the day as well as at night, whereas during gametogenic calcification, it occurs primarily in the late afternoon (Spero, 1986). During pre-gam calcification (Fig. 3a), the symbiotic algae lie on the surface of the spines during the day and reside within the shell at night. During gametogenic calcification, however, the symbiotic algae are adjacent to the rapidly thickening sphere because the foraminiferal spines have been resorbed (Bé, 1980) (Fig. 3b).

The δ^{13}C value of CO_2 available for calcification is controlled by gas diffusion rates and two biological processes. Respiration by the foraminifer and its symbiotic algae release CO_2 that is depleted in ^{13}C relative to the ambient CO_2 pool (Park and Epstein, 1961; DeNiro and Epstein, 1978). In contrast, photosynthesis by the symbiotic algae increases the ^{13}C content of the CO_2

pool, since $^{12}CO_2$ is utilized preferentially during photosynthesis (Park and Epstein, 1961). During pre-gametogenic calcification, a slow chamber thickening rate (Spero, 1986) coupled with a high gas diffusion rate through the spine matrix (Jørgenson et al., 1985) is responsible for calcite being deposited with a $\delta^{13}C$ value little affected by respiration or symbiont photosynthetic activity (Fig. 3a). During gametogenic calcification, the accumulation of photosynthesizing symbionts on the shell surface would create a microenvironment in which the carbon isotopic composition of available HCO_3^- was controlled by respiration and the photosynthetic rate of the symbiotic algae rather than by diffusion (Fig. 3b). As light intensity decreased, the photosynthetic rate of the symbiotic algae decreased proportionately (Spero and Parker, 1985). Thus, the trend towards more negative shell $\delta^{13}C$ values at lower light intensities (Fig. 1) can be explained by the increased influence of respired CO_2 on the $\delta^{13}C$ value of the CO_2 pool available for calcification (Goreau, 1977; Weber and Woodhead, 1970; Cummings and McCarty, 1982).

At an irradiance level between the lowest light intensity and dark group, the isotopic effect of respired CO_2 dominates the microenvironment around the calcifying shell. Regression analysis of the carbon isotope values from the illuminated groups yields the relationship:

$$\delta^{13}C = 1.99 \times 10^{-3}I + 2.05 \ (r = 0.77)$$

where δ and I are the $\delta^{13}C$ value and irradiance level respectively. The light intensity at which the $\delta^{13}C$ value of the shell equals the estimated ambient CO_2 value of $+2.08°/\circ\circ$ (Grossman, 1984), is 15 $\mu E \ m^{-2} \ s^{-1}$. This irradiance level is reasonably close to the compensating light intensity of 30 $\mu E \ m^{-2} \ s^{-1}$ recently determined for the symbiotic foraminifera, *Globigerinoides sacculifer* (Jørgensen et al., 1985). These results, while preliminary, could suggest that the large ^{13}C depletion observed in shells from the dark group may begin once the compensating light intensity has been passed. Experiments are in progress to resolve this question.

The data presented in Fig. 2 demonstrates that the final size of the *O. universa* test is correlated with symbiont photosynthetic rate. Maximum shell dimensions were observed at a non-saturating light intensity of 130 $\mu E \ m^{-2} \ s^{-1}$, although the maximum size could have been attained at a slightly lower light level. Although light-enhanced calcification has been documented in a number of symbiotic associations including foraminifera (Crossland and

Barnes, 1974; Duguay, 1983; Goreau, 1959; Vandermeulen and Muscatine, 1974), differences in calcification rate may not be responsible for the differences in test size observed here.

Unlike most planktonic foraminifera that reach their final size through the continuous addition of chambers, the final size of *O. universa* is effectively determined at the time the sphere forms. Following the initial deposition of calcite onto the organic matrix secreted by the foraminifera (Spero, 1986), the shell dimensions can only increase through wall thickening. Thus, the sphere diameter is a function of the physiological condition of the foraminifera at the time of sphere formation.

These experimental results suggest that symbiont photosynthesis enhances the amount of cytoplasm/organic matrix that the foraminifera initially secretes. Based on these observations, one would predict that trochospiral *O. universa* growing at depths with light intensities greater than 130 $\mu E\ m^{-2}\ s^{-1}$ should produce spherical chambers of maximum size while specimens at deeper depths should produce smaller spherical chambers.

Correlations between *O. universa* sphere diameter and shell $\delta^{13}C$ values have been reported by several investigators from fossil material (Berger et al., 1978; Weiner, 1975; Williams et al., 1981a). These studies showed that larger diameter spheres were enriched in ^{13}C relative to smaller shells. These observations are consistent with the results reported in this study. The final size and $\delta^{13}C$ values of *Orbulina universa* represent an integration of a number of biological and environmental parameters including temperature, salinity, ambient light intensity, food availability, respiration, symbiont photosynthesis and the $\delta^{13}C$ value of ambient CO_2. It is clear that the photosynthetic activity of the symbiotic algae play a major role in controlling both.

Acknowledgements

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