Temperature dependance of endosymbiontic relationships? Evidence from the depth range of mediterranean *Amphistegina lessonii* (Foraminiferida) truncated by the thermocline

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ABSTRACT

Off the shores of Eastern Crete (Eastern Mediterranean Sea), the depth distribution of *Amphistegina lessonii* is truncated by the thermocline while other organisms including elphidiids, depending as well on light by their photosynthesis or their symbiosis with algae, reach the much deeper lower end of the photic zone. The difference of depth distribution in respect to the thermocline in amphisteginids and elphidiids is explained by their different type of symbiosis, complete cells growing and reproducing within the host shell of amphisteginids, chloroplast husbandry in elphidiids. Therefore, we suggest that too low temperatures do not hamper photosynthesis but rather the growth and reproduction of the symbionts.

RESUME

Autour des côtes Est de l'Ile de Crète (Méditerranée Orientale), la distribution en profondeur d'*Amphistegina lessonii* est tronquée par la thermocline à 60–70 m tandis que d'autres organismes, elphidiidés inclus, dépendant aussi bien de la lumière par leur activité photosynthétique ou par leur symbiose avec des algues, atteignent la limite inférieure de la zone photique à 135–140 m. La différence de répartition des populations d'amphistégines et d'elphidiidés par rapport à la thermocline est expliquée par leur différent type de symbiose. Les amphistégines abritent des diatomées capables de croître et de se reproduire, les elphidiidés portent des chloroplastes isolées dans leur protoplasme. Il en est conclu que des températures trop basses du milieu n'empêchent pas le fonctionnement de la photosynthèse des symbiotes mais bloquent la croissance et/ou la reproduction des algues symbiotiques.

Introduction

Paleobathymetry is a major issue in current sequence stratigraphy. Independant methods to estimate depth of deposition are needed to control the depth estimates derived from sedimentological arguments and basin analysis. We consider methods as independant if they are based on biological processes governed by water depth and reflected by the distribution of fossils in sedimentary sequences. The latter register sealevel rise and fall in the most accurate way where the ecological gradients linked to water depth (light, water energy, temperature and nutrient supply) are steepest, i.e. in shallow water. The present paper attempts to offer some understanding of the interplay between the different ecological factors in the depth gradient in order to enhance the ecological interpretation of the distribution of benthic foraminifera, the most important depth indicators in shallow sediments of Late Cretaceous to recent age.

Symbiont-bearing corals and foraminifera are supposed to be restricted to climatic belts defined by minimum winter temperatures in surface water of 18°C for most hermatypic corals and 16°C for symbiont-bearing *Heterostegina depressa* and *Amphistegina lobifera*. These two species are considered as lessepsian migrants by Reiss and Hottinger (1984), i.e., immigrants from the tropical realm with winter minimum temperatures around 18°C. Their geographic distribution in the Mediterranean, as known so far, corresponds to the winter isotherm of 16°C, (see Murray 1991, Fig. 11.2, p. 185). However, this kind of correlation constitutes rather poor evidence because biogeographic data are always incomplete and must include data from literature with doubtful or questionable identifications of species in need of interpretation. This is particularly the case for larger, symbiont-bearing foraminifera such as, for instance, amphisteginids and soritids cited from the available literature by Murray (1991).

A survey of the foraminiferal faunas on the coasts of Eastern Crete permitted to study the depth distribution of *Amphistegina lessonii* in the presence of a thermocline in order to

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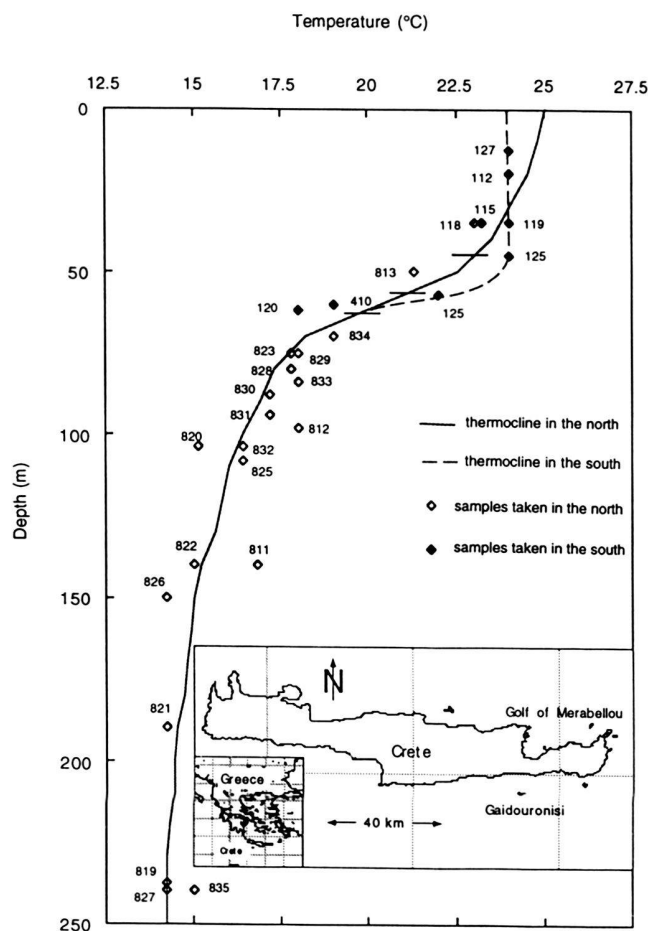
Fig. 1. Location of study area and depth distribution of temperature in September off the coasts of Eastern Crete. Discrete temperature gradient discontinuities are marked by horizontal bars.

compare it with its tropical occurrences, where the thermocline is absent or too deep to interfere with the light-dependant ecosystems in the photic zone. The present paper reports the depth distribution of dead shells of *Amphistegina lessonii* in sediments collected from depths between 3 and 230 m and compares it to the depth distribution of selected other species and to water temperature measured at the sites of sampling. This is an attempt to show the temperature dependance of this particular species and to discuss its significance by correlating the frequency rates with the thermocline in the depth gradient rather than with the winter minimum isotherm extending over large areas of the mediterranean.

Material and methods

Sediment sampling off Crete was carried out during autumn 1974 by SCUBA diving down to about 60 m and by grab to 230 m. The grab was lowered by a hand-driven winch mounted

on a large rubber boat constructed with one half of a World War II military ponton bridge element (Hottinger, 1976). Field activities were carried out by the Swiss Academy of Natural Sciences (on behalf of the Swiss National Foundation for Scientific Research) aimed at the preliminary exploration of the benthic life in coastal waters in order to decide about an implantation of a marine biological station on Crete. 21 sediment samples were taken on the North-Eastern coast of Crete in the Gulf of Merabellou (Hagios Nikolaos), 23 samples around Gaidouronisi Island off the South-Eastern coast of Crete (Fig. 1). For the present study, 13 samples from the North and 11 samples from the South were selected for quantitative analysis. They represent depths between 3 and 230 m. Temperatures (Fig. 1) were measured by a minimum-maximum thermometer fixed on the line of the grab about 30 cm above ground or by ordinary diving thermometers carried by the SCUBA divers who noted the values over sampling sites on their underwater note-pad. Levels of sharp discontinuity in the temperature gradient can be seen by the diver and were noted on the pad during the dives.

Sediment samples were washed in freshwater and dried in air. Sample splits of 0.3 cm^3 were picked under the binocular microscope for all identifyable organisms. The standard volume of sediment chosen yielded between about 300 and 1500 foraminifera. The foraminifera were identified to species level and counted. 96 species could be identified, mainly by using the illustrated inventory of mediterranean foraminifera by Cimerman and Langer (1991) but also by Wiesner (1923) and Hottinger et al. (1993). Some samples from the Gulf of Merabellou are contaminated with reworked Miocene foraminifera washed into the sea from steep coastal outcrops of marine marls. The fossil contaminants are easily detectable by their vivid brownish coloration and by their lack of transparency. As they originate from open marine deposits far below the photic zone, their occurrence does in no way interfere with the scope of the present paper.

Additional 13 sediment samples collected by SCUBA diving on the Maledivan Islands representing 1–68 m depth, were selected from exposed and sheltered reef slopes of the Maledivan Islands (Indian Ocean; Hottinger 1980). *A. lessonii* was picked and counted from standardized splits in order to note their coiling direction.

Foraminiferal depth distribution in Crete

1. In Crete Island, the amphisteginids are represented by a single species, *A. lessonii* (see Hottinger et al. 1993, Pl. 184–185). Specimen abundance is highest in the uppermost 20 m of the water column reaching about 1600 specimens per unit sediment volume in the shallow deposits around Gaidouronisi which consists almost exclusively of recently produced shells on the site of their deposition. The depth range of *A. lessonii* in Crete is clearly limited to 60 m (Fig. 2).
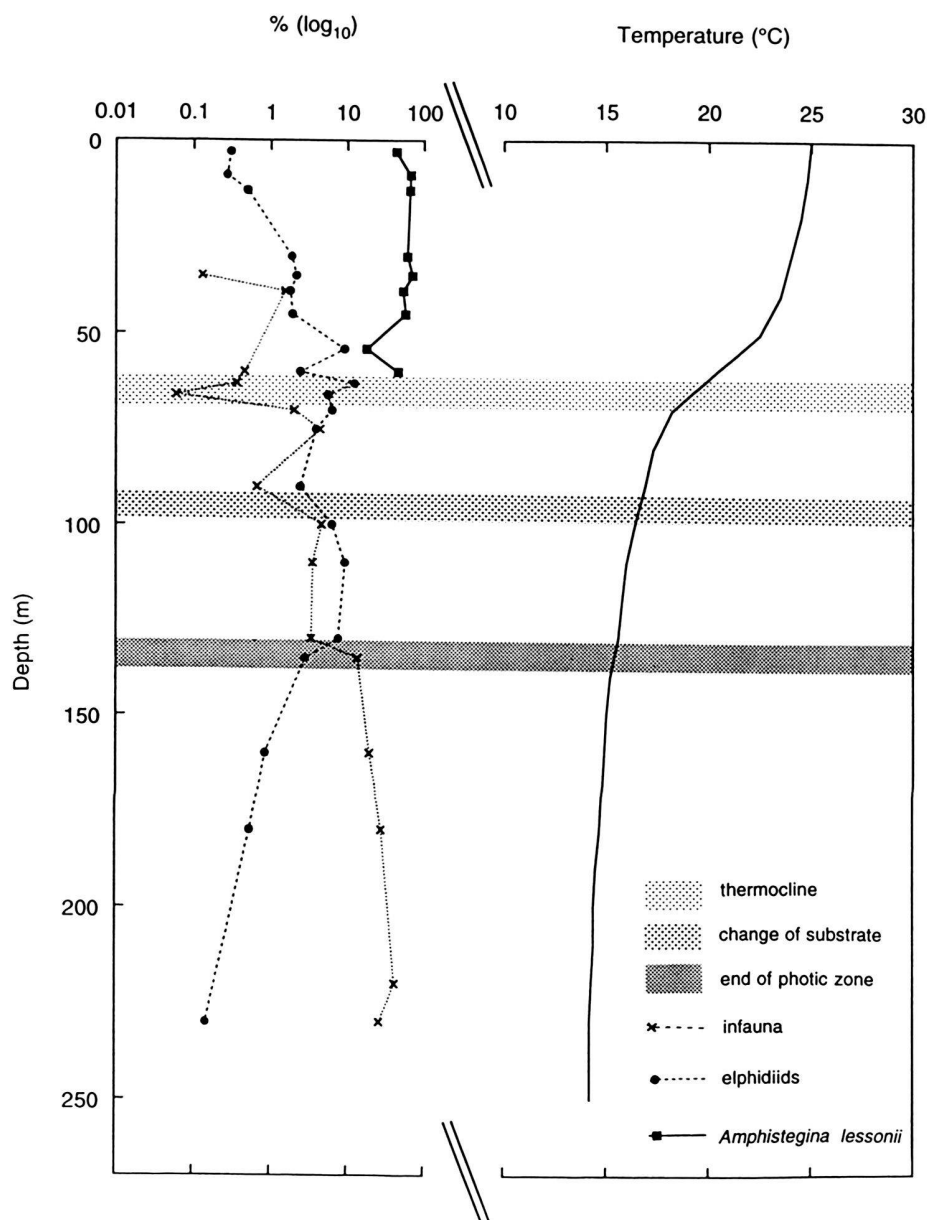
Fig. 2. Depth distribution of foraminiferal shells in the sediment from infaunal species, elphidiids and *Amphistegina lessonii* compared to depth gradient discontinuities in Eastern Crete. Frequencies are given in percent of total specimens in unitary sediment volumes. Note logarithmic scale of the frequency distribution.

2. The elphidiids, represented mainly but not exclusively by *Elphidium crispum*, reach their maximum frequency at 63– 66 m and their lower limit of the depth range at 135 m. Deeper specimens are few and might have been transported considering their small size (Fig. 2).

3. *Miniacina miniacea*, the permanently sessile, filterfeeding pioneer, reaches 93 m depth in significant numbers: between 93 and 110 m depth, the number of specimens per unit volume of sediment drops from 140 to 5.

4. Infaunal species such as *Uvigerina mediterranea*, *Bulimina marginata* or *Brizalina earlandi* appear in significant numbers at 100 m increasing in abundance towards depth (Fig. 2).

5. The peneroplids, i. e. *Sorites orbiculus*, *Peneroplis* sp. and *Coskinospira hemprichii* reach 68 m depth. Strikingly enough, the abundance of these porcelaneous larger foraminifera except *C. hemprichii* increases with depth: percentages relative to the total number of foraminifera present in a sample reach 12–25%, numbers of specimens per 0.3 cm^3 sediment about 200.

6. The numbers of *Textularia bocki* never reaching 20 specimens per sample between 3 and 66 m suddenly increase their frequency to over 50 between 75 and 100 m depth.

7. Fragments of corallinacean red algae have been observed to depths of 93 m.

Discussion

The ecological factors governing the depth distribution of the foraminifera are diverse and numerous. In each area and season, their combination and the impact of each factor may be different. Therefore, the single factors determining the depth ranges of the foraminifera have to be discussed one by one if we want to identify the relationship of a single factor to the depth range of a particular species. The most important factors governing the depth distribution of benthic foraminifera in the Gulf of Aqaba were identified by Reiss and Hottinger (1984) as light penetration in the water column. The nature of the substrate, i. e. solid substrates such as rock bottom, reefs or maerl and soft substrates such as fine sands and muds thick enough (20 cm at least) to admit infaunal life is indirectly and partially depth dependant by the water movement distributing the grains. This is the case under conditions of constant temperature in the depth gradient, i. e. in the permanent absence of a thermocline.

The overriding general condition of the ecosystem, however, governing also light penetration, is the trophic level of the water body as a whole: the Gulf of Aqaba was identified as a "blue desert" having very low contents of nutrients from bottom to top in the open water body. As light penetration depends on the production of planktonic organisms in the open water column, the position of the lower limit of the photic zone, as is reflected by the depth range of benthic organisms needing light for photosynthesis or for symbiosis with assimilating organisms, indicates the trophic level. In this respect, the Gulf of Aqaba and the Eastern Mediterranean around Crete are perfectly comparable, the lowest level of photosynthesis occurring at 135–140 m. In Crete, this is documented by the depth range of the elphidiids living in a so-called husbandry relationship with isolated chloroplasts of marine algae, mostly diatoms, in their cytoplasm (Lee and Anderson 1991). The elphidiids occur in significant quantities down to 135 m. The depth range of the coralline red algae reaching 140 m in the Gulf of Aqaba obviously is truncated around Crete by the change of substrate around 100 m depth. This is documented by the relief at this depth level of sessile filterfeeders (*Miniacina*; Langer 1993) by infaunal species (buliminids, bolivinids, uvigerinids) living in fine-grained soft sediments. The change of hard bottom substrate ("coralligène" facies; Perez & Picard 1964) to soft bottom must be due, as in the Gulf of Aqaba, to a change in topographic features, particularly in the steepness of the slope and corresponding to the base level for silt fractions during high water-energy events produced by winter storms (Hottinger 1983). Under similar conditions of exposure and seaway, an analogous change of substrate was observed at analogous depths at the south coast of Elba Island (Northern Tyrrhenian Sea; Hottinger 1983), on Lipari Island (Southern Tyrrhenian Sea; Langer 1993, Cimerman & Langer 1991) and in the Adriatic Sea (Drobne 1984).

The thermocline as a significant ecological discontinuity

In contrast to conditions in the Gulf of Aqaba, the depth gradient off Crete Island is characterized by a thermocline between 60 and 70 m (Fig. 2). During September 1974, discrete discontinuities of the temperature gradient have been observed at 45, 58 and 62 m during the SCUBA dives. Their position in the depth gradient is inconstant, depending on weather conditions and therefore irrelevant for the depth ranges of dead shells accumulating over considerable periods of time. On the exposed side of the Island of Crete, around Gaidouronisi, the gradient of the thermocline is notably steeper than in the more protected Gulf of Merabellou. This indicates a more thorough mixing of the warm surface layers with the cooler deeper layers on the exposed side of the island at the end of the warm summer season.

Textularia bocki was shown in the Adriatic to be dependant from temperature by its appearance below the thermocline (Drobne 1984) located there at 20–25 m depth. The same fact was observed by Venec-Peyré (1984) in Banyuls-sur-Mer, South-Eastern France. In Crete, we observe the same relation to the thermocline, in spite of its much deeper position. Therefore, we consider *Textularia bocki* as a temperature-depending species indicating the position of the thermocline. In this special case, the nature of this dependance is unknown. It might be the food source (Langer and Gehring 1993), the conditions for reproduction or the competition with other, "warmer" species. However, the species' reaction to the thermocline at various depths in different places indicates that the position of the thermocline as a mean value measured at the end of the warm season is a significant factor modifying associations of dead shells from temperature-dependant species accumulating in the sediment during the seasonal cycle.

Thus, the depth gradient off the coasts of Crete is characterized by three discontinuities, i.e. by a thermocline at 60 m, by a change of substrate between 93 and 100 m and by the lower limit of the photic zone at about 135 m (Fig. 2). Depth ranges of a species ending or starting at one of these limits are therefore considered as linked to the respective ecological factor.

In Crete, *Amphistegina lessonii* has a depth range limited by the thermocline, indicating a link between the area of distribution of this species with a minimum temperature of about 16°C. Since the other discontinuities in the gradient are located at much deeper levels, light penetration into the water column as well as the nature of the substrate can be excluded as a limiting factor, although *A. lessonii* has symbionts needing light. Therefore, we interpret *A. lessonii* 's depth distribution in Crete as truncated by the thermocline.

Support for a truncation of the depth range in Amphistegina: coiling ratios

In the depth gradient in the Gulf of Aqaba, which is undisturbed by temperature gradients or, locally, by changes in sub-

Tab. 1. Percentage of left- and right-coiling *Amphistegina lessonii* in Crete and in the Maldive Islands. Samples correspond to grain size fractions > 500 μm (finer fractions devoid of amphisteginids) and are listed corresponding to their origin (north or south of Crete, restricted or exposed in the Maldive atoll).

CRETE: GAIDOURONISI (EXPOSED)

Sample No	Depth	Total	% Sinistral	% Dextral
74121	3 m	267	90.6 %	9.4 %
74127	13 m	576	90.3 %	9.7 %
74122	35 m	1011	87.83 %	12.16 %
74125	45 m	327	88 %	12 %
74124	60 m	510	90.1 %	9.9 %

CRETE: GULF OF MERABELLOU (PROTECTED)

74417	9 m	1729	94.2 %	5.8 %
74416	30 m	602	90.7 %	9.3 %
74415	39 m	209	87 %	13 %
74414	54 m	41	78 %	22 %
74410	66 m	10	80 %	20 %

MALDIVE ISLANDS (EXPOSED)

80019	20 m	93	80 %	20 %
80014	40 m	99	64 %	36 %
80013	50 m	61	61 %	39 %
80012	60 m	64	70 %	30 %
80023	65 m	85	72 %	28 %
90024	68 m	130	69 %	31 %

MALDIVE ISLANDS (RESTRICTED)

80004	1 m	48	98 %	2 %
80003	9 m	58	96 %	4 %
80002	15 m	137	87 %	13 %
80001	20 m	150	85 %	15 %
80005	38 m	45	87 %	13 %
80007	40 m	78	81 %	19 %
80029	48 m	93	81 %	19 %

strate, representing therefore a pure light gradient, Pécheux (1995) has shown intraspecific variation to change with depth either in a linear way, parallel to the light gradient, or showing optimal values at intermediate depths of the specific depth range for *Assilina ammonoides*. The sexual reproduction producing microspheric specimens, predominantly takes place at optimal depths, while at the extreme upper and lower ends of the specific depth range asexual reproduction dominates or is exclusive under the stress of extreme conditions. In amphisteginids, the proportion of sexually produced, microspheric specimens is reflected by the coiling direction ratio because megalospheric forms are predominantly dextral or sinistral (about 95%) while microspheric forms are random. Thus, minority coiling ratio increase means an increase of sexual reproduction under optimal conditions. If the coiling ratio is distributed in an asymmetric way over the depth gradient, the factors delimiting the species' depth range are not progressive, excluding the light gradient but cutting off the depth range by means of a second factor consisting of a limiting threshold value.

In Crete, around the exposed Gaidouronisi, minority coiling ratios change insignificantly from 9.4 to 12.1% down to a depth of 35 m and fall back to 10% down to 60 m. In the more protected Gulf of Merabellou, we observe a minority coiling ratio rising systematically from 5.8 to 20–22% in the depth gradient. Similar trends are observed on the exposed reef slope of the Maledivan Islands where high minority values rise slowly from 20 to 30% in the depth range between 20 and 68 m while in the protected lagoons the minority coilers are 2% at 1 m depth rising to 19% down to 48 m depth. In the Maledivan Islands, the depth gradient is cut off in the lagoons by the topography producing generalized bottom depths of 50 m (Ciarapica and Passeri 1995) while on the exposed side, sampling was limited to SCUBA diving depth limits of 70 m. In the Gulf of Aqaba, Morariu and Hottinger (1988) report a minority coiling maximum at 40 m depth reaching 12% compared to 8% at the ends of depth ranges between 1 and 80 m. In the tropical realm, the depth range of *A. lessonii* is compressed by the presence of competitive sister species, such as *A. lobifera* at the shallow, and *A. papillosa* at the deep end of the species' depth range. Even in the compressed depth range, the distribution of minority coilers is symmetrical if the depth gradient is more or less undisturbed. The data showing an obvious asymmetry of minority coiler distribution over the depth gradient in Crete, support the idea of a truncation of the depth range in *A. lessonii*.

Origin of temperature dependance

Keeping in mind the depth distribution of the elphidiids in Crete reaching the bottom of the photic zone, we may ask about the origin of the temperature dependance in *Amphistegina lessonii*. Amphisteginids and elphidiids, both have symbionts but their endosymbiosis is different. In amphisteginids, the diatomacean symbionts grow and multiply within their host shells, in elphidiids, the symbiont husbandry does not involve growth processes of their symbiontic chloroplasts. Consequently, if the difference in symbiosis between the two groups is responsible for their respective relation to temperature, the higher minimum temperature above the thermocline necessary for the survival of the *Amphistegina* population signal their limiting character for symbiont growth and reproduction rather than for the photosynthetic activity of their chloroplasts. This is a hypothesis. Its support by additional circumstancial evidence or by experimental work is beyond the scope of the present paper.

Conclusions

1. Off the shores of Crete Island, the lower depth limit of *Amphistegina lessonii* populations is truncated by the thermocline at 60–70 m depth and not determined by the lack of light at the lower limit of the photic zone at 135–140 m.
2. The significance of the thermocline measured at the end of the warm season in September as a delimiting factor for temperature-dependant foraminifera is supported by the drastic reduction of frequency in the occurrence of the agglutinated *Textularia bocki* that is known to follow the thermocline in the Adriatic Sea at 20–25 m depth.
3. The idea of a truncation of the depth range in *A. lessonii* is supported by the asymmetric distribution of its chirality in the depth gradients, i. e. of the minority coilers indicating optimal conditions for sexual reproduction immediately above the thermocline in Crete and in intermediate depths of their range in purely light-dependant depth gradients of tropical seas.
4. The occurrence of porcelaneous larger foraminifera symbiontic with red algae or dinophyceans (*Peneroplis, Sorites* etc.) is in general also limited to warmer surface waters above the thermocline, although, there may be secondary factors complicating the picture what is documented also by their geographic distribution.
5. The depth range of the elphidiids characterized by chloroplast husbandry is not affected by the thermocline. Their frequency is significantly reduced at the lower limit of the photic zone.
6. Considering the effect of temperature on foraminiferal species with a true endosymbiosis where the symbionts grow and multiply within the host cell while chloroplast husbandry is not affected by low temperatures, it is suggested that too low temperatures do not hamper or suppress the photosynthesis of the symbionts but their growth and/or reproduction within the host cell.

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