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**ENDOLITHIC ALGAE IN LIVING STONY CORALS: ALGAL CON-  
CENTRATIONS UNDER INFLUENCE OF DEPTH-DEPENDENT  
LIGHT CONDITIONS AND CORAL TISSUE FLUORESCENCE IN  
AGARICIA AGARICITES (L.) AND MEANDRINA MEANDRITES  
(L.) (SCLERACTINIA, ANTHOZOA)**

by

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ABSTRACT

DELVOYE, L., 1992. Endolithic algae in living stony corals: Algal concentrations under influence of depth-dependent light conditions and coral tissue fluorescence in *Agaricia agaricites* (L.) and *Meandrina meandrites* (L.) (Scleractinia, Anthozoa). *Studies Nat. Hist. Caribbean Region* 71. Amsterdam 1992: 24-41.

The relation between Scleractinians and their endolithic algae was studied in the depth range of 10 to 35 m in Curaçao. Endolithic algal concentrations are found in the skeleton under the living tissue of stony corals and never in dead parts or in coral rubble. The influences of depth-dependent light conditions and coral tissue fluorescence on endolithic algal concentrations were studied in a non-fluorescent and a fluorescent form of both *Agaricia agaricites* and *Meandrina meandrites*.

Spectroscopy shows that this fluorescence has a photosynthetic potential for both their zooxanthellae and their endolithic algae. The hypothesis that the width of the algal concentrations and their depth below the tissue are correlated with depth on the reef could not be confirmed, with one exception. This only can be explained by the redistribution of zooxanthellae in the coral tissue with increasing depth, making it more transparent. No evidence was found that fluorescence is indeed enhancing the photosynthesis in the endolithic algae of both corals.

Ground section histology shows that endolithic algae are in contact with soft coral tissue and are associated with fungi.

**Key words:** Endolithic algae, stony corals, fluorescence, spectroscopy, algal pigments.

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## INTRODUCTION

It has long been known that endolithic green algae of the genus *Ostreobium* are present in the skeletons of living reef corals (DUERDEN 1902). And in more recent times, also bacteria (DISALVO 1969) and fungi (KENDRICK *et al.* 1982; BAK & LAANE 1987) have been found.

It is clear that endolithic algae and fungi play a role in the erosion of marine carbonate substrates (GOLUBIC 1969; KOHLMAYER 1969). Microborings by such organisms in carbonate deposits occur early in the geological time scale (KOBALUK & RISK 1974).

Therefore it is generally assumed that microboring organisms in living corals do indeed contribute to the destruction of reefs, but in fact little is known about their ecology or their relationships to living corals (HUTCHINGS 1986). However, on basis of this geologically old relationship, one may assume that endolithic micro organisms and their coral hosts have become mutually adapted. In some coral species (*Agaricia* sp., *Meandrina meandrites*) the green algal band is found deeper in the skeleton than in other species living in about the same depth range (*Sideastrea siderea*, *S. radians*, *Porites* sp.). This observation suggests that this adaption has species-dependent aspects.

Recent histological work has revealed contacts between endolithic algae, fungi and the living coral tissue (PETERS 1984 & pers.comm., E. H. GLADFELTER pers. comm.) and associations between endolithic algae and fungi (this paper), lending support to the idea that there is an established relationship between boring micro-organisms and living corals.

One of the most important abiotic factors in the ecology of endolithic algae will be the availability of photosynthetically active light. Depending on spectral composition and penetration in the coral skeleton, the intensity of this light may vary between  $10^{-6}\%$  and 2.0% of the incident flux (HALLDAL 1968).

In seawater, the light intensity decreases with depth. At the same time, the longer wavelengths are progressively filtered out. Between 15 and 20 m there is a transition zone, as most red and yellow light is absorbed (JERLOV 1968; DUSTAN 1979).

Depth-dependent light conditions may have an effect on the behaviour of endolithic algal concentrations in living corals. An other effect on endolithic algae is to be expected from the fluorescence of living corals, as compared to non-fluorescent corals of the same depth on the reef. This fluorescence

is caused by substances in the living coral tissue, which are excited by blue and ultraviolet rays in sunlight. This part of the solar spectrum penetrates deep in clear oceanic waters (JERLOV 1968; SCHLICHTER *et al.*, 1987). In this paper the results of a study on endolithic algae in living corals on a reef along the S.W. coast of Curaçao (Netherlands Antilles) are presented, focussing on the following questions:

- Does the presence of concentrations of endolithic algae in coral skeletons depend on the presence or absence of living coral tissue?
- Is there a relationship between the width of the green algal band in the skeletons of living corals and their depth on the reef?
- Is there a relationship between the distance of the green band from the light receiving surface of the coral and the water depth?
- Is fluorescence light from coral hosts active in the photosynthesis of their endolithic algae?

#### MATERIALS AND METHODS

The study was carried out in two steps: first a survey to obtain a general picture of the distribution of endolithic algae and the occurrence of fluorescence in living corals. Second, a closer examination of species selected during the survey with regard to the questions stated above.

The composition of the fluorescence light of corals was studied with spectroscopy for its photosynthetic potential. In order to reduce local variations and to minimize seasonal effects, samples for the detailed investigation during the second step, have been collected at the same stretch of reef and within a three month's interval of time. Coral colonies or fragments of colonies were collected by means of SCUBA-diving between Buoy 1 and 1 near Piscadera Bay (DELVOYE 1989) on the SW-coast of Curaçao (June – Augustus 1988).

Samples of non-fluorescent *A. agaricites* were collected from about 10, 20 and 30 m, of fluorescent *A. agaricites* between 17 and 35 m. Both the fluorescent and non-fluorescent forms of *Meandrina meandrites* were collected from depths of about 10, 20 and 30 m. Samples were carried to the laboratory in separate plastic bags containing seawater. In the laboratory, the samples were labeled and kept in small aerated aquariums.

The samples were tested for fluorescence in the laboratory at night or in the dark during daytime, using a Philips 8 W 08 UV-A 'black light' lamp. This type of lamp emits a continuum around 350 nm on which several mercury emission lines are superimposed. Photographs and spectrograms of fluorescence, if occurring, were taken when possible.

For spectroscopy, a prism spectrograph with a resolution of 5 nm in blue light was employed. A SLR-camera, equipped with a F/3.5 135 mm objective, recorded the spectrograms on Kodak TMax-400 film (Fig. 1). Exposure times ranged from one to ten minutes. Spectrograms were measured with a calibrated eyepiece micrometer in a stereo binocular microscope. The mercury emission lines at 404.66 and 435.83 nm of the 'black light' lamp and the Fraunhofer absorption lines B, C, D, E, b1, F, G, H and K in the solar spectrum, photographed with the same set-up, were chosen as references (NORTON 1959).

Subsequently, the samples were slabbed on a rock saw, taking care to saw through the

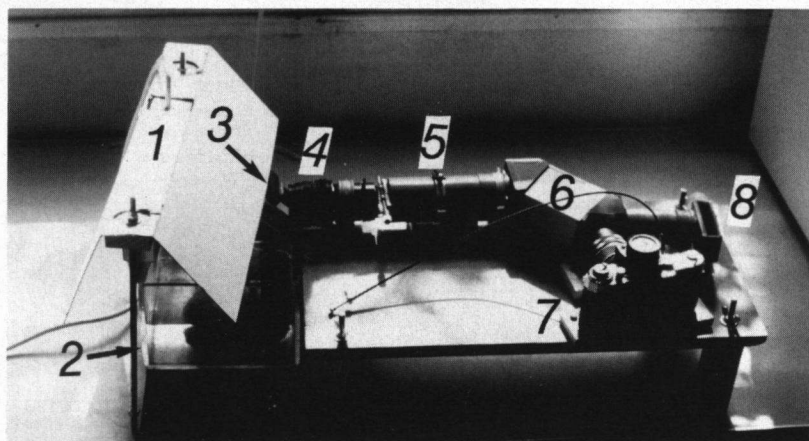


FIGURE 1. Spectrograph set-up. 1. 'Blacklight' lamp under cardboard hood (black inside). 2. Coral sample in small aquarium, with black cardboard on bottom. 3. Front surface aluminized mirror, reflects fluorescence light into: 4.  $F/2 - 50$  mm SRL objective covered with UV-haze filter, acting as a collector and projecting light source on: 5. Adjustable slit in collimating unit. 6. Unit containing three identical  $45^\circ$  prisms. 7. SRL-camera with modified viewfinder for maximum transmission and eye relief, equipped with a  $F/3.5 - 135$  mm objective. 8. Coarse wavelength scale, for use with bright spectra.

point of attachment of the colony and perpendicular to the coral surface. Then the distance (taken from the top of the 'hills' on the coral surface to the bottom of the algal concentration) and the width of the green layer in the skeleton were measured with a pair of calipers, with an accuracy of 0.5 mm. This was done for several positions within 2/3 of the distance from the centre to the rim of each colony. For each colony, the mean value of a sequence was calculated. The variation around these mean values ranges from 0.5 to 1 mm.

For ground section histology according to DONATH (1987) selected sample slabs were fixed in a mixture of 36% formalin and seawater (1+9, by volume) and stored in sealed plastic bags. Slabs from material up to five years old, fixed in the same manner were also used. Sections perpendicular to the coral surface were sawn, ground and polished in a thickness range from 10 to 40 micrometer and stained with Weigert's iron hematoxylin-erythrosin-orange-G (DELVOYE 1989; modified), toluidin blue or Heidenhain's Azan (DONATH 1987). In these sections the coral skeletons with endolithic organisms and soft tissue can be studied under the compound microscope, using a magnification of 100-200x.

TABLE I  
PRELIMINARY RESULTS OF A SURVEY ON THE PRESENCE OR ABSENCE OF GREEN  
BANDS AND FLUORESCENCE IN 27 SPECIES OF STONY CORALS

Species	N	Green algal band	Fluorescence and colour
Family Pocilloporidae			
<i>Madracis decactis</i>	6	+	+ O
<i>Madracis mirabilis</i>	3	-	+/- O
Family Acroporidae			
<i>Acropora palmata</i>	1	-	-
<i>Acropora cervicornis</i>	1	-	-
Family Agariciidae			
<i>Agaricia agaricites</i>	47	+	+ Y, O
<i>Agaricia lamarcki</i>	10	+	+ Y
<i>Agaricia grahamae</i>	2	+	+ Y
<i>Agaricia undata</i>	4	+	+ Y
<i>Agaricia fragilis</i>	2	+	+ Y
<i>Agaricia humilis</i>	9	+	+ Y
<i>Helioseris (Leptoseris) cucullata</i>	6	+	+ Y
Family Siderastreidae			
<i>Siderastrea siderea</i>	3	+	-
<i>Siderastrea radians</i>	1	+	-
Family Poritidae			
<i>Porites porites</i>	1	+	+/- O
<i>Porites astreoides</i>	2	+	-
Family Faviidae			
<i>Montastrea annularis</i>	3	+	+ Y
<i>Montastrea cavernosa</i>	2	+	+ Y
<i>Favia fragum</i>	1	+	-
<i>Colpophyllia natans</i>	1	+	+ Y, O
Family Meandrinidae			
<i>Meandrina meandrites</i>	50	+	+ Y
<i>Dichocoenia stellaris</i>	1	+	-
<i>Dendrogyra cylindrus</i>	1	+	-
Family Mussidae			
<i>Scolymia lacera</i>	1	-	+ Y
<i>Scolymia cubensis</i>	1	-	+/- O
<i>Mycetophyllia ferax</i>	1	-	+ O
Family Caryophylliidae			
<i>Eusmilia fastigiata</i>	2	+	-
Family Dendrophylliidae			
<i>Tubastrea coccinea</i>	2	-	-

+ = present, - = absent, +/- = weak or doubtful. O = orange, Y = yellow. Note: Both *A. agaricia* and *M. meandrina* have different fluorescing forms. Classification after WELLS & LANG (1973).

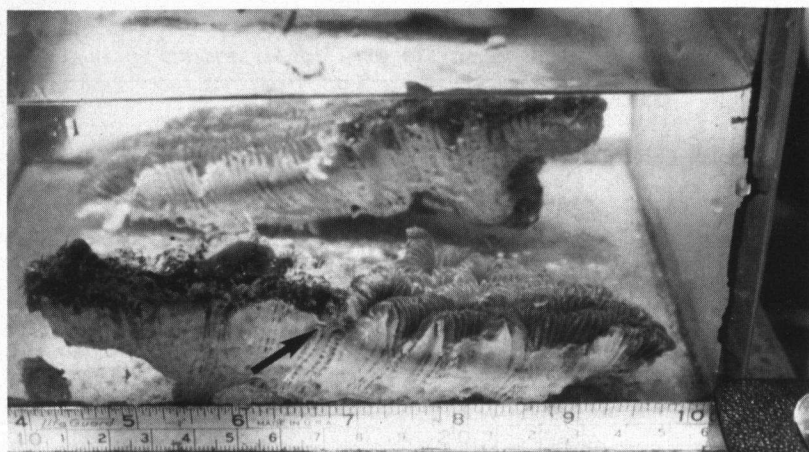


FIGURE 2. Sliced colony of *Meandrina meandrites*. Both halves are visible. The arrow points at the transition between the dead and living parts of the skeleton. Note that only under the living part the green algal band is present.

## RESULTS

### *General*

Table I presents the results of a survey in 27 species of scleractinians belonging to 10 families with respect to the presence or absence of green algal bands and fluorescence on the living surface. However, since in many species only one or a few colonies have been examined, these results must be considered to be preliminary.

Without exception green algal bands have been found only under living parts of the coral surface. They are not present in dead parts of a colony (Fig. 2, *M. meandrites*). Coral rubble from several depths has been examined, but algal concentrations have not been found. In some species (*Meandrina meandrites*, *Sideastrea siderea*, *Madracis decactis*) diffuse pink or red discolorations were observed. In *Acropora palmata*, *Acropora cervicornis*, *Mycetophyllia ferox*, *Scolymia lace-ra*, *Scolymia cubensis* and *Madracis mirabilis* no green bands were present (Table I). The older colonies of *Agaricia lamarcki* often showed a sponge-like secondary skeletal growth near the base. The algal concentration was always located between this secondary growth and the coral surface, but never in it.

TABLE II  
FLUORESCENCE PATTERNS IN *AGARICIA* SP. AND *HELIOSERIS CUCULLATA*

Species	Fluorescence pattern
<i>A. agaricites</i> non-fl. form	Only polyp mouths. Orange.
<i>A. agaricites</i> fl. form	Bright over complete living surface. Yellow to yellow-green.
<i>A. lamarcki</i>	Bright polyp mouths. Septal ridges weak, except around polyp mouths and occasional spots. Yellow.
<i>A. grahamae</i>	As <i>A. lamarcki</i> , but septal ridges stronger. Greater surface brightness.
<i>A. undata</i>	Polyp mouths dark. Bright septal ridges, concentrated around polyp mouths. Surface weak. Yellow.
<i>A. fragilis</i>	Polyp mouths dark. Bright septal ridges, evenly illuminated. Yellow-green.
<i>A. humilis</i>	Bright polyp mouths. Less brilliant septal ridges. Surface weak, but present. Yellow.
<i>H. (L.) cucullata</i>	Bright polyp mouths and septal ridges. Surface dark. Yellow.

TABLE III  
PEAK WAVELENGTHS IN NM OF FIVE BANDS PRESENT IN FLUORESCENCE  
SPECTROGRAMS OF 10 SPECIES OF LIVING STONY CORALS

Species	Spectral bands				
	1	2	3	4	5
<i>A. agaricites</i> non-fl. form	—	—	—	605	—
<i>A. agaricites</i> fl. form	479	533	567	605	—
<i>A. lamarcki</i>	479	533	567	605	—
<i>A. grahamae</i>	479	533	567	605	—
<i>A. undata</i>	479	533	567	605	—
<i>A. fragilis</i>	479	533	563	601	—
<i>A. humilis</i>	474	530	567	605	—
<i>H. (L.) cucullata</i>	489	533	563	601	—
<i>M. cavernosa</i>	450	540	—	601	—
<i>C. natans</i>	501	533	570	601	663
<i>M. meandrites</i>	489	533	567	605	663
Algal tufts	—	—	—	605	663

The estimated error in the given values is 10 nm, except for *M. cavernosa*. The quality of the spectrogram for this species did not allow an accurate determination of wavelengths.

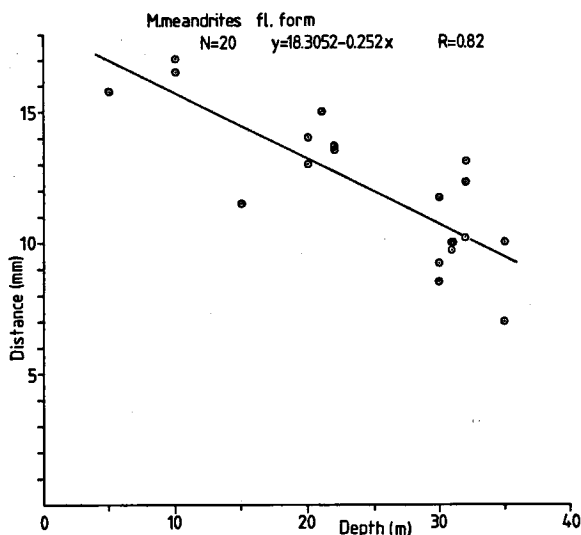


FIGURE 3. *M. meandrites* fluorescent form. Linear regression of distance of endolithic algal concentration in the skeleton versus depth on the reef. The correlation coefficient is significant.

The strongest fluorescence was found in the agariciids and in *M. meandrites*. It is in most instances concentrated around the polyp mouths, but may also spread over the surface. The colour of the fluorescence can be yellow, yellow-green or orange. The fluorescence patterns of the agariciids are described in Table II. In this group, each species has its specific fluorescence pattern.

Table III presents the spectrographic results of 10 species. The coral fluorescence spectra consist of four to five broad emission bands in the wavelength range from 450 to 700 nm. The maximum values in nm for the bands are given. The spectral composition of the fluorescence is roughly the same for all species. The values around 605 and 663 nm probably originate in the zooxanthellae and endolithic algae, as they are identical with emission bands from algal tufts on coral rubble. In slabbed samples, green endolithic algae displayed an orange-red fluorescence. However, the intensity was too low to obtain spectrograms from them.

In ground sections of *A. agaricites*, *A. lamarcki*, *A. grahamae*, *A. undata* and *M. meandrites*, endolithic algae can be seen as thalli having diameters of 6 micrometers, and nodi at distances of 50 micrometers (Fig. 4). They make contact with the



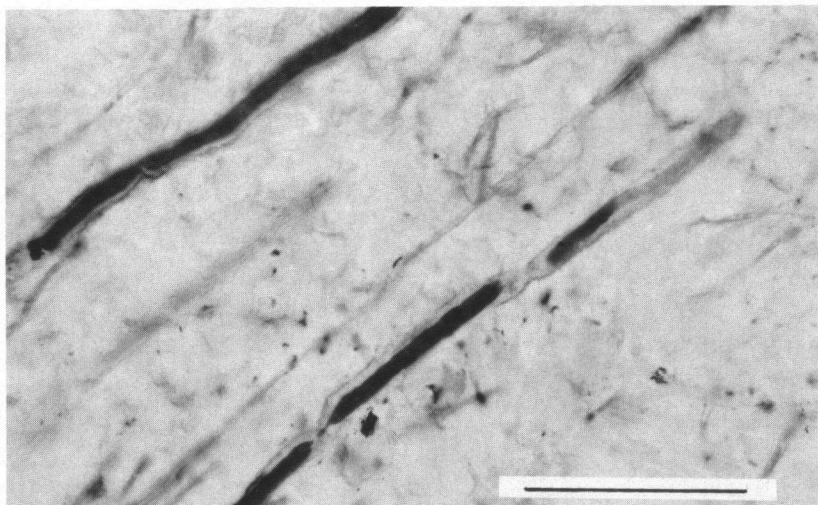


FIGURE 4. Endolithic algae in skeletal matrix as seen in a ground section of *A. agaricites*. Direction of living coral tissue is at right. Distance between two nodi is about 50 micrometers. Generally speaking, most thalli run towards the illuminated surface of the colony. The smaller thalli between the larger ones are associated fungi. Section thickness about 20 micrometers, iron hematoxylin-erythrosin-orange-G stained. Scale bar 50 micrometers.

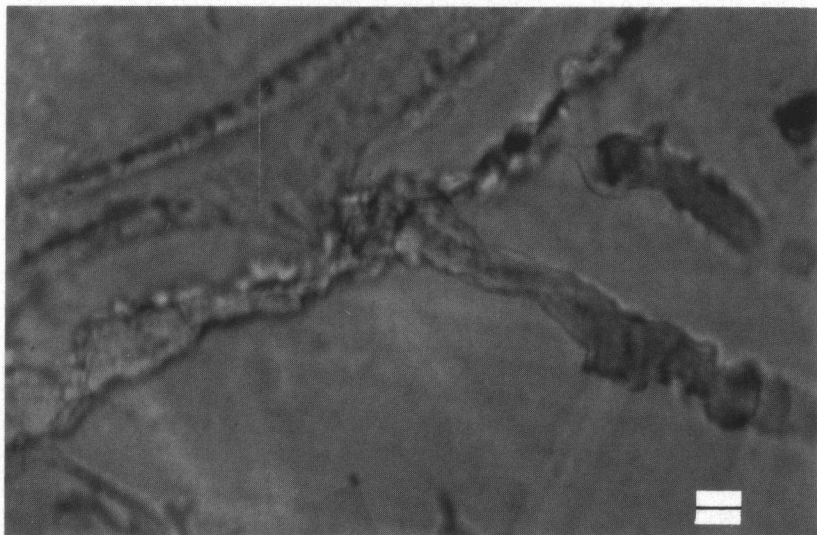


FIGURE 5. Endolithic alga making contact with soft coral tissue in a ground section of *A. agaricites*. Thickness about 15 micrometers, Azan stained. Scale bar 10 micrometers.

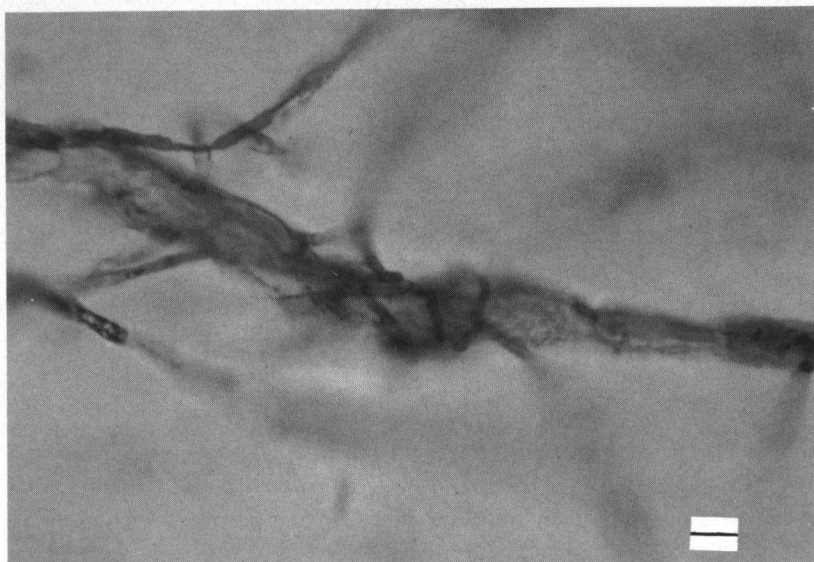


FIGURE 6. Endolithic algal thallus with associated fungus in a 15 micrometers thick ground section of *A. agaricites*. Azan stained. Scale bar 10 micrometers.

soft coral tissue (Fig. 5) and are associated with fungi (Fig. 6). The skeleton of *M. meandrites* is much more transparent than that of the agariciids. Analysis of variance (SOKAL & ROHLF 1981) on algal concentration distance data of both species shows that they stem from different distributions, hence indicating different transparencies. (Number of groups: 4. Significance level:  $P > 0.01$ . Degrees of freedom: 3 and 93. Critical value for F: 4.04. Calculated F-value: 61.68).

Fungi seem to be the dominant endolithic organisms in ground section of *Madracis decactis*, *Mycetophyllia ferox*, *Sideastrea radians* and *Porites porites*.

A *P. porites* colony slab from St. Martin shows the same type of black discoloration as described in Pacific *Porites* by BAK & LAANE (1987).

#### *Agaricia agarites* and *Meandrina meandrites*

These species were selected to investigate the relationships between the distance and the width of the green zone in the skeleton *versus* the depth on the reef. Both are common on the reef slope in the investigated depth range. They have a relatively massive skeleton, in which the green zone of endolithic algae stands out sharply and can be measured with sufficient ac-

TABLE IV  
SUMMARY OF THE CORRELATION COEFFICIENTS IN FIGURES 3 TO 10

Species	N	Width	- R	Distance	- R
<i>A. agaricites</i> non-fl. form	20	0.38 95 % : 0.444	ns	0.32 95 % : 0.444	ns
<i>A. agaricites</i> fl. form	27	- 0.11 95 % : 0.381	ns	- 0.05 95 % : 0.381	ns
<i>M. meandrites</i> non-fl. form	30	0.41 95 % : 0.361	s	- 0.13 95 % : 0.361	ns
<i>M. meandrites</i> fl. form	20	- 0.42 95 % : 0.444	ns	- 0.82 99 % : 0.561	s

N is the number of samples. Under R correlation coefficients of Width (mm) and Depth (m) are given, with the critical values of R for the confidence interval of 95 or 99%.

ns = non-significant, s = significant. Idem for Distance (mm) and Depth (m).

curacy. As it turned out, both *Agaricia agaricites* and *Meandrina meandrites* have forms that only show fluorescence around the polyp mouths, and forms that display a bright fluorescence over the complete living surface. In *A. agaricites*, the non-fluorescent form fits the descriptions of *Agaricia agaricites purpurea* (Lesueur), and the fluorescent form those of *Agaricia agaricites agaricites* (Linnaeus) by WELLS (1973) and by VAN MOORSEL (1983). However, to avoid confusion with other, apparently depth-dependent, ecoforms (*A. a. danai* M. Edw. & Haime and *A. a. carinata* Wells (VAN MOORSEL, 1983), I will refer to *A. agaricites* non-fl. and fl. for the non-fluorescent and fluorescent forms, respectively. The same distinction will be made in the non-fluorescent and fluorescent forms of *Meandrina meandrites* respectively.

*A. agaricites* non-fl. was found over the total investigated depth range, while *A. agaricites* fl. was absent at depths shallower than 17 m. Both forms could easily be recognized in the field.

Except in the shape of the columella in young polyps and massiveness of the skeleton, no differences between skeletons of both forms could be found. In the fluorescent form the columella is more pronounced and the colonies tend to be thicker.

In two colonies of *A. agaricia* fl. part of the surface was dark, while the rest of it was displaying a vivid fluorescence. Careful examination did not reveal any evidence of fusion between two colonies in these cases.

The two forms of *M. meandrites* were found over the whole depth range. On the reef no distinction between these two forms could be made. A substantial portion of the fluorescent form (7 out of 20) displayed partial fluorescence,

light and dark areas showing a patchy distribution over the coral surface. Nevertheless, as this condition may be the result of stress during collection and transport or due to some unknown physiological phenomenon, all data from fluorescent and partial fluorescent colonies were pooled. Comparison of dried skeletons of both *M. meandrites* forms revealed no differences. In Table IV the correlation coefficients for distance *vs.* depth and width *vs.* depth are summarized for both species. In two cases they rise above the 95% confidence limits: For *M. meandrina* non-fl. a weak association between the width of the algal concentrations and depth is shown. In *M. meandrina* fl. there is a strong negative association between the distance of the algal concentrations and depth. Figure 3 represents this last case as an example. The other correlation coefficients are below the 95% confidence interval and therefore have no significance (SOKAL & ROHLF 1981).

## DISCUSSION

### *General*

Algal concentrations occur only under living coral tissue. There are three hypothetical advantages for this situation:

- Corals resist sedimentation (BAK & ELGERSHUIZEN 1976) on their living surfaces, thus preventing blocking of light.
- Corals resist settling of sessile organisms on their living surfaces, preventing blocking of light and predation.
- In case of fluorescence of the living coral tissue, this light source can contribute to the photosynthesis of endolithic algae.

In sliced samples of the Acroporidae, Mussidae and some species from other families (Table I), no green band has been found. However, this does not exclude the presence of other, colourless endolithic micro-organisms. The pink and red discolorations in the samples mentioned earlier already indicate the presence of other boring micro-organisms than algae. This is confirmed by ground section histology, since endolithic fungi have been found in all samples.

An exchange of metabolites is suggested by the contacts of endolithic algae with the living coral tissue (Fig. 5). Transfer of nitrogen and phosphorus containing compounds from the coral tissue to the algae may be of importance. From their position within the coral skeletons, the possibility for the algae to take up such nutrition from the surrounding seawater in an environment poor in free nitrogen and phosphorus compounds seems limited.

Fungi in symbiosis with algae are generally known as lichens. HENSSEN & JAHNS (1974) mention four criteria which are to be met to recognize such a symbiosis as a lichen:

1. A very close association between fungus and alga, in which the fungus is in physical contact with the alga.
2. The formation of a habitus, specific for the fungal/algal combination. This habitus is different from the fungal and algal habitus.
3. The association should physiologically be successful.
4. The presence of a typical mode of vegetative reproduction for the lichen as such.

In the association between fungi and endolithic algae in living corals criterium 1 and probably criterium 3 are met. Criterium 2 is not met, unless the green band itself is considered to be the habitus of the association. Structures as mentioned in criterium 4 have never been found. Therefore it is not possible to classify this association as a lichen.

In other instances fungi may scavenge on the organic matrix of the skeleton. More research is needed to clarify their role.

Not-infested secondary growth in *Agaricia lamarki*, over parts inhabited by boring algae, shows that corals are able to repair or prevent skeletal damage.

Secondary growth in relation to endolithic algae has also been found in the Indo-Pacific scleractinians *Pachyseris speciosa* and *Galaxea fascicularis*.

#### *Coral tissue fluorescence and zooxanthellae*

The differences in spectral composition of the fluorescence light are small among the species listed in Table III. The error in the observations is estimated to be about 10 nm. The brightest band around 479 nm matches the broad absorption maximum around 450 nm in the action spectrum of the zooxanthellae from *Favia* sp. (HALLDAL 1968). The other bands around 533 and 567 nm match the maximum around 540 nm in the same action spectrum. The emission peak around 479 nm coincides with the absorption maxima of the photosynthetic pigments beta-carotene, diadinoxanthin, dinokanthin, peridinin and an unknown pigment of the zooxanthellae in *Pocillopora* sp. (JEFFREY & HAXO 1968).

The absorption spectra of zooxanthellae from *Goniopora planulata* and *Lep-toseris fragilis* as determined from chloroform extracts by SCHLICHTER *et al.* (1987) show a maximum between 380 and 510 nm, broad enough to match the 479 nm emission band.

The bands around 603 and 663 nm (Table III) are weak, the latter is probably caused by chlorophyll-a excitation. For *L. fragilis* it has been made plausible by SCHLICHTER *et al.* (1987) that fluorescence light from the tissue amplifies the photosynthesis in the zooxanthellae. This coral has a maximal

occurrence between depths of 100 and 145 m in the Red Sea, at which no other zooxanthellate coral species are known.

These results support the hypothesis that short wavelengths of the solar spectrum are converted into longer wavelengths by corals to enhance photosynthesis in their zooxanthellae (SCHLICHTER *et al.* 1987). If true, this mechanism can be one of the reasons for the large depth range of the agariciids, *Montastrea* sp. and *M. meandrites* on Caribbean reefs (DUSTAN 1979; BAK & ENGEL 1979). The reverse argument is not necessarily true, although many corals with a limited depth range display only a weak fluorescence or nothing at all (in Table I: *Acropora palmata*, *Acropora cervicornis*, *Porites porites*, *Madracis mirabilis*, *Sideastrea radians*, *Favia fragum*, *Dendrogyra cylindrus*) (ROOS 1964, 1971; BAK & ENGEL 1979). Whether the species-specific fluorescence has a biological significance and whether the intensity of fluorescence is depth-dependent or not, are questions that will need further investigation (Table II).

#### *Coral tissue fluorescence and endolithic algae*

There is a broad absorption feature between 340 and 480 nm, and a second one between 645 and 720 nm in the action spectrum of endolithic algae in *Favia* sp. (HALLDAL 1968).

JEFFREY (1968) found that these absorption maxima are mainly due to the photosynthetic pigments chlorophyll-a, beta-carotene and siphonein from *Ostreobium*. The most important fluorescence emission band around 479 nm (Table III) has therefore a photosynthetic potential for endolithic algae. However, as no intensities of this fluorescence are known, one can only speculate about its importance in this respect.

#### *Agaricia agaricites and Meandrina meandrites*

The overlap in habitat on the reef of both forms of *A. agaricites* is not complete. However, the differences in skeletal build between them are small. So evidence for the recognition of both forms as distinct species is inconclusive. The same arguments apply to both forms of *M. meandrites*. Being collected at random, the 3:2 ratio between the non-fluorescent and the fluorescent forms is considered to be approaching their actual ratio on the reef.

On basis of the decreasing light intensity with increasing depth in the sea, one should expect a negative correlation between this depth and the quan-

tities width and distance of algal concentrations in living coral skeletons. However, in both forms of *A. agaricites* no such correlations have been found (Table IV).

An explanation may be found in the changing photosynthetic properties of the zooxanthellae in the coral tissue. According to WYMAN *et al.* (1987), the number of zooxanthellae per unit area of coral tissue decreases with increasing depth. At the same time, their chlorophyll-a content increases. This chlorophyll-a redistribution leads to a change in the percentage of light absorption by coral tissue. This means that the remaining percentage of light that is reflected by the coral tissue and transmitted to the coral skeleton also changes. The total flux  $E$  falling on a living coral can be divided in:

$$E = A + R + T$$

This can be rewritten as:

$$R + T = E - A$$

where  $A$ ,  $R$  and  $T$  stand for the Absorbed part, the Reflected part and the Transmitted part respectively. Absolute values for each quantity can be found by multiplication with the light intensity in absolute units for that particular depth (Table V).

TABLE V  
A. AGARICITES

Depth	E	A(%)	R+T(%)	R+T(E)
1	1500	81	19	285
10	600	91	9	54
30	200	62	38	76
50	75	51	49	36.75

The first three tabulated quantities are after WYMAN *et al.* (1987). Depth is in m.  $E$  is the flux of light in  $E.m^{-2}.s^{-1}$ .  $A\%$  is the absorption percentage of incident light for the coral tissue. The remaining percentage of light that is reflected and transmitted is calculated as  $R+T(\%) = 100\% - A(\%)$ . This portion is then expressed in  $E.m^{-2}.s^{-1}$ , according to:  $R+T(E) = E.(R+T(\%))/100$ .

This has been done for the data of *A. agaricites* and the light intensities at noon for several depths as given by WYMAN *et al.* (1987). The quantities of  $R$  and  $T$  cannot be presented by separate values because only values for quantity  $A$  are given. The resulting  $R+T(E)$  values are presented in Table V. Although the data are only valid for Jamaica, the situation in Curaçao can be considered to be similar. The absolute amount of  $R+T$  light at noon in *A. agaricites* is about 40% larger at 30 m than at 10 m. But the difference, as measured in absolute units is only  $22E.m^{-2}.s^{-1}$ . Therefore, taking into ac-

count local small scale variations, e.g. shading, the vicinity of reflecting stretches of sediment, it seems reasonable to expect that the light conditions for endolithic algae in *A. agaricites* will remain within the same order of magnitude for depths between 10 and 30 m. As can be seen by comparing the results of both forms, fluorescence is not important as a source of photosynthetic light for their endolithic algae.

As no data on chlorophyll-a redistribution for *M. meandrites* are known, any interpretation of the data is speculative. However, the distances for both forms (Table IV and Fig. 3) differ significantly, while their widths do not. As the skeletal transparency is higher than in *A. agaricites*, this suggests an influence of tissue fluorescence. Further research is needed to clarify these points.

Considering their apparent benefits, it seems unlikely that endolithic algae themselves are destructive agents in a living coral. This is contrary to opinions about the rôle of endolithic algae in corals (DUERDEN 1902, HUTCHINGS 1986). However, it cannot be excluded, that endolithic algae are preparing the substrate for other, but destructive, boring organisms.

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#### REFERENCES

- BAK, R. P. M. & J. H. B. W. ELGERSHUIZEN, 1976. Patterns of oil-sediment rejection in corals. *Mar. Biol.* 37: 105-113.  
BAK, R. P. M. & M. S. ENGEL, 1979. Distribution, abundance and survival of juvenile her-



- matypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar. Biol.* 54: 341-352.
- BAK, R.P.M. & R.W.P.M. LAANE, 1987. Annual black bands in skeletons of reef corals (Scleractinia). *Mar. Ecol. Prog. Ser.* 38: 169-175.
- DELVOYE, L., 1989. Gametogenesis and gametogenic cycles in *Agaricia agaricites* (L) and *Agaricia humilis* Verrill and notes on gametogenesis in *Madracis mirabilis* (Duchassaing & Michelotti) (Scleractinia). *Publ. Found. Sci. Res. Surinam & Neth. Ant.* 123: 101-134.
- DISALVO, L.H., 1969. Isolation of bacteria from the corallum of *Porites lobata* (Vaughan) and its possible significance. *Am. Zool.* 9: 735-740.
- DONATH, K., 1987. *Die Trenn-Dünnschliff-Technik zur Herstellung histologischer Präparate von nicht schneidbaren Geweben und Materialien. Apparate- und Methodenbeschreibung.* EXAKT-/Kulzer-Druckschrift, Norderstedt.
- DUERDEN, J.E., 1902. Boring algae as agents in the disintegration of corals. *Bull. Am. Mus. nat. Hist.* 16: 323-332.
- DUSTAN, P., 1979. Distribution of zooxanthellae and photosynthetic chloroplast pigments of the reef-building coral *Montastrea annularis* Ellis and Solander in relation to depth on a West Indian coral reef. *Bull. mar. Sci.* 29 (1): 79-95.
- GOLUBIC, S., 1969. Distribution, taxonomy and boring patterns of marine algae. *Am. Zool.* 9: 747-751.
- HALLDAL, P., 1968. Photosynthetic capacities and photosynthetic action spectra of endozoic algae of the massive coral *Favia*. *Biol. Bull.* 134: 411-424.
- HENSSEN, A. & H.M. JAHNS, 1974. *Lichenes.* Georg Thieme Verlag Stuttgart.
- HUTCHINGS, P.A., 1986. Biological destruction of coral reefs. A review. *Coral Reefs* 4: 239-252.
- JEFFREY, S.W., 1968. Pigment composition of Siphonales algae in the brain coral *Favia*. *Biol. Bull.* 135: 141-148.
- JEFFREY, S.W. & F.T. HAXO, 1968. Photosynthetic pigments of symbiotic dinoflagellates (zooxanthellae) from corals and clams. *Biol. Bull.* 135: 149-165.
- JERLOV, N.G., 1968. *Optical Oceanography.* Elsevier Publishing Company, Amsterdam-London-New York.
- KENDRICK, B. & M.J. RISK & J. MICHAELIDES & K. BERGMAN, 1982. Amphibious microborers: Bioeroding fungi isolated from live corals. *Bull. mar. Sci.* 32: 862-867.
- KOBLUK, D.R. & M.J. RISK, 1974. Devonian boring algae or fungi associated with micrite tubules. *Can. J. Earth Sci.* 11: 1606-1610.
- KOHLMEYER, J., 1969. The role of marine fungi in the penetration of calcareous substances. *Am. Zool.* 9: 741-746.
- VAN MOORSEL, G.W.N.M., 1983. Reproductive strategies in two closely related stony corals (*Agaricia*, Scleractinia). *Mar. Ecol. Prog. Ser.*, 13: 273-283.
- NORTON, A.P., 1959. *Norton's Star Atlas*, 22. Gall & Inglis, Edinburgh and London.
- PETERS, E.C., 1984. A survey of cellular reactions to environmental stress and disease in Caribbean scleractinian corals. *Helgol. Meeresunters.*, 37: 113-137.
- ROOS, P.J., 1964. The distribution of reef Corals in Curaçao. *Stud. Fauna Curaçao* 20: 1-51, 16 figs., 14 pls.
- ROOS, P.J., 1971. The shallow-water stony corals of the Netherlands Antilles. *Stud. Fauna Curaçao* 37: 1-108, 47 figs.
- SCHLICHTER, D. & H.W. FRICKE & W. WEBER, 1987. Light harvesting by wavelength transformation in a symbiotic coral of the Red Sea twilight zone. *Mar. Biol.* 91: 403-407.
- SOKAL, R.R. & F.J. ROHLF, 1981. *Biometry.* Freeman and Company, New York: 400-498.

- WELLS, J.W., 1973. New and old scleractinian corals from Jamaica. Coral Reef Project-Papers in Memory of Dr. Thomas F. Goreau. *Bull. mar. Sci.* 23 (1): 16-58.
- WELLS, J.W. & J.C. LANG, 1973. Systematic list of Jamaican shallow-water Scleractinia. Coral Reef Project-Papers in Memory of Dr. Thomas F. Goreau. *Bull. mar. Sci.* 23 (1): 55-58.
- WYMAN, K. D. & Z. DUBINSKY & J.W. PORTER & P.G. FALKOWSKI, 1987. Light absorption and utilisation among hermatypic corals: a study in Jamaica, West Indies. *Mar. Biol.* 96: 283-292.