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THE IMPORTANCE OF FEEDING IN TWO SPECIES OF SORITID FORAMINIFERA WITH ALGAL SYMBIONTS

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ABSTRACT

The carbon budgets and rates of calcification of *Archaias angulatus* and *Sorites marginalis*, two species of symbiont-containing soritid foraminifera, were studied *in situ* in Key Largo Sound, Florida. Respirometric and radionuclide techniques were used to measure mid-day primary production, calcification, and feeding rates. The algae used in the tracer-feeding studies were prominent species from the local *Thalassia* community and species which are excellent food sources for other species of littoral benthic foraminifera. Tracer feeding studies clearly indicated that feeding was the more important process at mid-day; the ratio of carbon gain in both foraminifera-symbiont systems by feeding to primary production was $\geqq 10:1$. The rate of primary production was generally greater in *A. angulatus* than in *S. marginalis*. The diets of the two species of foraminifera were relatively non-overlapping. Under the experimental conditions both species deposited $\sim 4\%$ of dry weight in additional calcium per day. Small specimens of *A. angulatus* deposited $\sim 1.8\times$ more calcium than did larger specimens. Under the experimental conditions, light did not enhance the rate of calcification.

Many researchers (Goreau, et al., 1971; Kohn and Helfrich, 1957; Odum and Odum, 1955) believe that the high localized productivity of coral reefs is achieved through very tightly interwoven and efficient recycling systems that reduce external losses to the outside ocean water to a minimum and maintain the local nutrient levels at very high steady state values. Although there is still some controversy (Franzisket, 1969, 1970; Goreau et al., 1971; Johannes et al., 1970; Muscatine, 1973; Taylor, 1973a, b), there is general agreement that zooxanthellae fix a significant quantity of carbon and that a portion of the photosynthetate is translocated into host animals (Goreau and Goreau, 1960; Muscatine, 1967; Muscatine and Cernichiari, 1969; Trench, 1971a-c; also reviewed in Muscatine, 1971, 1973; Taylor, 1973a, b). Regardless of their contribution to the welfare of their hosts, the algae occupy a considerable part of the protoplasmic volume of the host-symbiont system. Recent estimates of animal to plant protein in a non-fleshy (relatively thin coenosarc) coral, *Pocillopora damicornis*, suggest that the coral is $\sim$ 50% plant material (Muscatine and Cernichiari, 1969).

Foraminifera abound in coralline environments and many species contain chambers which are solidly packed with symbionts. Judging from recent reviews of algal symbiosis in invertebrates (Muscatine, 1973; Taylor, 1974), we know comparatively little about symbiosis in foraminifera (Lee, 1974). Studies of *Heterostegina depressa* indicate that this species can grow without feeding if incubated in the light (Röttger, 1972a, b). Light enhanced calcification in another large foraminiferan, *Archaias angulatus*, but feeding seemed to be the primary carbon route since $\sim 2\times$ more carbon was taken up via food than by photosynthesis. Recent fine structural studies of another symbiont-containing foraminifer, *Sorites marginalis* (Müller-Merz and Lee, 1976) from the same semitropical shallow benthic habitat, suggested that it too must be an active feeder. The present study is a logical extension of the fine structure studies and is aimed at assessing the relative importance of the algal-foraminifer symbiosis to the carbon budget of the system at mid-day when symbiont primary production might be at peak.

Materials and Methods

The algae used in tracer-feeding studies were either organisms which have been found to be excellent food organisms for a variety of littoral benthic foraminifera (Lee, 1974) [*Phaeodactylum tricornutum* (strain 39), *Nitzschia acicularis* (strain 8), *Dunaliella salina* (strain 13)], the *Archaias* symbiont (*Chlamydomonas hedleyi* (Lee et al., 1974; Lee and Zucker, 1969), or diatoms *Achnanthes haukiana* (SF-30-7), *Cocconeis placentula* (CS 20-5), *Mastoglea* sp. (SF 32-8), *Amphora coffeaeformis* (SF 1A) previously isolated into axenic culture from the surface of *Thalassia testudinum* blades on which were found large numbers of *A. angulatus* or *S. marginalis*. A series of differential media (Lee, et al., 1975) modified to give higher salinities was used for the latter isolations. Tracer feeding techniques followed the procedures outlined previously (Lee and Muller, 1973). The ^{32}P labeled algae were brought to the field where they were washed with the aid of a hand centrifuge before introduction into 30 ml polystyrene vessels. The flasks were fastened with rubber bands to an anchored plastic rack and incubated for 6 hr under natural conditions at mid-day in Key Largo Sound. All experiments were conducted in sextuplicate.

With the aid of radionuclides ^{45}Ca and ^{14}C, rates of primary production and calcification were also measured in the same experimental apparatus. Unfed foraminifera were incubated in either the light or dark. Dark flasks were wrapped in heavy aluminum foil. In some flasks 1 μM 2-acetyl-amino-1,3,4-thiadiazole-5-sulfonamide (Diamox) was added to inhibit calcification. In other flasks 10^{-5} to 10^{-6} M 3-(3,4-Dichlorophenyl)-1, 1-dimethylurea (DCMU), a pre-emergence herbicide was added to inhibit photosynthesis. Experiments were conducted in duplicate.

The natural seawater from the collection site was enriched with 100 μCi of ^{14}C ($NaHCO_3$) to yield a specific activity of carbonate carbon of 0.55 mCi/mM or ^{45}Ca ($CaCl_2$)/ml to yield a calcium specific activity of 28 μCi/g Ca. At the conclusion of experiments the animals were rigorously agitated in unlabeled seawater. Radioactivity was measured with a liquid scintillation counter using a PPO-1-dimethyl POPOP in toluene cocktail.

The animals used in these experiments, *A. angulatus* and *S. marginalis*, were collected and removed from *T. testudinum* with the aid of #00 sable brushes or scalpels immediately before inoculation into experimental vessels.

The *A. angulatus* in experimental vessels were mixed populations of ~ 20 juveniles (< 0.5 mm, ~ 2.6×10^{-4} g [dry wt]/foram) and ~ 25-30 intermediate and adult forms (< 1-4 mm, average 2.2 mm, 9.16×10^{-4} g/foraminifera). Although *S. marginalis* were moderately abundant, large numbers were not harvested from random samples of *T. testudinum*. We were only able to obtain sufficient animals by intensive snorkel surveys of large areas of *T. testudinum* beds. Since the blades with *S. marginalis* were identified under water while we were snorkeling, the experimental animals were biased in favor of large, mature organisms (1.5-5 mm).

Measurements of primary productivity and respiration were also made in the field using Gilson #5 all glass differential manometers mounted on a float. The manometers were secured to the float by means of stainless steel holds and brackets used in the laboratory model (Gilson Medical Electronics, Middleton, Wisconsin 53562). The reaction flasks were mounted so that they floated 11.5-12.5 cm below the surface of the water. Dark flasks were wrapped in heavy duty aluminum foil. A piece of filter paper saturated with 20% KOH was placed in the center well of the dark flasks. After the radioactivity of the animals was measured, or after they were harvested from respiration experiments, the animals were gently decalcified in HCl, dried to constant weight, and then weighed. We felt that com-

Table 1. Carbon budget of two species of symbiont-bearing soritid foraminifera

	Net carbon fixed*				Food eaten†			
	Archaias		*Sorites*		*Archaias*		*Sorites*	
Food organisms	mean	range	mean	range	mean	range	mean	range
Control (no food added)	0.3	0.1–0.4	0.7	0.4–0.8		—		—
Chlamydomonas hedleyi (Arch symb)	1.1	0.9–1.3	1.1	0.9–1.2	0.7	0.6–0.8	0.4	0.3–0.5
Cocconeis placentula (Cs 20-5)	3.6	2.7–4.0	2.4	1.9–2.8	0.8	0.6–0.9	0.4	0.4
Achnanthes haukiana (S F 30-7)	0.7	0.3–1.0	0.7	0.4–0.9	0.33	0.3–0.4	0.53	0.5–0.6
Phaeodactylum tricornutum (39)	1.2	0.9–1.3	0.2	0.7–1.4	0.1	0.06–0.15	0.3	0.2–0.4
Amphora coffeaeformis (S F 1A)	3.6	2.7–4.1	0.9	0.4–1.1	0.97	0.8–1.2	0.1	0.04–0.18
Nitzschia acicularis (8)	0.8	0.6–1.0	0.6	0.3–0.9	0.1	0.03–0.18	0.2	0.1–0.8
Dunaliella salina (13)	1.2	0.8–1.3	1.2	0.9–1.3	0.1	0.08–1.2	0.7	0.6–0.8
Mastoglea sp (S F 32-8)	2.4	2.0–2.6	1.8	1.5–2.1	0.9	0.7–1.0	1.2	0.9–1.3

* Mean and range, mg/g organic weight of foram/0.25 day, high natural light.
† Mean and range, gC/g organic weight of foram/0.25 day, high natural light.

parison of the animals on the basis of their organic weight was more reasonable since the two species of animals differ greatly in their degree of calcification. There was very little sky cover on the days on which we ran experiments. Observations by the National Weather Service, N.O.A.A., at Miami suggest that the average daily radiation during the periods of our studies were ~ 375 Langleys/day.

We also surveyed portions of Key Largo Sound, with the aid of snorkels and face masks, in order to estimate populations of epiphytic foraminifera. Blooms of foraminifera on *T. testudinum* or algae were gently harvested into plastic bags to be separated, dried, and weighed later.

Results

Tracer studies clearly indicated that both feeding and photosynthetic fixation of carbon by symbionts within the animals contributed significant fractions to the carbon budgets of both foraminifera-symbiont systems (Table 1). The feeding (ingestion) rates of both foraminiferan species varied, depending upon the species of algae fed, but were generally several orders of magnitude greater than photosynthetic rates. With only one exception (*Mastoglea* sp.), the diets of the two species of foraminifera were relatively non-overlapping. *A. angulatus* ate two times more *C. hedleyi* and *C. placentula*, and almost 10 times more *A. coffeaeformis* than did *S. marginalis*. *S. marginalis* ate 7 times more *Dunaliella* than did *A. angulatus*. *P. tricornutum* and *N. acicularis* were eaten in very small numbers by both species.

Feeding seemed to enhance carbon fixation but there was no direct correspondence between the mass of the algae eaten by the animals and the ^{14}C measured in the foraminifera [e.g., compare the data for *C. hedleyi* (*Archaias* symbiont) and *C. placentula* (Cs 20-5)]. Carbon fixation in both host-symbiont systems was greatest in the presence of *C. placentula* and *Mastoglea* sp. *A. coffeaeformis* greatly stimulated (~ 10 ×) C fixation in *A. angulatus* but not in *S. marginalis*. We found all three of these algal species to be abundant in the epiphytic communities of *T. testudinum*. In several cases carbon fixation was 33-50% greater in *A. angulatus* than in *S. marginalis* and in one case *A. angulatus* symbionts fixed four times more C than those in *S. marginalis*. In the dark, *S. marginalis* incorporated only 4% of the labeled carbon ($H^{14}CO_3^-$) as did organisms incubated in the light. Specimens of *A. angulatus* in the dark incorporated more labeled bicarbonate (~ 15%)

Table 2. Carbon budget of 2 species of symbiont-bearing soritid foraminifera

	Light*†		Dark‡	
	mean	range	mean	range
Sorites	2.2×10^{-6}	$2.0–2.6 \times 10^{-6}$	1.6×10^{-6}	$0.9–2.1 \times 10^{-6}$
Archaias	8.2×10^{-7}	$7.8–8.6 \times 10^{-7}$	6.6×10^{-7}	$6.1–6.9 \times 10^{-7}$

* Net moles O_2 produced/mg dry organic wt/hr in the absence of food organisms; average of 6 replicates.
† Incubated in mid-day–early afternoon natural light in Key Largo Sound.
‡ Moles O_2 consumed/mg dry organic wt/hr.

than did *S. marginalis*. In the light both foram-symbiont systems evolved slightly in excess of twice as much oxygen as they consumed in the dark (Table 2). On a dry organic weight basis *S. marginalis* symbionts incubated without food fixed three times more carbon than did *C. hedleyi* in *A. angulatus*.

Under the experimental conditions (4 hr mid-day incubation *in situ*) both foram species deposited 2% of their dry (calcified) weight in additional calcium. In the test DCMU depressed calcification in *S. marginalis* to 60% of controls and in *A. angulatus* it was 74% of controls. Calcification in *A. angulatus* was depressed 83% by Diamox, but *S. marginalis* was unaffected. On a basis of weight, small *A. angulatus* deposited 1.8 times more calcium than did larger specimens.

Neither species of foraminifera was uniformly distributed throughout Key Largo Sound. Over the years we have found that patches of *A. angulatus* and *S. marginalis* are more likely to occur in some parts of Key Largo Sound than in others. For this reason most of our collections and experiments were made near North Sound Creek (80°23.1'W 25°08.5'N). *A. angulatus* is far more abundant in the sound than is *S. marginalis*. In many blooms *A. angulatus* are found in clusters on a single blade of *T. testudinum* or algae. Most of the animals are attached aperturally and are at right angles to the blades. In the extreme we collected thalli of *Boodlea* sp. which looked like underwater Christmas trees with foraminifera as ornaments. From one specimen of *Boodlea* weighing (dry weight) 5.74 g, occupying ~ 500 cm^3 in space above the substrate, we recovered 1.91 g of *A. angulatus*. In contrast, a mature specimen of *S. marginalis* is sometimes surrounded by 20 or more young specimens but only rarely have we found clusters of 3 or more *S. marginalis* on a single blade of *T. testudinum* or on an algal thallus. Specimens of *S. marginalis* tend to be located on the distal half of *T. testudinum* blades and, in contrast to *A. angulatus*, they lie flat on the blade. At peak abundance perhaps 30% of the *T. testudinum* blades have one or more specimens of *S. marginalis*. Many times, however, we have found specimens on less than 1% of the *T. testudinum* blades examined.

Discussion

Evidence obtained in this study dovetailed nicely with data from previous studies on the species (Lee and Zucker, 1969; Müller-Merz and Lee, 1976), and seems to suggest some similarities and perhaps some differences between foraminifera with symbionts and reef corals (e.g., Goreau et al., 1971, Muscatine, 1973; Taylor, 1973a, b). Symbiotic algae in both corals and soritid foraminifera are capable of producing more oxygen than is consumed by the host-symbiont systems and their ratios of maximum photosynthesis to respiration (P:R = ~ 2-5) are quite similar (Kanwisher and Wainwright, 1967; Muscatine, 1973; Taylor, 1973a, b). In both corals and soritids feeding seems to be the major carbon pathway. Our experiments were not

designed to yield data which would allow us to construct daily or annual carbon budgets for the two foraminifera species under investigation, but they lend themselves to some speculations along these lines.

In making our estimates of primary production of the foraminifera-symbiont systems, two factors, both potential sources of error, were not measured: (1) ^{14}C fixed in primary production and incorporated into the ^{32}P labeled food organisms which were then ingested by the forams and (2) losses due to ^{14}C fixed and respired during the experiment. If we neglect the first factor, primary production will be overestimated. If we assume that rate of feeding of the animals was uniform during the experimental incubation ($\sim$ 0.1 gC/g foraminifera/hr), and if we assume that under the experimental conditions the algae eaten were fixing carbon at a uniform rate (estimated at 0.1 to 1 $\times$ 10^{-6} M CO_2/mg dry weight of algae/hr; Saks, pers. comm.), then, by integrating the potential additional ^{14}C label gained from an increasingly labeled but declining population of cells, we can estimate a potential error of $\sim$ 0.03 mg/g organic weight of foraminifera 0.25 day. This is an approximate over estimation of primary production by the host-symbiont system of 1-10%. As for the second factor we have already measured the rate of respiration of the host-symbiont systems ($\sim$ 1 $\times$ 10^{-6} M O_2/mg dry organic wt/hr; Table 2). The rate of total CO_2 released by the flasks during algal photorespiration is difficult to estimate because it will vary depending upon the metabolic pathways available to the algal species (e.g., presence or absence of glycolate dehydrogenase), but the hypothetical CO_2/O_2 quotient of photorespiration would be < 1. In our own laboratory we have measured photorespiratory rates for algae similar to species used in these experiments ($\sim$ 0.1-10 $\times$ 10^{-7} M carbon/mg dry wt/hr). If we had trapped the $^{14}CO_2$ respired during the carbon budget experiments in filter paper saturated with KOH or phenethylamine we would have had to subtract some estimate of the photorespiratory rates of the non-eaten free algae to get host-symbiont respiration of label fixed. The estimate itself would have had an estimated error of $\sim$ $\pm$ 10%. To get the trapped $^{14}CO_2$ we would have had to use a different experimental vessel, one less conductive for the foraminifera feeding part of the experiment. Therefore, it seemed wiser to avoid this difficulty by assuming that the P:R ratio of the host-symbiont systems are similar to those in corals. Assuming the worst case, we may have underestimated primary production by the host-symbiont systems 20-30%. Since the carbon fixed by both foraminifera host-symbiont systems was $>$ than the carbon ingested (by several orders of magnitude) our preliminary estimates are quite satisfactory for our purposes.

If we assume no mechanical trauma to the animals and their symbionts as they were harvested from *T. testudinum* and manipulated for experiments, and assume on the basis of studies on other shallow benthic foraminifera (Lee and Muller, 1973) that the ecological growth efficiency (E_e) of the soritids lies between 1-20%, and if we assume that the rate of release of photosynthetate by the symbionts in their host is similar to the rate of release of *C. hedleyi* in axenic culture ($\sim$ 60%, Lee et al., 1974) then the ratio of carbon gain in both foraminifera-symbiont systems by feeding to that by photosynthetic fixation at mid-day is $\geqslant$ 10:1. On a daily or annual basis the carbon ratio might be higher.

Possible benefits of the symbiotic relationship to the nutrition of the symbiont seem easier to demonstrate than those to the host. *Symbiodinium microadriaticum* can use urea, uric acid, guanine, adenine, and several amino acids as nitrogen sources and glycerophosphate and nucleotides as phosphate source (McLaughlin and Zahl, 1959). All of these are possible metabolites which could be host by-products or available in food consumed by the host. *C. hedleyi* grew well in a minimal medium but its growth was tripled in the presence of thiamine and

stimulated (50%) in the presence of biotin, glutamic acid, histidine, and methionine (Lee et al., 1974). Urea 20 μM was the best N source; purines and pyrimidines did not satisfy nitrogen requirements. Biotin and thiamine are vitamins which might be made available to the symbionts from the bacteria and algae eaten by the foraminifera.

While it has been shown that materials pass from zooxanthellae into the tissue of host coelenterates (Pearse and Muscatine, 1971; Trench, 1971a-c, Von Holt and Von Holt, 1968a, b), and that the *A. angulatus* symbiont, *C. hedleyi*, has the same potential (Lee et al., 1974), the precise significance of the substances in the context of the nutrition of the host animals still is not understood. *S. microadriaticum* releases glycerol, glucose, alanine, lipids, organic acids, and organic phosphates. *C. hedleyi in vitro* releases mannitol (Lee et al., 1974) but it is entirely possible that *in vivo* host tissues might influence the rate and quality of released materials. Several studies (Muscatine, 1967; Trench, 1971a-c) have shown, for example, that homogenates of host tissues effect excretion by *S. microadriaticum*.

Symbiont derived nutrients may enchance calcification in some, as yet not clearly perceived, way. Goreau (1959) found that the dark corals with zooxanthellae sometimes calcified 2-3 times faster than corals which had lost their zooxanthellae. This evidence suggested to him that translocation of organic materials from the zooxanthellae may have been responsible for this dark enhancement of calcification. Further evidence along these lines was provided in later studies by Pearse and Muscatine (1971). They found that there is a gradient in calcification of *Acropora cervicornis* from rapid calcification at the tips of the branches of coral to less at the basal portions even though the tips contain fewer zooxanthellae than the basal portions of the branches. They found rapid calcification when the tip was experimentally darked and the lower portions illuminated. They also suggested that calcification might be stimulated through an organic photosynthetic product, translocated to the tip.

A number of workers have suggested light together with zooxanthellae significantly accelerate calcification in corals (Droop, 1963; McLaughlin and Zahl, 1966; Muscatine, 1973; Taylor, 1973a, b, Vandermeulen, et al., 1972). The situation is not as clear in the soritid foraminifera studied. In a laboratory study, light enhanced calcification of *A. angulatus* 3-4 fold after 19 days incubation (Lee and Zucker, 1969). There was no difference in calcification between fed and starved animals over the same period. In the present study, however, we were unable to demonstrate significant differences in calcification between organisms incubated for 6 hr either in the light or the dark. The organisms in the present study may have had sufficient symbiont "calcification enhancement product(s)" so that in the relatively short (6 hr) incubation period it was not rate limiting.

Fine structural studies of mature specimens have shown that in *S. marginalis* (Müller-Merz and Lee, 1976) feeding and symbiotic activities are morphologically separated. The symbiotic dinoflagellates are densely packed in the intermediate chambers along with many amorphous somatic nuclei. Only a few symbionts and somatic nuclei are found in the inner and outer chambers. A very few symbionts were also found in the embryonic apparatus. Food vacuoles were numerous but restricted to the outer chambers. We have not yet completed fine structural studies of *A. angulatus* but we have noted that *C. hedleyi* in their host were smaller and lacked the thick cell walls characteristic of the cells in axenic culture.

The compartmentalization of the symbiotic activities and the feeding activities in *S. marginalis* presents some interesting problems for the cell. One imagines that the digestive enzymes of the *S. marginalis* cells are either restricted to the outer chambers or are blocked from entering or turning

a symbiotic algal vacuole into a digestive vacuole. Recent data from another protozoan-symbiont relationship, *Paramecium bursaria-Chlorella* suggests that the latter might be a logical possibility (Karakashian and Karakashian, 1973). Cytochemical techniques for the demonstration of acid phosphatase, a digestive enzyme, are well-developed and provide an excellent means to find localized sites of digestive activities. The enzyme is present in food vacuoles and cytoplasmic vesicles but not present in adjacent perialgal vacuoles. Under appropriate experimental conditions both aposymbiotic *P. bursaria* and *Chlorella* can be grown separately from each other. Strains of *Chlorella* placed in cultures of aposymbiotic *P. bursaria* are ingested in large numbers. Most of the newly ingested algae are digested, but some of certain strains are not, and these live to establish a symbiotic relationship with their hosts. When heat-killed *Chlorella* were mixed together with an equal mixture of live algae, digestion was greatly delayed (50% in 43 hr). In control cultures, fed only dead algae, the paramecia completely digested all the algae within 24 hr.

Though the symbionts in both species of soritid foraminifera are quite unrelated to each other the host-symbiont systems seem to be functionally quite similar. Primary production is not the primary carbon route and both systems fix more carbon when the host is actively feeding. Since *S. microadriaticum* seems to be so pandemic in different types of coelenterates (McLaughlin and Zahl, 1959; 1966; Taylor, 1973b), and may also be the *S. marginalis* symbiont, and since soritids seem so well adapted or preadapted for symbiosis (Haynes, 1965; Lee, 1974; Lee et al., 1974) one wonders why one never finds this dinoflagellate in *Archaias* spp. collected in the field. It seems reasonable to suggest that this and many other interesting questions could be answered if aposymbiotic soritids and potential symbionts could be studied in gnotobiotic cultures.

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