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Microsensor studies of photosynthesis and respiration in the symbiotic foraminifer *Orbulina universa*

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Abstract Oxygen and pH microelectrodes were used to investigate the microenvironment of the planktonic foraminifer *Orbulina universa* and its dinoflagellate endosymbionts. A diffusive boundary layer surrounds the foraminiferal shell and limits the O_2 and proton transport from the shell to the ambient seawater and vice versa. Due to symbiont photosynthesis, high O_2 concentrations of up to 206% air saturation and a pH of up to 8.8, i.e. 0.5 pH units above ambient seawater, were measured at the shell surface of the foraminifer at saturating irradiances. The respiration of the host–symbiont system in darkness decreased the O_2 concentration at the shell surface to $<70\%$ of the oxygen content in the surrounding air-saturated water. The pH at the shell surface dropped to 7.9 in darkness. We measured a mean gross photosynthetic rate of 8.5 ± 4.0 nmol O_2 h^{-1} foraminifer^{-1}. The net photosynthesis averaged 5.3 ± 2.7 nmol O_2 h^{-1}. In the light, the calculated respiration rates reached 3.9 ± 1.9 nmol O_2 h^{-1}, whereas the dark respiration rates were significantly lower (1.7 ± 0.7 nmol O_2 h^{-1}). Experimental light–dark cycles demonstrated a very dynamic response of the symbionts to changing light conditions. Gross photosynthesis versus scalar irradiance curves (P vs E_o curves) showed light saturation irradiances (E_k) of 75 and 137 μmol photons m^{-2} s^{-1} in two *O. universa* specimens, respectively. No inhibition of photosynthesis was observed at irradiance levels up to 700 μmol photons m^{-2} s^{-1}. The light compensation point of the symbiotic association was 50 μmol photons m^{-2} s^{-1}. Radial profile measurements of scalar irradiance (E_o) inside the foraminifera showed a slight increase at the shell surface up to 105% of the incident irradiance (E_d).

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Introduction

Planktonic symbiont-bearing foraminifera often occur in oligotrophic ocean waters. Probably due to their close relationship with autotrophic dinoflagellates, they can survive in nutrient-limited environments. Symbiont-bearing foraminifera populate the euphotic zone, where the symbionts are exposed to light levels sufficient for photosynthesis. It has been suggested that the zooxanthellae live well-protected in the cytoplasm of the host where they benefit from the respired CO_2 as well as from nitrogen and phosphorus from prey digested by the foraminifer (Bé 1977; Jørgensen et al. 1985; Gastrich and Bartha 1988). The density of endosymbionts can reach a mean of 3300 cells per foraminifer, and specific photosynthetic rates of 1.72 pmol C symbiont^{-1} h^{-1} were measured at saturating irradiances (Spero and Parker 1985). The importance of the endosymbionts for the host was demonstrated in experiments, where the symbionts were treated with the photosynthetic inhibitor DCMU [3-(3,4-dichlorophenyl)-1,1-dimethylurea]. Bé et al. (1982) thus found significantly shorter survival times, reduced shell growth rates, and a smaller final shell size after inhibition of zooxanthellae photosynthesis.

Spinose planktonic foraminifera have a perforate calcareous shell with thin spines. The spines can reach a length of several millimeters and enlarge the effective surface area of the foraminifera, thereby increasing the chance of capturing prey with its sticky rhizopodial network (Bé 1977). Due to the enormous productivity of foraminiferal shells large parts of the ocean floor are covered with them and constitute the so-called "globigerina ooze". Because the geochemical composition, i.e. the stable carbon and oxygen isotope composition, of

planktonic foraminiferal shells can be used for paleoenvironmental reconstructions of the last 120×10^6 years of the world's oceans, these organisms have become a major tool in geology to reconstruct the productivity of past oceans. However, photosynthesis of endosymbionts can affect the isotopic composition of the foraminiferal shells due to the higher affinity of the CO_2 fixing enzyme for $^{12}CO_2$ (see e.g. Spero and de Niro 1987).

Symbiotic associations of planktonic spinose foraminifera with microalgae have been reported for at least seven species. The predominant algal symbionts are coccoid dinoflagellates (Hemleben et al. 1989). They are found in the species *Orbulina universa*, *Globigerinoides sacculifer*, *G. ruber* and *G. conglobatus* (Spindler and Hemleben 1980; Hemleben and Spindler 1983; Spero 1987). The endosymbiont of *O. universa*, an opportunistic species from the temperate to tropical provinces (Bé 1977), is the dinoflagellate *Gymnodinium béii*. The foraminifera *Globigerinella aequilateralis*, *Globigerina cristata* and *G. falconensis* host symbiotic chrysophycophytes (Spindler and Hemleben 1980; Gastrich 1987; Faber et al. 1988). All symbionts exhibit a diurnal migration from the shell interior to the distal parts of the foraminiferal spines in the light. Spero (1987) suggested that the migration also involves a daily endo-/exocytotic cycle.

Oxygen and pH microelectrodes have already been used to study symbiotic associations, such as the foraminifer *Globigerinoides sacculifer* and the hermatypic corals, *Favia* sp. and *Acropora* sp. (Jørgensen et al. 1985; Kühl et al. 1995). Microsensor techniques proved to be useful tools for measuring the processes of photosynthesis and respiration with a high spatial and temporal resolution in these symbiotic associations (Revsbech and Jørgensen 1986). The light–dark shift technique (Revsbech et al. 1981; Revsbech and Jørgensen 1983) measures gross photosynthetic rates independent of the respiration process, and light and dark respiration rates in symbiont–host systems can be assessed independently. Due to their small tip diameter, microsensors can be used without any destruction of the organism, and several measurements in one specimen, e.g. under changing light or temperature conditions, are possible.

Photosynthesis in planktonic symbiotic foraminifera has previously been investigated with two different techniques. Jørgensen et al. (1985) used O_2 microsensors to measure the gross and net photosynthetic rates of *Globigerinoides sacculifer* (Jørgensen et al. 1985). Radio tracer ^{14}C methods have been used to estimate the cell-specific carbon uptake of symbionts of two different species (Spero and Parker 1985; Gastrich and Bartha 1988). It was estimated that a single *Orbulina universa* specimen would contribute approximately 0.2% of the fixed carbon in 1 m^3 of seawater (Spero and Parker 1985). The foraminifer–algal association has been characterized as a "hot spot" of productivity in oligotrophic seawater.

Symbiont-bearing planktonic foraminifera are cosmopolitan calcifying organisms, but there are still a lot of open questions about their biology and the physiological and biochemical interactions of the host–symbiont association. Several hypotheses about their mutual benefit, e.g. the nutritional relationship, the transport of metabolic gases, and the calcification process, are discussed in the literature (e.g. Erez 1983; Jørgensen et al. 1985; Hemleben et al. 1989; Lea et al. 1995). Although the photosynthetic rates of the symbionts of *Orbulina universa* have been studied (Spero and Parker 1985), the microenvironment of this foraminifer and its importance for host–symbiont interaction are still unknown. We used O_2 and pH microsensors and a fiber-optic scalar irradiance microprobe to investigate the physico-chemical microenvironment of this symbiotic system. Our study demonstrates the influence of changing light conditions on the foraminiferal–algal symbiosis and a close coupling of photosynthesis and respiration in *O. universa*.

Materials and methods

Collection

Adult *Orbulina universa* with sphere diameters ranging between 290 and 550 μm (Fig. 1A) were hand-collected by SCUBA divers from the surface waters of the Southern California Bight, near Santa Catalina Island, California between July and August 1995. Individual specimens were sampled in glass jars at a depth of 5 to 10 m (Fig. 1B). During the collection period the mean water temperature was 19.2 °C. Light measurements at the collection site showed an average downwelling irradiance of 2100 μmol photons m^{-2} s^{-1} at the water surface in full sunlight (S. Anderson, personal communication). After sampling in the morning hours (09:00 to 11:00 hrs), individual foraminifera were kept in separate glass vessels at 22 °C and ~80 μmol photons m^{-2} s^{-1} without feeding. Experiments were conducted within less than 24 h after collection, in the laboratory of the Wrigley Institute for Environmental Studies (WIES).

Experimental setup

For microsensor measurements, a specimen was placed on a nylon mesh in a small Plexiglas chamber (10 ml volume) with filtered seawater (Figs. 1C, 2A). The microsensors were manually positioned with a micromanipulator (Märtzhäuser, Germany). The angle of inclination of the microsensor was 30° relative to the vertically incident light. Positioning of the microsensor tip relative to the foraminiferal shell surface was adjusted under a dissection microscope. Measurements were performed at room temperature (20 to 22 °C) in a dark room under defined light conditions. The light source was a fiber optic halogen lamp (Schott KL-1500) equipped with a collimating lens, and incident irradiance (0 to 1000 μmol photons m^{-2} s^{-1}) was adjusted by neutral density filters (Oriel). Downwelling quantum irradiance (400 to 700 nm) was measured with a quantum irradiance meter (LiCor, LI 189). The light was controlled by a mechanical shutter, installed in the light path of the halogen lamp, without influencing the light quality. The specimens were allowed to adapt to conditions in the measuring chamber for 0.5 to 1 h, and the experiments were started when the symbionts were distributed in a concentric halo around the shell (Figs. 1A, 2B).

Oxygen microelectrodes

Photosynthetic rates and radial concentration profiles of O_2 from the ambient seawater to the shell surface were measured with a Clark-type O_2 microelectrode with a guard cathode connected to a

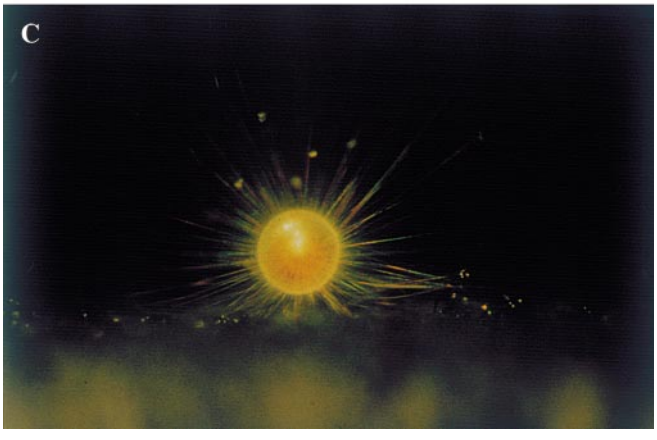

Fig. 1A Adult *Orbulina universa* with dinoflagellate symbionts surrounding the shell. Juvenile trochospiral shells are visible in the center of the transparent spherical chamber (diameter of the spherical shell was ~500 µm) (photo: T. Mashiotta). **B** Collection of planktonic foraminifera by SCUBA diving. Individual specimens are sampled in glass jars (photo: E. Meesters). **C** *O. universa* sticking to the nylon mesh inside the measuring chamber

picoammeter and a strip chart recorder (Revsbech 1989). The microelectrodes had an outer tip diameter of 5 to 12 µm, a 90% response time of < 0.4 to 1.8 s and a stirring sensitivity of 0 to 2%. Linear calibration of the electrode signal was done at room temperature in air-saturated seawater and in O_2-free seawater (reduced with sodium dithionite). The O_2 concentration of the air-saturated seawater was determined by Winkler-titration (Grasshoff et al. 1983).

pH microelectrodes

pH was measured with glass pH microelectrodes (Revsbech et al. 1983) in combination with a calomel reference electrode (Radiometer, Denmark), both connected to a high impedance mV meter. The pH electrodes had a pH-sensitive tip of 12 to 25 µm diameter and of 80 to 150 µm length. They were calibrated in NBS buffers (Mettler Toledo, pH 4, 7 and 9) at room temperature.

Scalar irradiance measurements

A fiber optic microprobe (Lassen et al. 1992) connected to a PAR meter (Kühl et al. 1997) was used for measuring radial profiles of quantum scalar irradiance (400 to 700 nm) from the surroundings towards the shell of *Orbulina universa*. The diameter of the scalar irradiance microprobe tip was < 100 µm. Linear calibration of the fiber optic scalar irradiance microprobe was done in darkness and in a collimating light field at a known downwelling irradiance over a black light trap (Kühl et al. 1997). Downwelling irradiance was measured with a quantum irradiance meter (LiCor, LI 189). All light measurements in this paper refer to visible light (400 to 700 nm), i.e. the available radiation for oxygenic photosynthesis.

Photosynthesis measurements

Oxygen microelectrodes with a fast response time (< 0.5 s) were used for measurements of gross and net photosynthesis. Gross photosynthesis was estimated with the light–dark shift technique (Revsbech et al. 1981; Revsbech and Jørgensen 1983) by measuring the initial decrease of O_2 in the first seconds after darkening. The O_2 depletion is equal to the photosynthetic O_2 production during the previous light period (more details in Revsbech and Jørgensen 1983; Glud et al. 1992; Kühl et al. 1996). Gross photosynthetic rates, $P(r)$, were measured inside the symbiotic swarm at 50-µm intervals starting at the shell surface. Radial profiles of photosynthetic activity were used to calculate the total gross photosynthetic production assuming that the symbionts surround the shell in spherical symmetry (Fig. 2B). The total gross photosynthetic rate, P_{total} (nmol O_2 h^{-1} foraminifer^{-1}), was calculated as the sum of the photosynthetic rates, measured per volume of each concentric segment in the symbiotic halo (Jørgensen et al. 1985):

$$\sum_i P(r_i)\left\{\frac{4}{3}\pi\left[(r_i + r_{i-1})^3 - (r_{i-1})^3\right]\right\} , \quad (1)$$

where $i = 0,\ 50,\ 100 \ldots$ µm.

Net photosynthesis and respiration rates were calculated from the measured steady-state O_2 profiles in light and in darkness, respectively. The area-integrated O_2 flux, Q_t (nmol O_2 h^{-1} foraminifer^{-1}), was calculated by the radial gradient, dC/dr, the molecular O_2 diffusion coefficient in seawater, D, and the surface area of the sphere, $4\pi r^2$ (Jørgensen et al. 1985; Ploug et al. 1997):

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

Respiration measurements

The respiration of the symbiont–host system in the light was calculated as the difference between total gross photosynthesis and net photosynthesis (Jørgensen et al. 1985). In the dark, the O_2 flux to the sphere is determined by the combined respiration rate of the foraminifer and the symbionts, and dark respiration was calculated from the O_2 profiles measured in the dark by using Eq. 2.

P versus E_o curves

Gross photosynthetic rates (nmol O_2 cm^{-3} s^{-1}) were measured with the light–dark shift method at the shell surface inside the symbiont

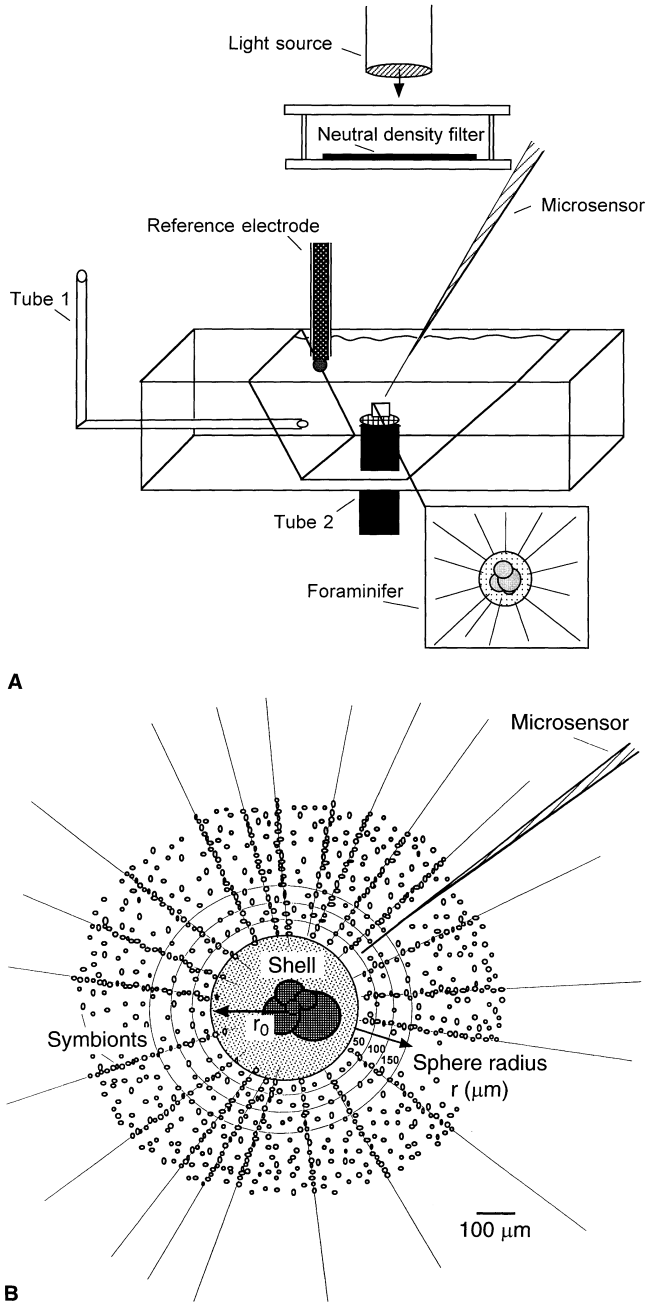

Fig. 2 A Schematic drawing of the measuring chamber (10 ml volume) with a single foraminifer placed on a nylon mesh. Microsensor positioning was done with a micromanipulator, and the incident light was adjusted by neutral density filters. **B** *Orbulina universa*. Schematic drawing of an adult. Concentric spheres of 50 μm thickness indicate the microsensor positioning for the photosynthesis measurements (r_o radius of the spherical shell; r distance to the shell)

swarm as a function of increasing scalar irradiance. *Orbulina universa* was exposed to each irradiance level for 15 to 30 min before the measurements started. Light intensities (0 to 700 μmol photons m^{-2} s^{-1}) were adjusted with neutral density filters (Oriel). An exponential function: $P = P_m [1 - \exp(-\alpha E_o/P_m)]$ (Webb et al. 1974) was fitted to the P versus E_o data measured at the shell surface, where P_m is the light-saturated photosynthetic rate and α the initial slope of the P versus E_o curve at subsaturating scalar irradiance (Geider and Osborne 1992).

Results

Microenvironment of the symbiotic *Orbulina universa*

The zooxanthellae of *O. universa* showed a diurnal migration pattern. During the day, the dinoflagellates spread out on the rhizopodial network between the spines, while at night they were located inside the shells. During our experiments the symbionts formed a 200 to 400 μm thick concentric halo surrounding the spherical shell of the foraminifer (Figs. 1A, 2B).

Around the shell, a diffusive boundary layer (DBL) was established that limited the solute transport between the surrounding seawater and the foraminifer. In the light, the O_2 concentration started to increase in the distal part of the spines, and very high concentrations were measured towards the shell (Figs. 3A, 7A). Profiles of gross photosynthesis inside the symbiont swarm showed highest rates at the foraminiferal shell, where a maximum gross photosynthesis up to 13.7 nmol O_2 cm^{-3} s^{-1} was measured (Fig. 3C). The photosynthetic activity of the symbionts and the presence of a DBL thus created a microenvironment of high pH and high O_2 concentrations around the shell of *Orbulina universa* as compared to the ambient seawater (Fig. 3A, B). At the shell surface, we measured O_2 supersaturation up to 206% of air saturation at high irradiances (Fig. 3A). During measurements of the dark profiles the symbionts moved into the shell. In darkness, the respiration of the foraminifer and the symbionts decreased the O_2 concentration to $< 80\%$ air saturation at the shell surface of this specimen (Fig. 3A). Due to photosynthetic CO_2 fixation in the light, pH increased to up to 8.8 at the shell surface under saturating light conditions. In darkness, pH was lowered down to pH 7.9 at the shell surface as a result of CO_2 release during respiration of the host and its symbionts (Fig. 3B). The average rate of gross photosynthesis per adult *O. universa* was 8.9 nmol O_2 h^{-1} $foraminifer^{-1}$ (Table 1), but rates of 13.9 nmol O_2 h^{-1} $foraminifer^{-1}$ at saturating irradiance (782 μmol photons m^{-2} s^{-1}) were found in one specimen (No. I). The net photosynthetic rate of the same specimen reached 8.7 nmol O_2 h^{-1}.

Radial O_2 and pH profiles measured at different positions in the foraminifer showed similar concentration gradients (data not shown) supporting our assumption of a radial symmetry of solute concentration and diffusion around the foraminiferal shell under stagnant conditions. Radial profiles of scalar irradiance from the ambient seawater to the shell showed values up to 105% of the incident irradiance (Fig. 3C). This increase probably resulted from light scattering and reflection within the spines and off the calcite shell surface.

Oxygen, pH and photosynthesis at the shell surface

Experimental light–dark cycles resulted in very dynamic changes in the O_2 production at the shell surface

(Fig. 4). After a steady-state O_2 level was reached, the light was turned off and the O_2 level decreased from 190 to 80% air saturation within 5 min. When the light was turned on again, the O_2 concentration increased immediately and reached 100% air saturation within 15 s. A steady-state supersaturation of 190% was reached again after 3 to 4 min.

Oxygen and pH conditions at the surface of the foraminiferal shell were investigated as a function of scalar irradiance (Fig. 5). The O_2 and pH versus scalar irradiance curves demonstrated the saturation of photosynthesis with increasing incident light. Both pH and the O_2 level at the shell surface saturated at approximately 250 µmol photons m^{-2} s^{-1}.

Gross photosynthetic rates at the shell surface increased with increasing scalar irradiance (Fig. 6A, B). The exponential function of Webb et al. (1974) was fitted to the P versus E_o measurements and estimated a maximum photosynthetic rate of 9.3 nmol O_2 cm^{-3} s^{-1} in one specimen. The initial slope α in the linear part of this P versus E_o curve was 0.07 (Fig. 6A). The onset of light saturation of photosynthesis expressed by the light saturation irradiance, E_k, was $P_{max}/\alpha = 137$ µmol photons m^{-2} s^{-1}. In a second specimen, we found a lower E_k of 75 µmol photons m^{-2} s^{-1} caused by a lower P_{max} of 5.6 nmol O_2 cm^{-3} s^{-1} and the same initial slope ($\alpha = 0.067$) (Fig. 6B). Up to 700 µmol photons m^{-2} s^{-1} no photoinhibition was observed in *Orbulina universa*.

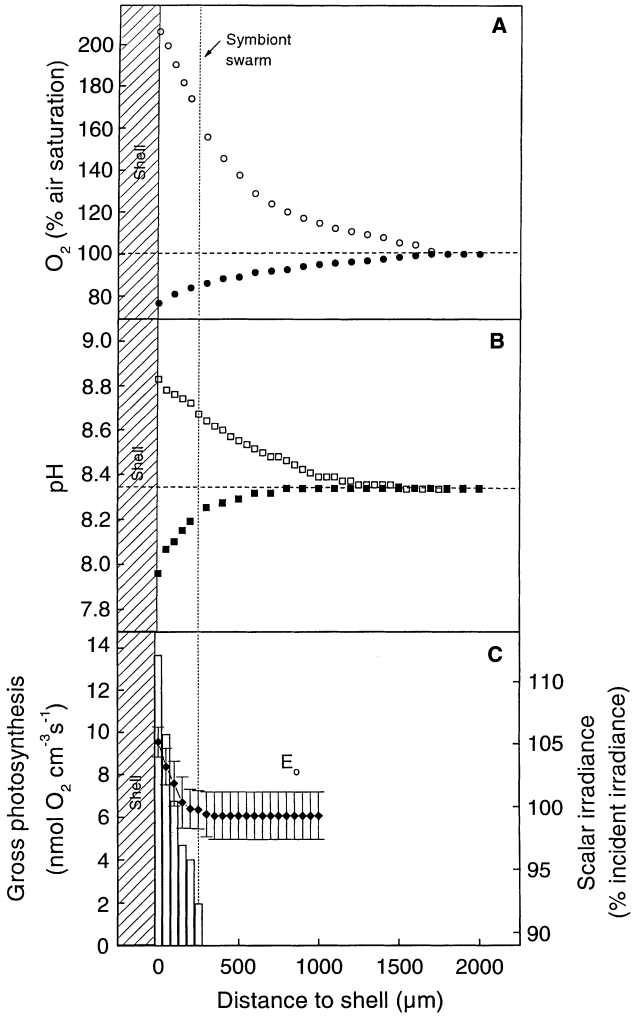

Fig. 3 Light profiles (○) and dark profiles (●) of O_2 (**A**) and pH light (□) and dark(■) profiles (**B**) measured from the ambient seawater to the spherical shell (E_o = ~700 µmol photons m^{-2} s^{-1}). Profiles of scalar irradiance (◆) and gross photosynthesis (*bars*) measured in steps of 50 µm towards the shell surface of *Orbulina universa* (**C**). *Vertical dotted line* indicates the outer periphery of the symbiont swarm

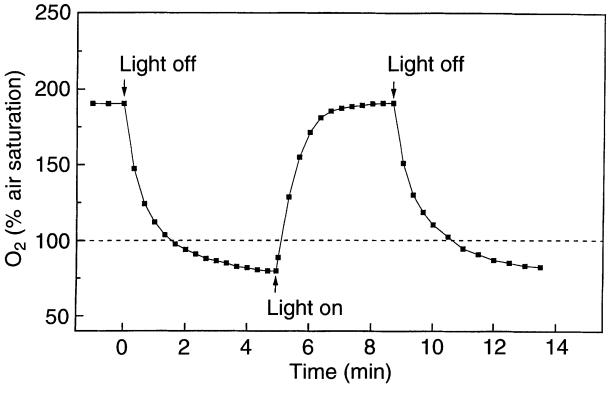

Fig. 4 O_2 dynamics at the shell surface of *Orbulina universa* during experimental light–dark cycles. Incident irradiance was 683 µmol photons m^{-2} s^{-1}. *Dashed line* indicates the O_2 concentration of the ambient seawater

Table 1 *Orbulina universa*. Photosynthesis and respiration measured in several individuals of different sizes at saturating irradiances

Foraminifer no.	Shell diameter (µm)	Incident irradiance (µmol photons m^{-2} s^{-1})	Photosynthesis (nmol O_2 h^{-1} foraminifer^{-1})		Respiration (nmol O_2 h^{-1} foraminifer^{-1})	Percentage of gross photosynthesis
			Gross	Net		
I	554	782	13.89	8.72	5.17	37
II	554	782	11.00	5.06	5.94	54
III	463	288	9.26	4.57	4.69	51
IV	473	446	8.16	6.45	1.71	21
V	297	750	2.29	0.57	1.72	75
Mean ± SD	468 ± 105	609 ± 228	8.92 ± 4.29	5.07 ± 2.99	3.85 ± 1.99	47.6 ± 20.14

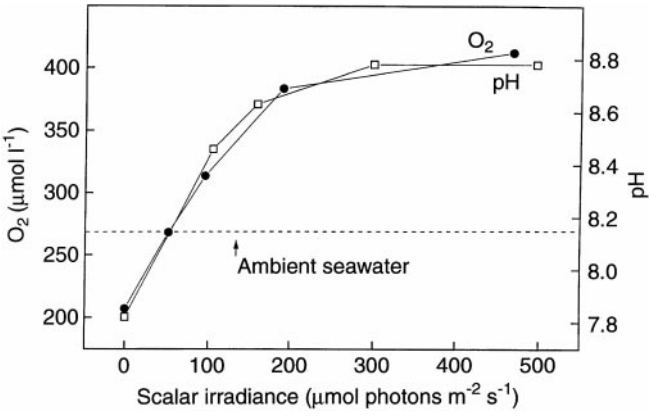

Fig. 5 O_2 (●) and pH (□) measured as a function of scalar irradiance (µmol photons m^{-2} s^{-1}) at the shell surface of *Orbulina universa*. *Dashed line* indicates ambient seawater level of O_2 and pH

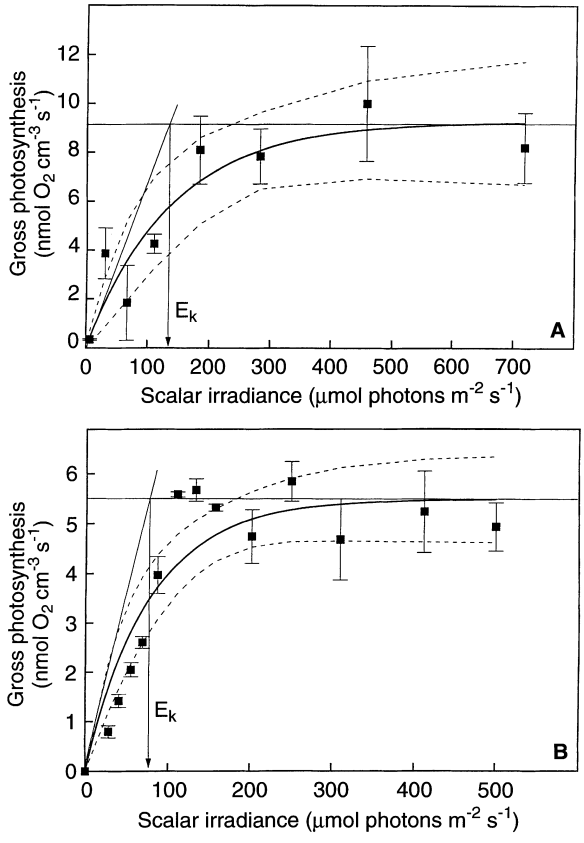

Fig. 6 Gross photosynthetic rates versus scalar irradiance (400 to 700 nm) measured at the shell surface of two *Orbulina universa* specimens (**A** and **B**, respectively). An exponential function (Webb et al. 1974) (*solid line*) was fitted to the data by a nonlinear least-squares Levenberg–Marquardt algorithm (Origin 4.1, MicroCal Software, Inc.) (**A**: $r^2 = 0.86$, $\chi^2 = 1.95$; **B**: $r^2 = 0.85$, $\chi^2 = 0.63$). *Dashed lines* indicate 95% confidence intervals and E_k the onset of light saturation

Radial distribution of O_2 and pH

Radial O_2 and pH profiles in dependence of the incident irradiance were measured from the ambient seawater

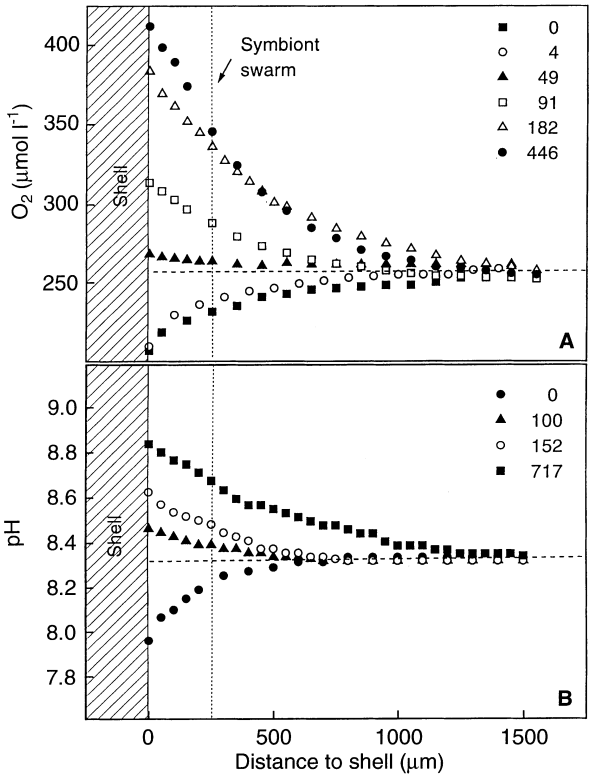

Fig. 7 Radial steady-state O_2 (**A**) and pH (**B**) profiles as a function of increasing irradiance. *Vertical dotted line* indicates the outer periphery of the symbiont swarm. *Numbers* indicate incident irradiance (µmol photons m^{-2} s^{-1}). *Dashed lines* indicate O_2 concentration and pH of the bulk seawater

towards the shell surface (Fig. 7). The O_2 concentration started to increase outside the spines and reached the highest values at the shell surface due to the presence of the DBL. The O_2 profiles varied as a function of the light level (Fig. 7A). At 50 µmol photons m^{-2} s^{-1} the compensation irradiance, E_c, where the respiratory O_2 consumption of the system balanced the zooxanthellae O_2 production, was reached at 50 µmol photons m^{-2} s^{-1} (Fig. 8). With increasing incident irradiance (> 50 µmol photons m^{-2} s^{-1}), the photosynthetic O_2 production exceeded the O_2 uptake, and net photosynthesis approached saturation at >450 µmol photons m^{-2} s^{-1} (Fig. 8).

The pH increased towards the surface of the shell from the ambient seawater level at the end of the spines. Due to increasing photosynthetic CO_2 fixation with irradiance and the presence of a DBL we measured increasing pH values at the shell surface (Fig. 7B). The highest pH of 8.8 was found at 717 µmol photons m^{-2} s^{-1}. In the darkness the surface pH of this specimen decreased to 7.9.

Respiration rates in light and darkness

In the light we observed a high variability of respiration rates in different specimens (Table 1). When light res-

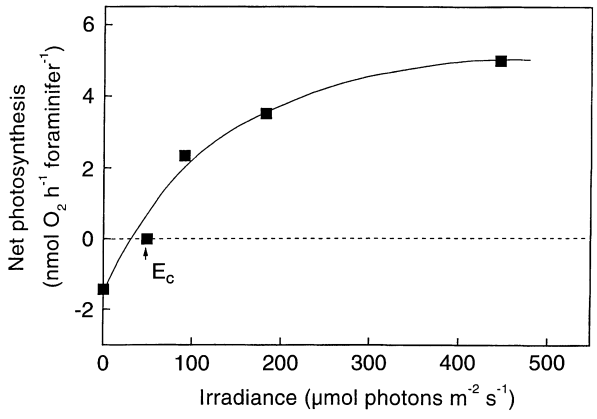

Fig. 8 Net photosynthesis of *Orbulina universa* (nmol O_2 h^{-1}) as a function of incident irradiance. The compensation light intensity, E_c, was found at 50 μmol photons m^{-2} s^{-1}

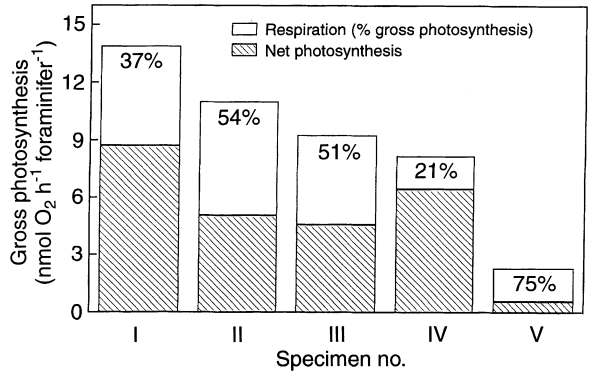

Fig. 9 Photosynthesis and respiration rates of different *Orbulina universa* specimens (*No. I to V*) calculated in a percent of gross photosynthesis

piration was calculated as a percentage of gross photosynthesis we found an average of 47.6 ± 20.1% ($n = 5$) (Table 1; Fig. 9). *Orbulina universa* and its zooxanthellae showed a lower average O_2 consumption in darkness (1.7 ± 0.7 nmol O_2 h^{-1}; $n = 24$, data not shown) compared to the respiration at light saturation (3.9 ± 1.9 nmol O_2 h^{-1}; $n = 5$, see Table 1). Thus respiration was stimulated in the light by a factor of 2.

Discussion

Foraminiferal microenvironment

The O_2 and pH of the microenvironment around the foraminiferal shell differ from the ambient seawater values, depending on the rates of photosynthesis and respiration of the host–symbiont association. The pH varied approximately one unit between saturating irradiances and dark conditions, and the O_2 level ranged between <70 and 206% of air saturation. The foraminifer and its endosymbionts thus live in a dynamic microenvironment of constantly shifting physico-chemical conditions.

The steep O_2 and pH gradients from the shell to the bulk medium at higher irradiances (>150 μmol photons m^{-2} s^{-1}) (Fig. 7A, B) are caused by the high photosynthetic activity of the endosymbionts and the existence of a DBL that surrounds the shell of the foraminifer (Jørgensen et al. 1985). The DBL constitutes a barrier for the mass transfer of gases, ions and other solutes between the foraminifer and the ambient seawater. The thickness of the DBL around a sphere is generally measured by extrapolating the gradient of O_2 at the sphere–water interface to the ambient seawater concentration (Jørgensen and Revsbech 1985; Ploug et al. 1997). While the DBL thickness around the shell of *Orbulina universa* could be estimated in the dark (~200 μm) when the symbionts reside inside the shell, the DBL thickness in light could not be estimated by the extrapolation method due to the presence of the symbiont swarm around the shell. The steady-state O_2 gradients towards the shell in the light are thus affected by diffusion as well as photosynthesis and respiration.

The relative importance of small-scale physical processes around the shell and between the spines (eddy and molecular diffusion) is still unknown and should be investigated to characterize the DBL in more detail. Due to the presence of the calcite spines, the DBL probably shows different characteristics than a sublayer over a sphere with a smooth surface (e.g. turbulent wakes) (Mann and Lazier 1991).

To understand zooxanthellae photosynthesis the scalar irradiance is the most relevant light-intensity parameter (Kirk 1994; Kühl et al. 1995). In hermatypic corals, Kühl et al. (1995) measured scalar irradiance profiles with a fiber optic microprobe and demonstrated that the scalar irradiance could reach up to 180% of the downwelling irradiance at the tissue surface. This increase was explained by multiple scattering and diffuse reflection of light within the coral tissue–skeleton matrix. Our measurements showed a slight increase of scalar irradiance towards the spherical shell of *Orbulina universa* that is probably caused by the combined scattering of the calcite spines and the reflection of light by the spherical shell (Fig. 3C). The light measurements thus demonstrated no significant self-shading of the dinoflagellate cells inside the swarm.

Photosynthetic rates

The photosynthetic rates determined for *Orbulina universa* are similar to published data. The photosynthetic productivity of *O. universa*, when measured with the ^{14}C method (Spero and Parker 1985), showed a photosynthetic rate per symbiotic dinoflagellate of 1.72 pmol C h^{-1}. Assuming an average symbiont density of about 3.3×10^3 algal cells per adult *O. universa* (Spero and Parker 1985), the total photosynthetic rate of a single foraminifer would amount to a rate of 5.7 nmol C h^{-1}.

Globigerinoides sacculifer showed a mean gross photosynthetic rate of 18 nmol O_2 foraminifer^{-1} h^{-1} and a net photosynthesis of 15 nmol O_2 foraminifer^{-1} h^{-1} (Jørgensen et al. 1985). The carbon fixation rates of symbiotic planktonic foraminifera collected in the surface waters near Bermuda ranged between 1.2 and 4.2 nmol C h^{-1} foraminifer^{-1} (Caron et al. 1995). Assuming an O_2/CO_2 conversion ratio of unity, these numbers compare well with the rates measured in the present study.

During our experiments some zooxanthellae remained in the calcite shell. Because we only measured the gross photosynthesis towards the shell surface, we did not record the O_2 production inside the shell, which may not be negligible. Earlier measurements of the photosynthetic rates inside the shell of the symbiotic *Globigerinoides sacculifer* showed a high O_2 production. Jørgensen et al. (1985) estimated an O_2 production of 3.8 nmol O_2 h^{-1} inside the shell. Thus the total gross photosynthetic rates per *Orbulina universa* specimen we report here could be underestimated.

Due to the close coupling of photoautotrophic and heterotrophic processes in the symbiont-bearing foraminifera, the photosynthesis measurements with the ^{14}C method show some disadvantages. Geider and Osborne (1992) pointed out methodological and interpretative problems of the ^{14}C method, e.g. the impossibility to measure the light respiration as well as the transport of carbon between the intracellular carbon pools. In symbiotic associations, the ^{14}C method probably underestimates the production rates due to the production of unlabeled CO_2 by respiration (Michaels 1991). Here we estimated the photosynthesis and respiration rates of *Orbulina universa* from O_2 gradients and discrete measurements inside the symbiont swarm. Because we did not determine the chlorophyll *a* content of the endosymbionts and the number of endosymbionts, we present the rates on a per foraminifer basis.

The radial profiles of gross photosynthesis inside the symbiont swarm of *Orbulina universa* showed a significant increase towards the shell surface. This is due to the fact that the symbiont density increased towards the shell. When measurements of gross photosynthetic rates were done by the light–dark shift technique, the zooxanthellae tended to move back into the shell of *O. universa* after a while. Our measurements of total gross photosynthesis are based on point measurements with a spatial resolution of 50 to 100 μm. This means that the O_2 production within the symbiont swarm was measured for a small volume around the electrode tip (Jørgensen et al. 1985). Consequently, a change of the spatial distribution of the zooxanthellae will affect the photosynthetic rates.

The variability of the gross photosynthetic rates is probably due to several reasons. First, the symbiont photosynthetic activity is affected by the available light and the nutrient supply. Second, the number of symbionts and their distribution may play an important role. Spero and Parker (1985) observed a positive correlation between the shell diameter and the symbiont number of juvenile *Orbulina universa*. The symbiont density depends on the rate of cell division of the endosymbionts and on the age of *O. universa*. The dinoflagellate *Gymnodinium béii* shows division rates of 0.65 d^{-1} (25 °C) in culture (Spero 1987). Although Spero and Parker (1985) could not determine a correlation between the size of the adult chamber and the number of symbionts, we observed a positive correlation between the size of the spherical shell and the total gross photosynthetic rate (Table 1). The specimen with the largest shell diameter showed the highest total gross photosynthesis. Lea et al. (1995) found that the shell diameter of *O. universa* specimens is independent of age. Therefore, the diameter of the spherical shell can not serve as an estimate for age. The correlation between the total gross photosynthetic rate and the foraminiferal shell size as well as the number of symbionts should be confirmed in further studies, e.g. by detailed pigment analysis.

The total photosynthetic rates of the symbiotic foraminifera can also be influenced by the pigment content of the symbiotic dinoflagellates. For example Bijma (1986) studied the pigment composition of symbionts of *Globigerinoides ruber* and *G. sacculifer* and found a ~1.5 times higher chlorophyll *a*/carotenoid ratio in the symbionts of *G. ruber*. The type of endosymbionts is a further important parameter affecting the total photosynthesis. In some planktonic foraminifera smaller chrysophyte symbionts occur in higher abundances than the bigger dinoflagellate symbionts (Caron et al. 1995). In addition, daily variations of the photosynthetic rates were demonstrated in ^{14}C-experiments with *Orbulina universa* (Spero and Parker 1985). The photosynthetic rates of the symbiotic dinoflagellates started to increase in the late morning and highest rates were found in the late afternoon.

Light regulation of photosynthesis

Measurements of O_2 profiles and pH profiles (Fig. 7A, B) showed a very dynamic response to the incident light intensity, and experimental light–dark cycles demonstrated a rapid reaction of the symbionts to changing irradiances (Fig. 4). Light–dark cycle experiments in *Globigerinoides sacculifer* showed similar O_2 dynamics at the shell surface (Jørgensen et al. 1985).

The onset of light saturation of the symbiont photosynthesis (E_k) was estimated in two specimens of *Orbulina universa* of different sizes. The E_k values were found at irradiances of 75 and 137 μmol photons m^{-2} s^{-1}, respectively. The difference is due to the different maximum photosynthetic rates (P_{max}) of the two specimens because both photosynthesis versus irradiance curves showed nearly identical slopes (α) of 0.067 and 0.07 (Fig. 6A, B). The specimen with the higher E_k value also had a larger diameter (483 μm compared to 297 μm). One explanation for the higher E_k is thus a higher number of endosymbionts. However, higher P_{max}

values can also indicate high growth irradiances (Herzig and Dubinsky 1992).

The study of photosynthesis versus irradiance curves in several symbiotic systems reported E_k values between 160 and 390 µmol photons m^{-2} s^{-1} (Jørgensen et al. 1985; Spero and Parker 1985; Kühl et al. 1995). *Globigerinoides sacculifer* collected in the Gulf of Aquaba showed higher E_k values of 160 to 170 µmol photons m^{-2} s^{-1} (Jørgensen et al. 1985) as compared to *Orbulina universa*. ^{14}C measurements of photosynthetic rates of *O. universa* showed a much higher E_k value of 386 µmol photons m^{-2} s^{-1} (Spero and Parker 1985). The onset of light saturation at higher light levels demonstrates the adaptation of the symbionts to high irradiances in the surface waters. An adaptation to high light exposure is also indicated by the fact that no photoinhibition was observed in our study even at high irradiances (Fig. 6A, B).

The calculation of the onset of light saturation (E_k) is also affected by the definition of the light field parameter (Kühl et al. 1995). Photosynthesis versus irradiance curves plotted against the downwelling irradiance (P vs E_d) result in a lower E_k compared to the photosynthesis versus scalar irradiance curves (P vs E_o) (Kühl et al. 1995). In our study, the E_k values estimated from the P versus E_d curves were only slightly lower due to the smaller difference between E_d and E_o at the shell surface. However, scalar irradiance is always the most relevant light field parameter when measuring light regulation of photosynthesis on a microscale (Kühl and Jørgensen 1994; Kühl et al. 1994).

The light compensation point (E_c) is dependent on gross photosynthesis and respiration of the host–symbiont system. In addition, processes that change the symbiotic light respiration, e.g. the mitochondrial respiration or photorespiration, may influence the light compensation point. A change of the foraminiferal light respiration due to growth rate or prey digestion may also result in a change of the compensation light intensity. Respiration measurements of *Orbulina universa* before and after feeding thus demonstrated an increase of the respiration rate within a few hours after feeding with 1-d-old *Artemia* nauplii (Rink, unpublished). Falkowski and Owens (1980) found a dependence of the light compensation point on the irradiance level during growth. The compensation light intensity of the symbiotic *Globigerinoides sacculifer* was 26 to 30 µmol photons m^{-2} s^{-1} (Jørgensen et al. 1985). Compared to *O. universa* this lower compensation point is probably caused by adaptation to lower irradiances (150 µmol photons m^{-2} s^{-1}) during maintenance in the laboratory several days before measurements (Jørgensen et al. 1985).

Light measurements in full sunlight at the collecting site showed irradiances up to 2070 µmol photons m^{-2} s^{-1} at the surface and 556 µmol photons m^{-2} s^{-1} at 12 m depth (S. Anderson, personal communication in 1995). Depth profiles of scalar irradiance (E_o) measured at the collection site showed a mean light attenuation

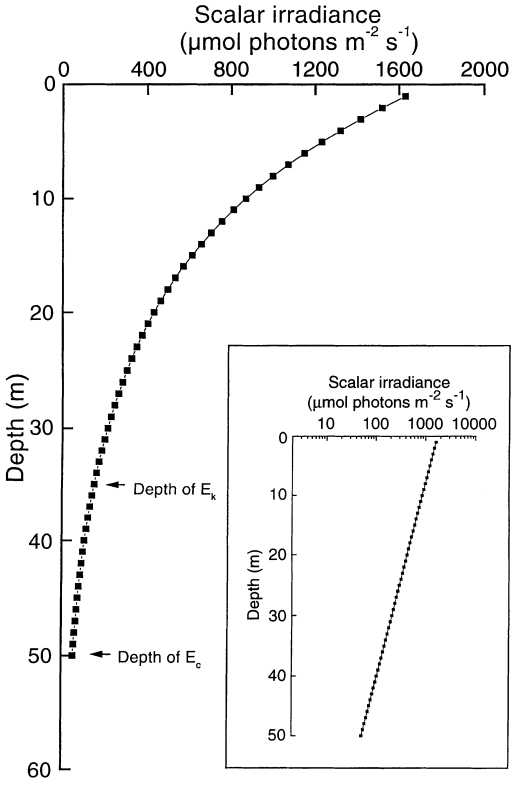

Fig. 10 Depth profile of scalar irradiance (E_o) calculated with the subsurface value $E_o(0) = 1747$ µmol photons m^{-2} s^{-1} and a light attenuation coefficient $K_o = 0.07$. $E_o(0)$ was measured under sunny conditions in the California Current (Catalina Island) (E_k = 137 µmol photons m^{-2} s^{-1}, E_c = 50 µmol photons m^{-2} s^{-1}). *Inset* shows log-transformed data

coefficient (K_o) of 0.07 (SD ± 0.023) (Fig. 10). The light compensation point (E_c) of *Orbulina universa* would thus be reached in a depth of ca. 50 m at the sampling site (Fig. 10). Theoretically, a net O_2 production of the symbiont–host system is possible down to this water depth at full sunlight. The O_2 production of *O. universa* exhibited a pronounced light dependency (Fig. 7A), and high net primary production rates of the symbiotic *O. universa* are limited to the regions of photosynthesis-saturating irradiances in the surface waters (0 to 35 m).

Primary production of planktonic foraminifera

The symbiont-bearing foraminifera constitute microenvironments of concentrated photosynthetic activity (Caron and Swanberg 1990) and were reported to have the highest rates of primary production in plankton communities because of the extremely high density of the endosymbiotic algae in their cytoplasm. Due to the high algal biomass, the amount of primary production occurring in the symbiont–host association is generally much higher than in an equivalent volume of seawater (Jørgensen et al. 1985; Spero and Parker 1985). Jørgensen et al. (1985) estimated that a single

foraminifer would increase the CO_2 fixation rate in a 125 ml productivity bottle fivefold above the CO_2 fixation in ambient seawater. Spero and Parker (1985) made the assumption that a single large *Orbulina universa* may represent a potential source of net primary production that would contribute approximately 0.2% of the fixed carbon in 1 m^3 of seawater.

Although the associations are packages of high productivity it is still difficult to estimate their total primary production. The foraminiferal part of the total phytoplankton primary production is dependent on their population density in the oceans (Bé 1977). Their productivity depends on the population dynamics and the patchiness of foraminifera. The distribution of most species shows a correlation with sea surface temperatures (Bradshaw 1959). Currents and mixing of surface waters may also cause a change of the foraminiferal distribution. Changes of the depth habitat due to the lunar periodicity of the reproductive cycle were reported by Hemleben and Spindler (1983).

Diurnal variations of the depth habitat, rising of the foraminifera during the daytime and falling in the night, are discussed by Berger (1969) and Boltovskoy (1973). Bradshaw (1959) suggested that the rapid production of O_2 by the symbiotic algae in the protoplasm could form oxygen bubbles that increase the buoyancy of the foraminifera during the day and could cause a rising to the surface. Fairbanks and Wiebe (1980) observed a maximum abundance of planktonic foraminifera in the deep chlorophyll maximum layer (DCM) with changing seasonal depth levels. They suggested that the foraminifera exploit the DCM as a major source for food and nutrients. Population studies of Bé et al. (1985) showed seasonally changing abundances of planktonic foraminifera in the Panama Basin. Because of this vertical and horizontal distributional patchiness, the estimation of planktonic foraminifer primary production is difficult and only possible for small oceanic areas that are well studied.

To calculate the net primary production of *Orbulina universa* from our microsensor data we assumed a density of five specimens per cubic meter (Spero and Parker 1985). An average net photosynthetic rate of 5 nmol O_2 h^{-1} $foraminifer^{-1}$ (Table 1) over a daily light exposure of about 10 h would result in a production of 0.25 μmol O_2 m^{-3} d^{-1} at light saturation. For the same parameters Jørgensen et al. (1985) found a three times higher primary production of 0.75 μmol O_2 m^{-3} d^{-1} for *Globigerinoides sacculifer* in the Gulf of Aquaba. The whole population of *G. sacculifer* would contribute about 0.1% of the mean yearly primary production in the Gulf. Caron et al. (1995) reported that the total symbiont production of sarcodines (Acantharia, Radiolaria, Foraminifera) in oligotrophic waters of the Sargasso Sea contributes only a small fraction (< 1%) of the total primary production. They found production rates of acantharia and foraminifera to contribute with an average of ~5% to the total annual primary production in the surface waters. A vertical biomass distribution for foraminifera was given by Michaels (1991) who formulated a depth-dependent relationship for symbiont productivity that is related to the exponential decline of the light field.

The percentage of the total primary production of planktonic foraminifera in 1 m^3 of seawater is probably overestimated, and the production rates are more variable because several parameters limit the primary production rates as mentioned before. Symbiont densities and productivities as well as light exposure and nutrient supply influence the maximum net O_2 production. If the planktonic foraminifera change their depth habitat due to vertical migration, light will be a limiting factor.

There are still open questions about the nutritional relationship in the foraminifer–dinoflagellate symbiosis. For instance, which kind of photosynthates are released by the dinoflagellates and how much of the primary fixed carbon is translocated to the host. With regard to the predation on plankton the significance of the photosynthate supply for the energy budget of the host will be of great interest. Due to the vertical ontogenetic migration of the planktonic foraminifera a combination of two energy sources, planktonic prey and photosynthates, is probably of importance. Detailed investigations of the migration patterns and changing abundances of *Orbulina universa* and other species in the water column would help to provide more information about their total primary productivity (Hemleben and Bijma 1994).

Respiration in light and darkness

One advantage of the microsensor technique compared to other methods is the possibility to estimate the respiration rate of the symbiont–host system in the light. We were able to calculate the light respiration of a *O. universa* by measuring the total gross photosynthesis and the net photosynthesis of the same specimen. Direct comparison of dark and light respiration rates was therefore possible. In the light, we found higher respiration rates of the symbiont–host association (3.9 nmol O_2 h^{-1} $foraminifer^{-1}$) compared to the dark respiration (1.7 nmol O_2 h^{-1} $foraminifer^{-1}$). This enhanced respiration in the light has been described for several symbiotic systems (Edmunds and Davies 1988; Harland and Davies 1995; Kühl et al. 1995) and for microalgae (Falkowski et al. 1985; Grande et al. 1989). Different mechanisms have been discussed to explain the enhanced respiration in the light (Falkowski et al. 1985; Weger et al. 1989).

The respiration of the host is enhanced in the light via the production of photosynthates by the dinoflagellate endosymbionts. Symbionts of larger benthic foraminifera have been shown to release soluble photosynthates like polyglucan, glycerol, glucose and lipids (Kremer et al. 1980). The zooxanthellae probably increase the quantity of respiratory substrates translocated to the host in the light. The tissue of larger foraminifera con-

tains some activating factors that stimulate the release of the photosynthates. Lee et al. (1984) found that the level of the photosynthate release of isolated endosymbionts increased dramatically in the presence of host homogenates. Due to the supply of carbohydrates and lipids by the endosymbionts foraminiferal respiration can thus be stimulated in the light.

Photosynthesis results in O_2 supersaturation around the foraminiferal shell, which may stimulate the respiration of the symbionts and the foraminifer. This internal O_2 supply alleviates the diffusion limitation due to the presence of the DBL. Experiments showed increased dark respiration when the symbiotic sea anemone *Anemonia viridis* was exposed to hyperoxic water (Harland and Davies 1995). These authors suggested, therefore, that the day time respiration is influenced by the O_2 release of the endosymbionts. Also, Jørgensen et al. (1985) suggested that the limited O_2 supply in the darkness due to the presence of the DBL caused reduced dark respiration rates. They measured a decrease of the O_2 at the shell of *Globigerinoides sacculifer* down to 50% of air saturation in darkness. In *Orbulina universa* we found an O_2 decrease to the shell surface down to 67% air saturation during darkness.

A higher O_2 consumption in the light can also be caused by photorespiration. Photorespiration is defined as a light-dependent O_2 uptake and CO_2 release due to the bifunctional enzyme Rubisco (Falkowski et al. 1985; Beardall and Raven 1990). The high O_2/CO_2 ratio produced by the photosynthesis of the zooxanthellae could promote the oxygenase activity of Rubisco. However, an efficient inorganic carbon uptake mechanism present in most microalgae seems to be able to decrease the importance of photorespiration (Beardall and Raven 1990). To our knowledge no investigation of photorespiration or inorganic carbon uptake by the foraminiferal symbionts has been reported in the literature.

In principle the pseudocyclic photophosphorylation (Mehler reaction) represents another light-induced O_2-consuming process (Raven and Beardall 1981; Falkowski et al. 1985). However, Glud et al. (1992) suggested that the measurement of gross photosynthetic rates with the light–dark shift method probably does not include the O_2 consumed by the Mehler reaction.

Due to the limitation of the ^{14}C method to measure respiration in the light, some authors investigated the dark respiration after exposure to high irradiances. This process of post-illuminated O_2 consumption in the darkness has been discussed for different microalgae (Burris 1977; Falkowski et al. 1985; Weger et al. 1989; Beardall et al. 1994) as well as for symbiotic sea anemones (Harland and Davies 1995) and corals (Edmunds and Davies 1988). Burris (1977) obtained a post-illumination burst of oxygen uptake in the dinoflagellate *Glenodinium* sp. and in the zooxanthellae of the coral *Pocillophora capitata* that lasted about 5 to 10 min. The dinoflagellates showed a longer post-illumination burst compared to other algae (1 to 2 min). Burris (1977) explained this increase by the possibility of a different photorespiratory pathway or by higher dark respiration rates. Beardall et al. (1994) demonstrated that low-light-adapted cells of *Thalassiosira weissflogii* were more susceptible to the enhanced post-illumination respiration compared to cells grown under high light conditions. Harland and Davies (1995) found a stimulation of dark respiration of 39% after 6 h exposure to saturating irradiance (300 μmol photons m^{-2} s^{-1}). The reef coral *Porites porites* showed a mean increased dark respiration rate of 39% relative to the pre-illumination dark respiration rate (Edmunds and Davies 1988).

The estimation of the light respiration with the microsensor technique showed much higher respiration rates during light conditions compared to the dark respiration rates (Kühl et al. 1995). Jørgensen et al. (1985) measured for *Globigerinoides sacculifer* a similar respiration rate in the light (3.0 nmol O_2 h^{-1} foraminifer^{-1}) as we did for *Orbulina universa*, but they did not find a lower dark respiration (2.7 nmol O_2 h^{-1}). In *O. universa*, we found a two times lower dark respiration (1.7 ± 0.7 nmol O_2 h^{-1}, $n = 24$). If we assume higher total photosynthetic rates per foraminifer due to additional O_2 production inside the shell, the difference between respiration rates in the light and darkness may be even larger. Generally, the dark respiration rates of microalgae are on the order of 10% of the gross photosynthesis (Beardall and Raven 1990). In our study we measured a mean total dark respiration of the symbiont–host association of 1.7 nmol O_2 h^{-1} and an average total gross photosynthetic rate of 8.9 nmol O_2 h^{-1}. If we assume that 50% of the total O_2 uptake is due to symbiont respiration (Jørgensen et al. 1985), the dark respiration rate of the zooxanthellae is nearly 10% of the gross photosynthesis.

The P/R ratio is used to estimate the physiological state of marine microalgae and to scale the relationship of consumption and production of organic material (Burris 1977). This ratio has been investigated for several algal species, and the numbers for dinoflagellates varied between 1.3 and 5.7 (Humphrey 1975; Burris 1977; Daneri et al. 1992). The zooxanthellae of coelenterate hosts can supply most of the carbon required by the host, as was demonstrated in 70 species of corals with P/R ratios of 2.4 ± 1.5 (Battey 1992). In our study we measured a mean net photosynthesis of 5.0 nmol O_2 h^{-1} during light saturation and an average dark respiration of 1.7 nmol O_2 h^{-1} foraminifer^{-1}. Consequently, the P_{net}/R_{dark} ratio of the symbiont–host system is about 3, which indicates that the required carbon for the foraminifer can be supplied by its symbionts. However, to estimate if the net primary production of the endosymbionts can provide the required organic carbon for growth and respiration of the symbiont–host association, the total net photosynthesis over the daily light period as well as the growth rates and the respiration rates of the host and the symbionts have to be calculated on a daily basis.

It has been suggested that foraminifera supply their endosymbionts with respired CO_2 (Bé 1977). The respiration of *Orbulina universa* in the light showed an

average rate of 48% of the gross photosynthesis. This value demonstrates a much higher CO_2 availability for the symbionts as compared to free-living dinoflagellates. Geider and Osborne (1989) reported that a dark respiration versus photosynthesis rate of 0.25 is generally found in dinoflagellates. *Orbulina universa* can, thus, supply its endosymbionts with additional CO_2, which may support photosynthetic CO_2 fixation. However, recent model calculations (Wolf-Gladrow et al. in preparation) as well as laboratory experiments (Bijma et al. in preparation) demonstrate that *Gymnodinium béii* in symbiosis with *O. universa* as well as isolated in culture also tap into the bicarbonate pool as a carbon source.

Conclusions

Microsensors are useful tools for studying photosynthetic processes in symbiotic systems and for comparing light and dark respiration rates. The respiration of *Orbulina universa* in the light was significantly higher than dark respiration. Possible mechanisms for this observation might be the increase of respiratory substrates (photosynthates) released by the symbionts and/or photorespiration.

Varying incident irradiances caused dynamic changes of the symbiont photosynthetic activity that affected the chemical microenvironment around the foraminiferal shell. High photosynthetic rates in combination with a slow efflux of O_2 and protons due to the diffusive boundary layer created an O_2 oversaturation and a pH increase in the foraminiferal microenvironment as compared to the ambient seawater. The symbiotic associations of *Orbulina universa* thus represent highly productive "hot spots" in the light-saturated photic zone of oligotrophic pelagic environments.

To understand the complexity of interactions between photosynthesis, respiration and calcification in symbiotic foraminifera, new methods have to be explored. A new CO_2 microsensor (de Beer et al. 1997) could provide more information about CO_2 uptake and dynamics. Furthermore the CO_2 microsensors could be used in combination with Ca^{2+} microelectrodes (Tsien and Rink 1980; Amman et al. 1987) to investigate the process of calcification in symbiont-bearing foraminifera.

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