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The Role of Feeding in the Metabolism of Larger Symbiont Bearing Foraminifera

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Abstract

The symbiont-bearing foraminifera *Amphistegina lobifera* and *Amphisorus hemprichii* feed on various species of unicellular algae found on their growth substrate. In this study we attempt to define the role of feeding in the carbon metabolism of the host-symbiont system. For this purpose, feeding rates and turnover of carbon taken up through feeding were measured with radiotracer methods. Following starvation, both species of foraminifera have high initial feeding rates on algae. Feeding rates later decrease and, after 8–24 hr, even net ejection may occur in the presence of food. Less than 5% of the carbon taken up through feeding is incorporated into the skeleton. The growth rate ratio of fed foraminifera compared to star fed specimens ranged between 1.0 to 6.9, depending on the species of food algae and the species of foraminifer. Over a two week period, the addition of inorganic dissolved phosphate and nitrate caused *A. lobifera* to grow 5 times faster than starved specimens, but fed specimens grew slightly faster. The growth of *A. hemprichii* was stimulated only two-fold by the addition of nutrients and four-fold by feeding. Pulse-chase experiments showed that *A. lobifera* ejects 75% of the carbon derived from food within 24 hr, while in *A. hemprichii* this process is more gradual. In a carbon/phosphorus double labelling pulse-chase experiment, *A. lobifera* retained, during a chase incubation of one week, 33% of the phosphorus but only 8% of the carbon. In *A. hemprichii*, there was no meaningful difference between the rates of retention of carbon and phosphorus. These observations indicate that *A. lobifera* uses feeding mainly as a source of nutrients while in *A. hemprichii* food may be a source of carbon and energy.

Keywords: foraminifera, feeding, egestion, retention, nutrients

1. Introduction

Although symbiont-bearing foraminifera may have a potential for autotrophy, some benthonic species are heterotrophic and feed on algae (Lee and Zucker, 1969; Lee and Bock, 1976; Lee et al., 1980, ter Kuile and Erez, 1984; reviews by Lee, 1974, 1980, 1983). In contrast, spinose planktonic species are more carnivorous, eating primarily zooplankton (Bé et al., 1981; Caron et al., 1981; Caron and Bé, 1984). Measurements of feeding rates compared with symbiont photosynthesis have been used to calculate carbon budgets (Lee and Bock, 1976; Lee et al., 1980). It was estimated that for all species examined carbon derived from feeding exceeds photosynthetic uptake by a factor of ten. The feeding rates reported were high when compared to the growth rates of these organisms. In these short term experiments it was not possible to distinguish between carbon uptake and incorporation, and no measurement was made of the amount of food egested (Lee and Bock, 1976; Lee et al., 1980). Based on microscopic observations Lee (1974) suggested that feeding is an episodic process in which the foraminifera gather large amounts of food to be digested later. Koestler and coworkers (1985) showed by means of electron microscopy that food algae are taken up by the pseudopodia and ingested in vacuoles while still outside the foraminiferal test. Digestion may already start at this stage, but occurs mainly inside the test. Vacuoles with digested food, possibly to be egested, were observed in the cytoplasm. In this study, the amounts of food incorporated into the structural organic matter, taken up by the skeleton, respired and egested were determined in order to complement these observations.

Some species of symbiont-bearing foraminifera can grow in the light without the addition of food as long as they are provided with nutrients, but cannot grow in the dark even when supplied with food (Rottger et al., 1980). It is therefore not clear which benefits they may derive from feeding. Jorgensen et al. (1985) suggested that the planktonic foraminifer, *Globigerinoides sacculifer* uses its food as a source of nutrients to stimulate photosynthesis of the symbionts, rather than as a carbon and energy source. Similarly, Falkowski et al. (1984) suggested that feeding in light adapted corals serves mainly as a source of nitrogen. Therefore we investigated the possibility that food is used as a nutrient source.

In this study we examine the role of feeding in the metabolism of two species of benthonic symbiont bearing foraminifera: *Amphistegina lobifera* and *Amphisorus hemprichii*. The following questions are addressed specifically: (1) What are the kinetics of the feeding process and is it a gradual

or a discontinuous process? (2) What fraction of the carbon that is ingested through feeding is incorporated into the organic matter and what fraction ends up in the skeleton? (3) Is feeding indeed more important as a source of nutrients than as a carbon and energy source?

2. Materials and Methods

Amphistegina lobifera, *Amphisorus hemprichii* and *Borelis schlumbergeri* were obtained from a *Halophila* sp. meadow 2 km south of the H. Steinitz Marine Biology Laboratory at 15 m depth, as described previously (ter Kuile and Erez, 1984; 1987). *Operculina ammonoides* and *Heterostegina depressa* were collected near the same location from a mud area and stones at 30–40 m depth respectively. Experiments on *A. lobifera* and *A. hemprichii* were conducted throughout the growth season, hence specimens of different age, having different size and weight, were used. The experiments were carried out in 100 ml beakers with 80 ml medium. Each data point is based on specimens incubated in one beaker. Results presented in one graph were obtained by incubating all beakers under equal conditions, starting at the same time. The foraminifera were concentrated on the bottom of the beaker, so that they were all equally exposed to the food. Prior to an experiment the foraminifera were starved for 2 days and preincubated in the beakers at least 24 hr in order to allow the pseudopodial networks to develop completely.

The foraminifera were fed on *Nitzschia ovalis*, a small diatom, and *Chlorella* sp. (AT), a chlorophyte, both from the collection of J.J. Lee (Lee, 1980; Lee and McEnery, 1983). The food algae were cultured in 100 ml Ehrlenmeyer flasks in Erdschreiber medium made with filtered seawater (FSW) Lee et al., 1975). The radiotracer used was primarily $NaH^{14}CO_3$ (5 μCi/100 ml); in one experiment, double labelling with $NaH^{14}CO_3$ (5 μCi/100 ml) and $Na_2H^{32}PO_4$ (10 μCi/100 ml) was applied. The label was added to algae that were in logarithmic growth, 3 days before harvesting. The algal cells were harvested by repeated centrifugation at 3000 RPM, followed by resuspension in nonlabelled FSW until the supernatant contained only background levels of radioactivity. The algae were then resuspended in FSW, mixed thoroughly and added in equal quantities to the experimental beakers containing the foraminifera. Triplicate aliquots of the suspension added to the beakers were filtered onto preweighed Nuclepore filters (pore diameter 0.4 μm) dried, weighed and counted with 10 ml of Instagel (Packard) in a Packard Tri Carb Liquid Scintillation Spectrometer. In this way the specific activity of the algae was measured as counts per

minute (CPM) per μg dry wt. algae.

The radioactivity in the various fractions of the foraminifera was analyzed as described previously (Erez, 1977; 1983; ter Kuile and Erez, 1987). At the end of the incubation the medium was replaced several times while shaking vigourously, whereby almost all the food not ingested was removed. The foraminifera were then rinsed 3 more times on a filter unit with FSW and one final rinse with double distilled water (DDW). The washwater never contained more than background levels of radioactivity. We therefore assume that this rinsing procedure did not cause loss of radioactivity because of lysis of the algae. After drying, the foraminifera were cleaned from adhering algae with brushes, sorted to species and crushed. Approximately 5 mg of crushed foraminifera was weighed on a Cahn 25 electrobalance and transferred to a liquid scintillation vial. Approximately 20 mg reagent grade $CaCO_3$ was added to drive all the inorganic carbon (the sum of CO_2, HCO_3^- and $CO_3^=$) out of solution after acidification. The vial containing the sample was placed in a 400 ml jar with a second vial containing 2 ml Oxisorb (New England Nuclear). The jar was tightly sealed and the sample acidified by injection with 2 ml of 8.5% H_3PO_4. The inorganic carbon was trapped in the vial with Oxisorb with an efficiency of 80±3% and counted with 10 ml Instagel. The contents of this vial is called "skeleton". The fraction left over in the vial originally containing the sample, onwards called "organic matter" was also counted with 10 ml Instagel. The channels ratio of the organic matter and the specific activity samples was constant and equal throughout the experiments, hence no quench correction was needed. This analytical method has been tested extensively before and was found to give an overall precision of ±5.2% (ter Kuile and Erez, 1987). The results of the organic matter were calculated in units of μg algae/mg foraminifera as follows:

$$\frac{\text{CPM sample}}{\text{Weight sample} \times \text{ specific activity}} = \mu\text{g algae/mg foraminifera}$$

The results of the skeleton fraction were corrected for the efficiency of the absorbtion in the Oxisorb. In the $^{14}C/^{32}P$ double labelling experiment, 3 windows were used for counting, 1 for only receiving ^{32}P counts. Standards containing only ^{14}C and ^{32}P and a repeated count 14 days after the first were applied to ensure separation of the ^{14}C and ^{32}P counts.

During the chase run of the pulse chase experiments, which were designed to follow the egestion of food after feeding, the animals were regularly cleaned of egested algae and provided with fresh non-labelled *Chlorella* sp (AT).

In one experiment the effect of different species of food algae an varying conditions (Table 1) on the growth of the foraminifera was determined by long term (10 days) non radiotracer methods. Growth, defined as the total addition of weight, was measured optically by converting sizes to weight (ter Kuile and Erez, 1984). The laboratory incubations were carried out in 100 ml beakers with excess quantities of specific food algae (Table 1). One incubation consisted of specimens that were allowed to resettle on leaves of *Halophila* of which all other foraminifera were removed by means of a forceps. The *in situ* incubation was in cages made of 4 cm long pieces of perspex tubing with an inner diameter of 5 cm, covered at both ends with 200 μm mesh plankton netting, permitting water and small particles to exchange freely (ter Kuile and Erez, 1984). The cages were incubated 5 cm above the bottom of the sea off the H. Steinitz Marine Biology Laboratory, Eilat at a depth of 10 m.

3. Results

The net uptake of *Chlorella* sp. (AT) and *Nitzschia ovalis* by *A. lobifera* and *A. hemprichii* as a function of time is shown in Fig. 1. The initial uptake was very rapid: between 8–30% of the maximum uptake, which was achieved in 8–48 hr, occurred in the first 6 min after addition of the food. Following this rapid initial uptake, the feeding rates strongly declined. Net uptake of *A. lobifera* feeding on *Chlorella* sp (AT) (Fig. 1A) stopped after 24 hr, even though a high concentration of labelled food was still present. Feeding by *A. lobifera* on *Nitzschia ovalis* basically followed the same pattern. Uptake in this case reached a maximum after 8 hr, but after 24 hr only half of that amount was still present. This suggests that net egestion occured even though labelled food was still available in the incubation medium. It must be stressed that the curves of Figs. 1,2 and 5 represent net uptake. The egestion rate at different times of the incubation period is not known, hence the actual feeding rates cannot be determined. The term *maximum uptake* is used to describe the maximum amount of food present at one time in the foraminifera.

The feeding kinetics of *A. hemprichii* differed only slightly from that of *A. lobifera* (Fig. 1B). The uptake in the first 2 hr may be less rapid and therefore the rates from 2 to 8 hr were slightly higher. The maximum uptake

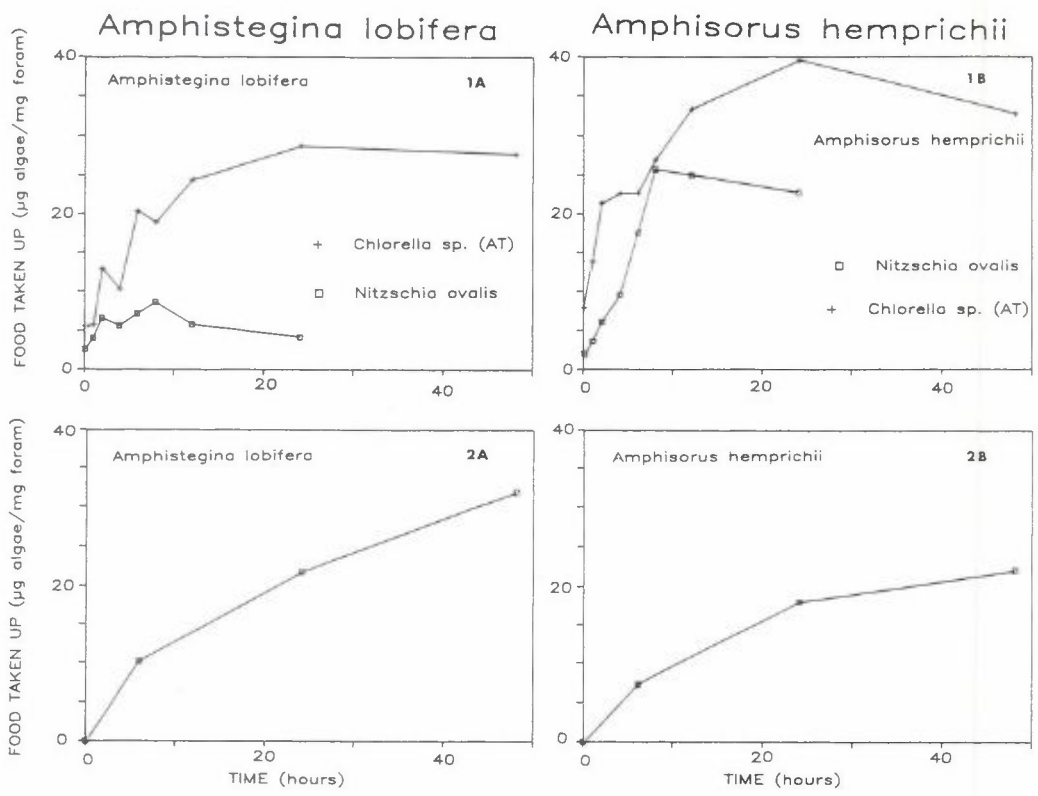

Figure 1. Uptake of algae as food by *A. lobifera* and *A. hemprichii*. The specimens were starved for 2 days prior to the start of the incubations. Food was provided in excess (roughly 150 µg dry weight/ml). Note that the data in this as well as in other figures are presented as net uptake for the duration of the experiment and not as rates. The average weight of *A. lobifera* feeding on *Chlorella* sp. (AT) and *Nitzschia ovalis* was 68 µg and 463 µg respectively, that of *A. hemprichii* 207 and 327 µg respectively.
1A. *A. lobifera* feeding on *Chlorella* sp. (AT) and *Nitzschia ovalis*. Much larger specimens were used in this experiment, which feed less per weight. Normalized to surface area slightly more *N. ovalis* was taken up than *Chlorella* sp. (AT). Note the net egestion after 8–24 hr and even net egestion can be noticed.
1B: *A. hemprichii* feeding on *Chlorella* sp. (AT) and *Nitzschia ovalis*. The uptake stopped after 8–24 hr and even net egestion can be noticed.

Figure 2. Feeding at low food concentrations (10% of that used in Fig. 1). *Chlorella* sp. was added to a concentration of 15 µg dry weight/ml. The average weight of *A. lobifera* and *A. hemprichii* was 137 µg and 331 µg respectively.
2A. The initial uptake rate by *A. lobifera* was still higher than in the later stages, but the difference is much less pronounced than when food is supplied in excess (compare to Fig. 1A).
2B. The uptake by *A. hemprichii* was only half of that when food was supplied in high concentrations. This was the only case that the total amount taken up by *A. hemprichii* was less than was taken up by *A. lobifera*.

of *Chlorella* sp. (AT) was reached after 24 hr and of *N. ovalis* after 8 hr. In both cases a slight net egestion in the presence of labelled food was observed after the maximum was reached.

In the experiments described in Fig. 1, food was supplied in excess. The results of a second experiment, where only a tenth of the original concentration (15 μg dry weight/ml *Chlorella* sp. (AT) instead of 150 μg dry weight/ml) was added are shown in Fig. 2. Both species had much lower initial uptake rates, but relatively higher rates afterwards, than when food was added in excess. In 48 hr *Amphistegina lobifera* (Fig. 2A) incorporated as much as when fed in excess. At the low food concentration *A. hemprichii* ingested half as much as animals grazing on high concentrations of food (Fig. 2B). This suggests that the food concentration was too low to reach the maximum feeding potential of *A. hemprichii*.

There were no basic differences between the two species of foraminifera examined with respect to the kinetic of the feeding process. The egestion of food in pulse-chase experiments after 48 hr of uptake (Fig. 3), suggested that food may play a different role in the nutrition of both species. *A. lobifera* (Fig. 3A) excreted 75% of the food taken up in 48 hr during the first 24 hr of "cold" chase (incubation with unlabelled food). An additional 19% of the food initially present was released during 9 days of chase incubation, leaving only 7% in the foraminifer after 10 days. The excretion of *A. hemprichii* (Fig. 3B) was much slower and more gradual. During the first 24 hr of chase incubation only 13% of the food initially present was released. After 10 days of incubation with cold food half of labelled food was still present. This may indicated that *A. hemprichii* is more dependent on feeding for its structural organic matter. Neither *A. lobifera*, nor *A. hemprichii* incorporated more than a few percent of the carbon taken up by feeding into their skeletons. Once incorporated into the skeleton, the amount of carbon did not decrease during the chase incubations.

The pulse-chase experiment raised the question: Why does *A. lobifera* feed at high rates and egest most of the food taken up within 24 hr? One possible hypothesis is that *A. lobifera* uses food more as a source of nutrients rather than carbon. If this is indeed true,then when ^{14}C is used as a label, a larger portion of the food taken up will be egested than when ^{32}P is used. In Fig. 4 the results of a feeding experiment using double labelling with ^{32}P and ^{14}C as tracers are are shown. The foraminifera were fed the labelled algae during 6 hr and the chase incubation was continued up to 1 week. With respect to carbon the results of this release experiment strongly resembled the outcome

Table 1. Growth of *A. lobifera* and *A. hemprichii* under different conditions and with different algal species as food. Growth was slowest for both species starved in the laboratory and fastest in cages incubated *in situ*. The enriched medium, mainly adding nitrate and phosphate, stimulated growth of *A. lobifera* more than growth of *A. hemprichii*. The effect of feeding on the different species of algae was different for each of the foraminifera.

	Growth in %/day	
Conditions	*A. lobifera*	*A. hemprichii*
Starved	0.29	0.41
Enriched medium	1.53	0.90
Cage *in situ*	3.06	2.19
Halophila	1.57	1.41
Chlorella sp (AT)	1.34	1.56
Nitzschia ovalis	2.01	1.18
Amphora sp.	0.50	0.50
Chaetoceras sp.	1.82	0.43

of the experiment described in Fig. 3. *A. lobifera*, however, retained much more labelled phosphorus than carbon. After 1 week, 8% of the carbon was left, whereas 32% of the phosphorus was still present (Fig. 4A). In the case of *A. hemprichii* there was no significant difference between the degree of retention of carbon and phosphorus (Fig. 4B). Both were gradually released at roughly the same rate as in the earlier experiment (Fig. 3).

The effect of feeding on growth of *A. lobifera* and *A. hemprichii* was determined in an optically measured growth experiment (Table 1) (methods as in ter Kuile and Erez, 1984). Starved specimens grew slowest, whereas individuals incubated *in situ* in cages grew fastest. In the latter case these specimens were probably exposed to a mixture of food sources. For *A. lobifera*, *Nitzschia ovalis* was the best food, in the sense that it stimulated growth most, *A. hemprichii* grew best on *Chlorella* sp. (AT). Also specimens allowed to climb on *Halophila* sp. leaves grew well. *Chaetoceras* sp. only supported growth of *A. lobifera* while *Amphora bigibba* did not stimulate growth in either species. It is noteworthy that the enriched medium, mainly providing dissolved inorganic phosphate and nitrate, enhanced growth of *A. lobifera* to a much higher degree than growth of *A. hemprichii*.

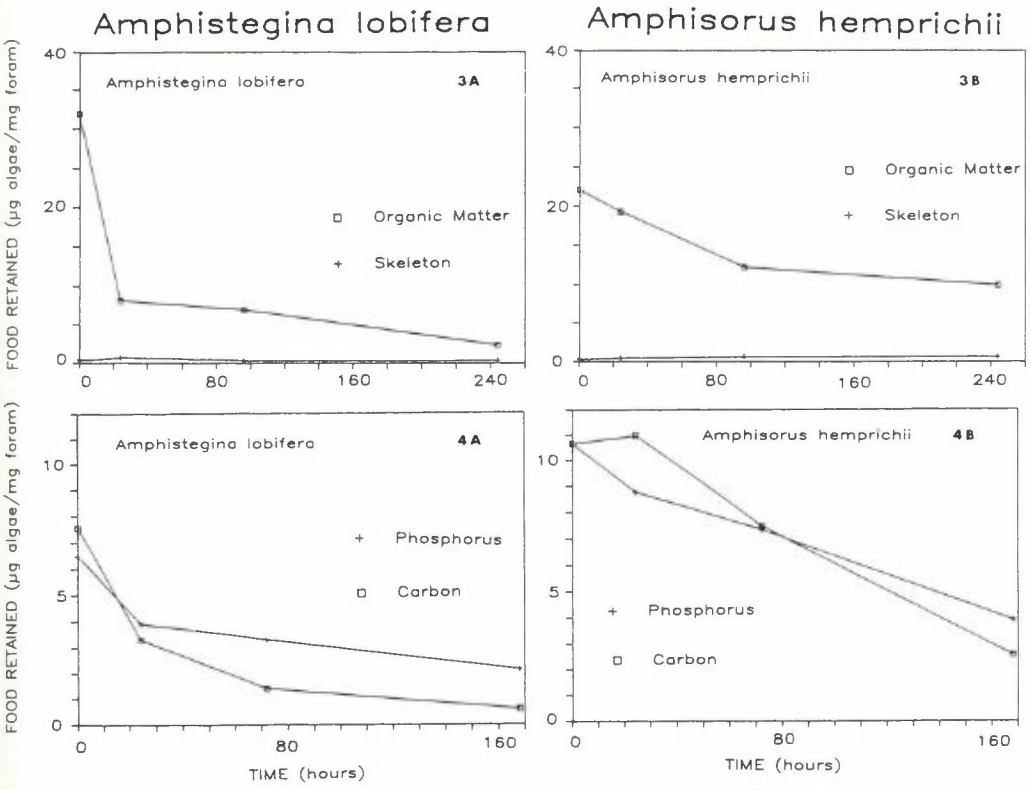

Figure 3. Release of food (*Chlorella* sp.) taken up during 24 hr. Cold food was added at the beginning of the chase incubation. The average weight of the foraminifera was equal to those of Fig. 2.
3A. *A. lobifera* showed a very rapid ejection during the first 24 hr of the chase period. The part that was left over after 24 hr was released much more gradually, while the amount incorporated into the skeleton hardly decreased.
3B. *A. hemprichii* release food much slower than *A. lobifera*. A larger percentage (almost 50% of the food ingested) was present 10 days after the labelling. The fraction that was incorporated into the skeleton was 2–3 times higher than in *A. lobifera*.

Figure 4. Comparison of the retention of carbon and phosphate derived from food taken up during 6 hr. Average weight of the foraminifera: *A. lobifera*: 690 µg; *A. hemprichii*: 1943 µg.
4A. *A. lobifera* again showed rapid release during the first 24 hr of the chase incubation. Afterwards phosphate is retained to a much higher extent than carbon.
4B. *A. hemprichii* released food more gradually, without a meaningful difference between carbon and phosphorus as tracers.

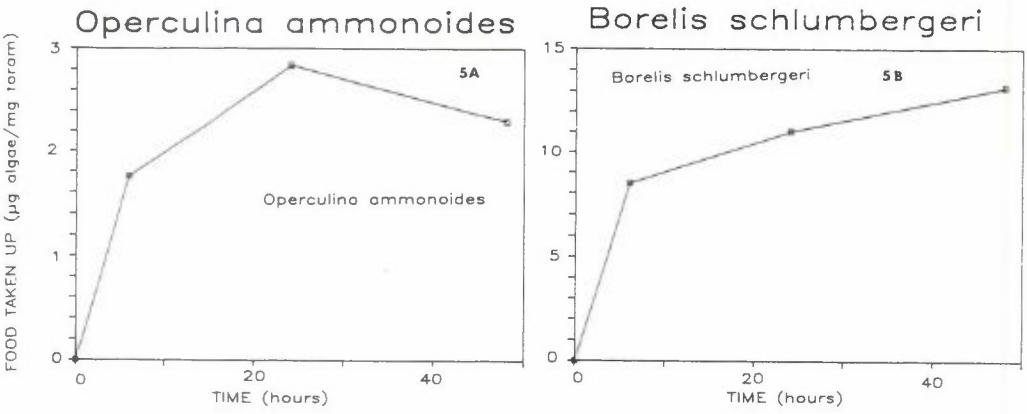

Figure 5. Kinetics of the uptake of *Chlorella* sp. as food by two other species of foraminifera: *Operculina ammonoides* and *Borelis schlumbergeri*. The average weight was 1344 μg and 339 μg respectively.
5A. The uptake of *O. ammonoides* was much lower than by the other species used in this study, but the kinetics were basically equal. A few percent of the carbon taken up as food is incorporated into the skeleton.
5B. The kinetics of feeding by *B. schlumbergeri* resemble those of other species. The amount eaten was intermediate between *O. ammonoides* and *A. lobifera* or *A. hemprichii*.

In order to examine the extent to which the feeding kinetics of *A. lobifera* and *A. hemprichii* can be generalized for other foraminiferal species, the experiments measuring uptake of food as a function of time were repeated on *Operculina ammonoides* and *Borelis schlumbergeri*. Compared to the other species *O. ammonoides* (Fig. 5A) ingested only small amounts of *Chlorella* sp. (AT). *B. schlumbergeri* ate only a quarter to a third of the amounts eaten by *A. lobifera* and *A. hemprichii*. The uptake kinetics were similar, however. The uptake by *O. ammonoides* did not increase from 24 to 48 hr (Fig. 5A). In the same period *B. schlumbergeri* added only a third of the amount taken up during the first 6 hr (Fig. 5B). Due to a lack of specimens of *Heterostegina depressa* measurements of feeding were only made during 24 hr (data not shown). The live uptake (0.200 μg algae/mg foram) was equal to the dead control (0.176 μg algae/mg foram) and was less than 1% of the uptake of *A. lobifera* and *A. hemprichii* (28.803 and 40.206 μg algae/mg foram respectively).

4. Discussion

The contribution of feeding to the total carbon budget

In this study the feeding rates of *A. lobifera* and *A. hemprichii* on algae were high when expressed as percent of the organic matter of the foraminifera. During 24 hr, up to 40 μg algae was taken up per mg foram. The organic matter content (dry weight) of *A. lobifera* and *A. hemprichii* was 70–90 μg/mg foram (Erez, unpublished), resulting in a feeding rate of 50%/day. The growth rate of thee organisms was 2–6%/day (ter Kuile and Erez, 1984). This indicates that on a basis of dry weight of organic matter, feeding exceeds growth by a factor of ten. Much higher values have been reported (Lee and Bock, 1976) for *Archaias angulatus* and *Sorites marginalis* (up to 0.97 g C/g organic matter in 6 hr) and for *A. lobifera* and *A. hemprichii* (9.3 μg C/μg protein/hr in a 4 hr experiment) (Lee et al., 1980). Since these measurements were made in short term experiments, they may represent the rapid initial uptake, rather than incorporation. While comparing feeding rates, it should be kept in mind that heavy (old) specimens have much lower feeding rates (compare Figs. 3 and 4). The results of the chase experiments (Figs. 3 and 4) suggest that *A. lobifera* incorporates only a small portion of the food taken up. *A. hemprichii* may incorporate a bigger part. In both species the carbon obtained from food is primarily retained in the organic fraction and little is incorporated into he skeleton. Moreover, it is possible that some of the label incorporated into the skeleton might originate from carbon respired by the algae before being taken up as food.

Feeding rates decrease strongly after rapid initial uptake (Figs. 1 and 2). Most of the food taken up is eventually egested (Figs. 3 and 4). Short term feeding experiments (Lee and Bock, 1976; Lee et al., 1980), therefore, considerably overestimate the contribution of feeding to total carbon incorporation. A more accurate estimate can be made if both uptake and the degree of retention are taken into account. Both *A. lobifera* and *A. hemprichii* retained photosynthetically acquired carbon almost completely during a chase incubation of 1 week (ter Kuile and Erez, 1987). *A. lobifera* egested 92% of the carbon taken up as food in 1 week, *A. hemprichii* approximately 50% (Figs. 3 and 4). *A. lobifera* specimens with an average weight of 70 μg incorporated approximately 1 μg C/mg foram through symbiont photosynthesis in 6 hr (ter Kuile and Erez, 1987) compared to a feeding rate of 20 μg algae/mg foram, of which approximately half is carbon (Sverdrup et al., 1942), in the same time. Taking only these data into account, the ratio between symbiont photosynthesis and feeding would be 1:10. A more realistic photosynthesis to

feeding ratio based on long-term incorporation is probably 2:1 for *A. lobifera* and 1:1.5 for *A. hemprichii*. Not taking egestion into account, Lee and Bock (1976) and Lee et al. (1980) reported a primary production to feeding ratio of 1:10. Lee et al. (1980) commented that this estimate may be exaggerated due to the experimental conditions, which were designed to increase feeding rates. Corrected for egestion, a ratio of 1:0.5–2 seems not unlikely for their data also. These estimates are based on feeding experiments using one food organism. In reality foraminifera are eating a mixture of algae and bacteria (Muller and Lee, 1969; Muller, 1975) and the total feeding rate may therefore be higher. The kinetics of feeding agree well with the microscopic observations of Lee (1974) and Koestler et al. (1985). The high initial uptake rates suggest that food algae that are taken up by the pseudopodial network are immediately transported inwards. The uptake continues till the foraminifera are filled to capacity with food, resulting in a strong decline of the feeding rates, even though food is still available. At reduced food levels more time is needed to gather the food, but the capacity of the foraminifera is unchanged (compare Figs. 1 and 2). A big portion of the food may be egested after partial digestion (Figs. 3 and 4). *A. lobifera* egests its food much faster than *A. hemprichii* (Fig. 3 and 4). Other species, like *O. ammonoides* and *H. depressa* may obtain considerably less or none of their carbon from feeding on algae. Possibly they feed on bacteria (Lee et al., 1980) or all their carbon is acquired through symbiont photosynthesis (Röttger et al., 1980). Based on measurement of the uptake only and assuming a similar egestion as in *A. hemprichii*, *B. schlumbergeri* seems to be intermediate in this respect. It probably derives about a third of its carbon from feeding.

The role of feeding in the metabolism of foraminifera

The function of feeding in foraminifera may be different in different species. In *A. hemprichii* it may serve mainly as a source for carbon and energy. The results of the carbon/phosphorus double labelling experiment (Fig. 4) suggest that *A. lobifera* uses its food mainly to provide nutrients; much more phosphorus is retained than carbon and *A. lobifera* respires 5 to 6 times less food than *A. hemprichii*. Röttger et al. (1980) observed no growth of fed specimens of *Amphistegina lessonii* in the dark. They concluded that foraminifera are mainly autotrophic. Feeding stimulates growth more in the light than in the dark (ter Kuile and Erez, 1984). Starved *Amphistegina* species provided with nutrients in the light grew 5 times faster than starved specimens in FSW (Röttger et al., 1980; Table 1 of this study), but growth

of *A. hemprichii* was stimulated only two-fold by the addition of nutrients. The effect of feeding or the addition of nutrients was approximately equal in *A. lobifera*, but nutrients were less effective than food in *A. hemprichii*. This suggests that in *A. lobifera* feeding stimulates photosynthesis of the symbionts by providing nutrients, rather than serving as a source for carbon and energy for the host. Similarly, planktonic foraminifera in oligotrophic waters can maintain their high rates of photosynthesis through the uptake of nutrients from food (Jorgensen et al., 1985). However, feeding frequency influences the growth rates of the planktonic foraminifer *Globigerinoides sacculifer* more than do changes in symbiont photosynthetic rate (Bé et al., 1981; Caron et al., 1981). This suggests that feeding may not solely affect the photosynthetic activity of the symbiotic algae in planktonic species.

It may be instructive here to draw a parallel with hermatypic corals. Szmant-Froelich and Pilson (1977) have demonstrated the transfer of nitrogen from ingested food to the symbionts in the coral *Astrangia danae*. It has been suggested that the primary importance of the feeding process in coral metabolism is its role as a source of nitrogen and phosphorus (e.g. Wafer et al., 1985). Jacques and Pilson (1980) reported that feeding stimulated photosynthesis by two-fold and calcification three-fold in the symbionts of *Astrangia danae*. They suggested that this effect was caused by ammonia production, in concurrence with our line of thought. Davies (1984) suggested that nitrogen rather than carbon translocated by the symbionts, was the limiting factor for growth in corals. A different hypothesis was proposed by Falkowski and coworkers (1984). They estimated that 80% of the carbon translocated by the symbionts was respired. They argued that the symbionts provided a nitrogen depleted energy source, which could not be incorporated into the structural organic matter of the coral. This leaves the host dependent on outside sources of nitrogen. Although they did not speculate on the nature of this source, feeding would be a plausible candidate. However, shade adapted corals may depend on feeding as a carbon source, since the estimated transfer of photosynthates by the symbionts is not sufficient to account for measured growth rates (Muscatine et al., 1984). Also, symbiont bearing zoanthids require feeding as a supplementary carbon source (Steen and Muscatine, 1984).

In conclusion it can be stated that feeding in algal symbiotic associations can either serve as nutrient source, as in *A. lobifera* and light adapted corals, or as a source of carbon and energy, as in *A. hemprichii*, shade adapted corals and zoanthids, or both. As to the foraminifera, it seems that the perforate

and imperforate foraminifera not only differ with respect to their calcification mechanisms (ter Kuile and Erez, 1987), but also with respect to the role of feeding in their metabolism.

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