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Light harvesting by wavelength transformation in a symbiotic coral of the Red Sea twilight zone

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Abstract

We report an extraordinary depth range for *Leptoseris fragilis* (Milne Edwards and Haime), a reef building coral of the Red Sea living in cytosymbiosis with zooxanthellae. The coral harbours an as yet unknown pigment system. We suggest that the heterotrophic host – the coral – provides its photoautotrophic symbionts with additional light. The supplementary light is provided by host pigments which transform light of short wavelengths into suitable wavelengths for photosynthesis, thus amplifying and increasing the transfer of photoassimilates from the zooxanthellae to the host.

Introduction

The platelike coral *Leptoseris fragilis* (Fungiina: Agariciidae) inhabits the upper twilight zone between 100 and 145 m depth with the highest densities of $\bar{x}=13$ ($s=5$, $n=10$) individuals m^{-2} between 110 and 120 m depth. This is the deepest *in-situ* record for a zooxanthellae containing scleractinian coral. In the Red Sea, the highest abundance and diversity of hermatypic, zooxanthellae harbouring corals generally occurs in shallow waters above 30 m (Loya, 1972; Mergner and Schuhmacher, 1974). Nine species can be found down to 100 m, but only *L. fragilis* can survive deeper than that (Fricke and Schuhmacher, 1983).

The unique depth distribution of *Leptoseris fragilis* living in an environment adverse to photosynthesis hints at adaptations to utilize low light intensities with a particular spectral composition. Recently Littler and Littler (1985) found photosynthesizing coralline algae at a depth of 268 m. The fact documents the capacity of photoautotrophic organisms to utilize light energy at great depths.

The basis for the singular depth distribution of *Leptoseris fragilis* may be due either to capacities of the cytosymbiotic algae (zooxanthellae) or the host or a combination of both. Adaptations which allow existence under dim light conditions may theoretically include: (a) a deep water adapted strain of the endosymbiotic algae (*Gymnodinium microadriaticum*) with increased pigment amounts, pigments with higher light or spectral sensitivity, or a complete new type of pigment; (b) the host provides its symbionts, at least temporarily, with metabolic energy or with additional light. Light provision could be accomplished by reflexion, bioluminescence or biofluorescence. A comparative study between a shallow water scleractinian coral (*Goniopora planulata*) and the deep water species should reveal which of these adaptations has been realized in *L. fragilis*.

Interactions between symbiotic algae and corals have been intensively studied for decades. Recent papers on this topic have been published by Muscatine *et al.* (1983, 1984), Dubinsky *et al.* (1984), McCloskey and Muscatine (1984) and Porter *et al.* (1984).

Material and methods

Leptoseris fragilis (Milne Edwards and Haime) was studied at Eilat, Gulf of Aqaba (Red Sea) with the research submersible GEO during three operational periods between 1982–1984. Individuals of *L. fragilis* were collected in the late afternoon and transported to shallow water (50 m). They were then transferred to the laboratory in darkened buckets in order to avoid light stress. The corals were observed under reduced light conditions or were deep frozen for biochemical studies. Small pieces were fixed for histological and ultrastructural studies (for details see Schlichter *et al.*, 1985).

Spectral composition of the downward irradiance was determined with a submarine photometer (G. M. MFG. Instrument Corporation, model 15 M 04) and different

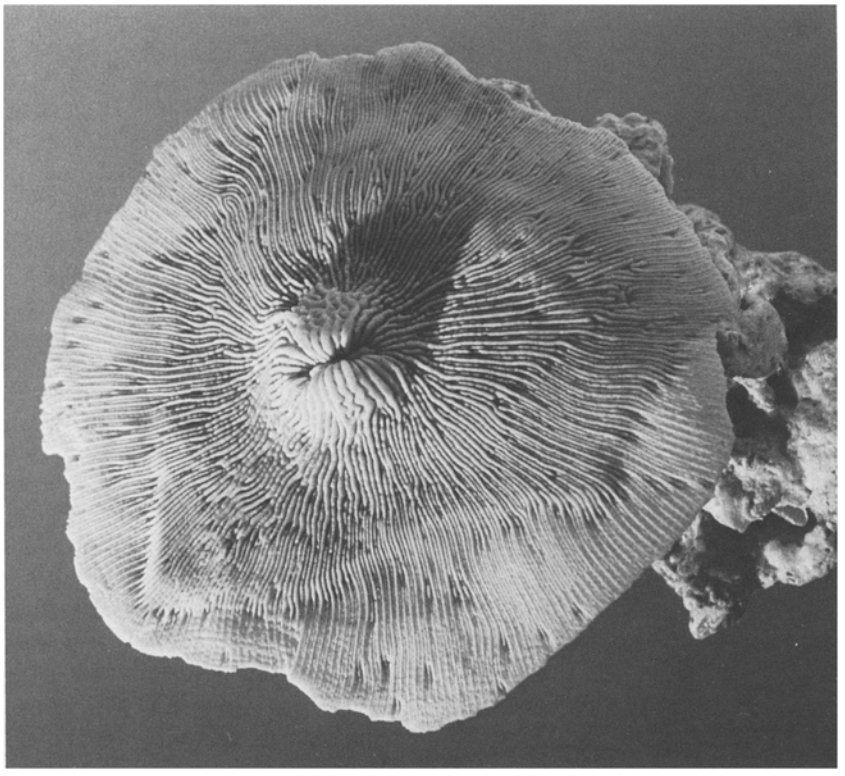

Fig. 1. *Leptoseris fragilis.* The scleractinian coral (up to 8 cm in diameter) lives at a depth between 100 and 145 m. Though the habitat receives a maximum of 0.15 to 1.7% of surface irradiation at noon, the association with symbiotic algae is successful

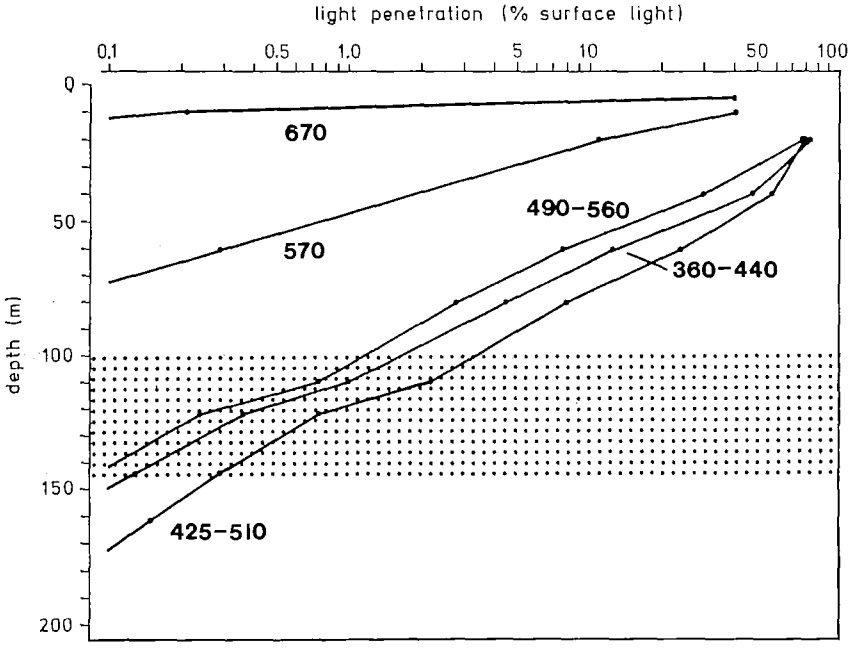

Fig. 2. Depth profile of the spectral composition of the downward irradiance in percent of surface irradiance (Eilat, Red Sea). The depth distribution of *Leptoseris fragilis* (dotted area) is extraordinary for a coral living in cytosymbiosis with algae

Schottfilters (Broad band filters: BG 18, BG 12, VG 8. The wavelengths inserted in Fig. 2 indicate the 80% range of maximum transmission. Edge filters; longpass: RG 5, OG 2, with 50% transmission at the wavelengths indicated in Fig. 2). The sensor was mounted in the upper observation domport of the submersible.

Fluorescence microscopy was performed with a Leitz Orthoplan, filter combination BF 355–425, LP 460. Absorption spectra were studied with a Hitachi 100–60 photometer and fluorescence emission spectra with an Aminco Bowman spectrofluorometer.

Results and discussion

The habitat of *Leptoseris fragilis* (Fig. 1) receives at noon on average 0.15 to 1.7% of surface irradiance or 0.5 to 10 μE m^{-2} s^{-1} in PAR (photosynthetic active radiation).

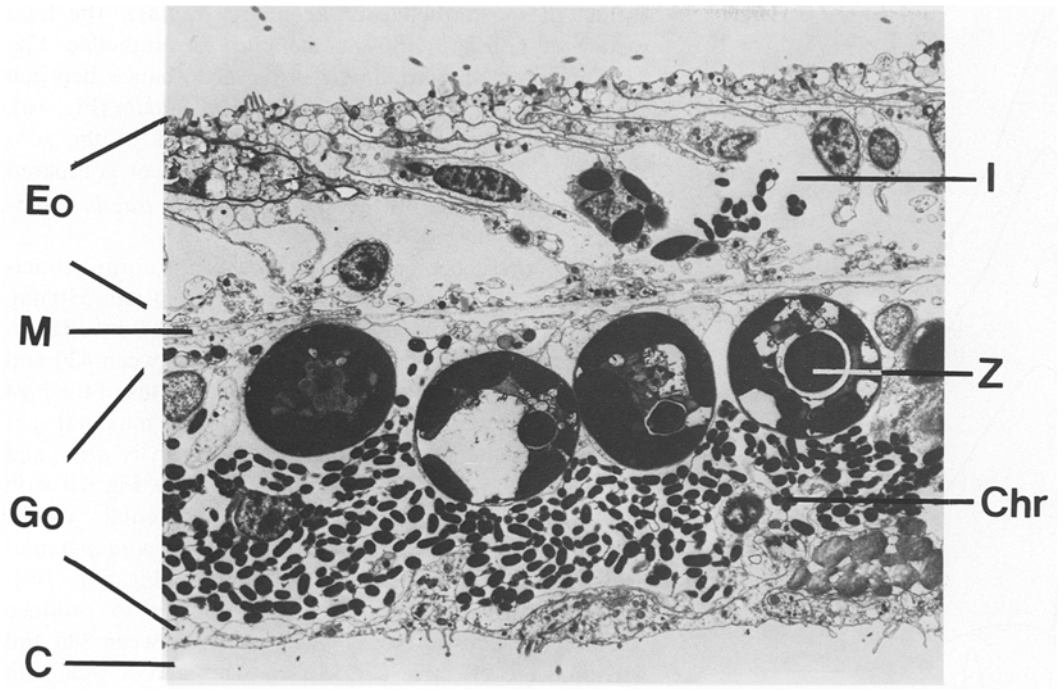

Fig. 3. *Leptoseris fragilis.* Ultrastructural organization of the external body wall (oral epidermis and gastrodermis). The symbiotic algae lie in a monolayer arrangement on a carpet of pigment granules which belong to a chromatophore system. 2 300×. E_o: oral epidermis; M: mesogloea; G_o: oral gastrodermis; C: coelenteron; I: intercellular space; Z: zooxanthellae (up to 7–9 μm in diameter); Chr: chromatophores, containing pigment granules (up to 1 μm diameter)

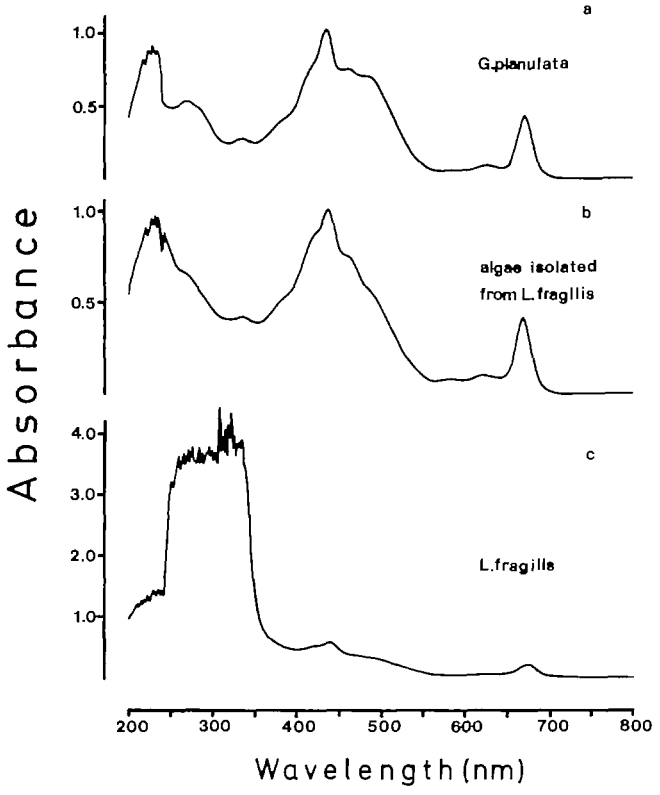

Fig. 4. Absorption spectra of chloroform extracts: (a) Extract of the shallow water coral *Goniopora planulata;* including host tissue and algae. (b) Extract of isolated zooxanthellae originating from *Leptoseris fragilis.* (c) Extract of *L. fragilis* including host tissue and algae. Consider the different amplification of the spectra that only simulates a lower content of algal pigments in Fig. 4c

Figure 2 shows the light attenuation of different wavelengths characterizing the water as oceanic water type I (Jerlov, 1976). Within the depth distribution of *L. fragilis,* wavelengths suitable for the photosynthesis of zooxanthellae have the best relative transmission (400–500 nm), but similarly high values are obtained for wavelengths down to 380 nm.

Electron microscopy revealed a hitherto unknown chromatophore system located in the oral gastrodermis of *Leptoseris fragilis.* The pigment granules form a dense stratum or carpet in the luminal part of the gastrodermis underlying the zooxanthellae, which are situated in a monolayered arrangement, probably to avoid mutual shading (Fig. 3; Schlichter *et al.,* 1985). In the shallow water species *Goniopora planulata,* such a chromatophore system is absent. Offered higher light intensities, *L. fragilis* discolours in less than one minute. The participation of the chromatophore system in this color change cannot be excluded, but the change in shade is mainly due to tissue retraction towards the skeleton, whereby the zooxanthellae are passively dislocated between the sclerosepta. In the histological section from corals fixed under low and strong light conditions respectively, the displacement can be observed. The functional significance of the close topographical relationship between the layer of zooxanthellae and the pigment cell system indicates that the hosts' chromatophores could have some function for the cytosymbiotic algae in the dim light environment.

Fluorescence microscopy reveals that the pigment granules display a reddish autofluorescence. Besides this, a

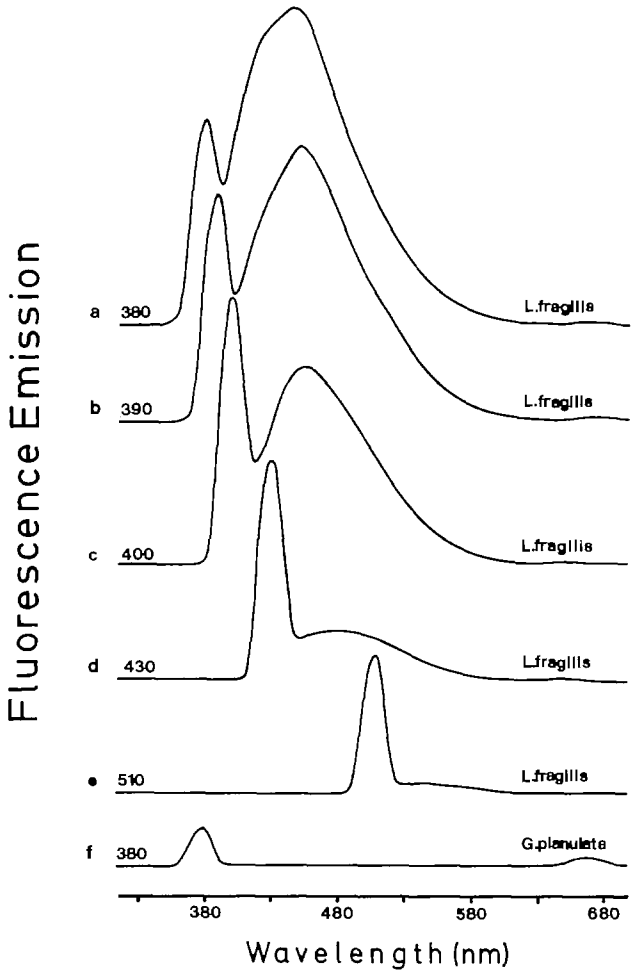

Fig. 5. Fluorescence emission spectra of chloroform extracts including host tissue and zooxanthellae. (a–e) Extracts of *Leptoseris fragilis* show intense fluorescence emission, depending on the excitation wavelength used (380–510). At higher amplification, additional fluorescence emission was traceable with peak emission shifting between 755 and 785 nm, depending on the excitation wavelengths used (380 to 400 nm). (f) The extract of *Goniopora planulata* shows no fluorescence emission over the set of excitation wavelengths offered, though on a chl *a* fluorescence basis (peak emission at 669 nm), the extracts were more concentrated. At much higher amplification, the extracts emitted low fluorescence between 440 and 550 nm, with peaks at 460 and 530 nm. The first peak in the spectra is due to the excitation. Especially shorter wavelengths, which are most prominent in the habitat of *L. fragilis,* produce strong fluorescence emission (see Fig. 2). The peak emission by the host pigments agrees well with the absorbance of the light trapping pigments of the symbiotic algae (compare with Fig. 4)

very intensive turquoise autofluorescence was observed that is not traceable to any specialized cell structures but seems to be a capacity of the cytoplasm. The shallow water coral, lacking pigment granules, showed no fluorescence other than the red one of the zooxanthellae.

Absorption spectra of chloroform extracts of both corals revealed no drastic qualitative differences in the content of pigments involved in photosynthesis (compare Fig. 4a, total extract of *Goniopora planulata* with Fig. 4b, extract of zooxanthellae of *Leptoseris fragilis*). The total extract of *L. fragilis* (host tissue plus zooxanthellae, Fig. 4c), however, showed an intensive absorbance between 350 and 260 nm that did not exist in *G. planulata* (Fig. 4a). The absorbance of the accessory pigments of the zooxanthellae of *G. planulata* is more prominent compared with the absorbance of the symbionts of *L. fragilis* (compare Fig. 4a with Fig. 4b).

For fluorescence emission spectra, chloroform extracts were excited with wavelengths between 380 and 510 nm. Using the excitation wavelength of 380 or 390 nm, *Leptoseris fragilis* showed an intense emission between 420 and 455 nm (Fig. 5a, b). Peak emission wavelengths of the host pigments fit almost identically with the maximal absorbance of the algae pigments (chlorophylls $a+c$ and accessory pigments; Jeffrey, 1980) (compare Fig. 4b with Fig. 5a, b). Under comparable experimental conditions, no emission was traceable in *Goniopora planulata* living in a well illuminated habitat (Fig. 5f). Testing different wavelengths for their power to produce fluorescence emission, only wavelengths between 380 and 410 nm were effective (Fig. 5a–e). This agrees well with the photic environment of *L. fragilis* (see Fig. 2, dotted area), where shorter wavelengths penetrate to the habitat.

Conclusions

Shorter wavelengths (380–500 nm) of the spectrum represent the greatest part of irradiance illuminating the habitat of the zooxanthellae containing the deep water coral *Leptoseris fragilis.* The radiation is not only absorbed by chlorophylls and accessory pigments of the zooxanthellae but also by host pigments. The wavelengths below 400 nm, which are less suitable for photosynthesis, particularly excite pigment granules of a chromatophore system and pigment localized in the cytoplasma of the host to autofluorescence. The absorbed light of shorter wavelengths is thus shifted into longer wavelengths which are then emitted and subsequently utilized by the endosymbiotic algae. The heterotrophic host thereby provides its autotrophic symbionts with additional light, thus, probably amplifying photosynthesis and increasing the export of photoassimilates. The mechanism, transforming available light of particular wavelengths into light of wavelengths which are suitable for photosynthesis of the algal symbionts, is a completely new type of contribution of the coral host for its symbiotic algae.

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Literature cited

Dubinsky, Z., P. G. Falkowski, J. W. Porter and L. Muscatine: Absorption and utilization of radiant energy by light- and shade-adapted colonies of the hermatypic coral *Stylophora pistillata.* Proc. R. Soc. London B *222,* 203–214 (1984)

Fricke, H. W. and H. Schuhmacher: The depth limits of Red Sea stony corals: an ecophysiological problem (a deep diving survey by submersible). Mar. Ecol. Prog. Ser. *4,* 163–194 (1983)

Jeffrey, S. W.: Algal pigment systems. *In:* Primary productivity in the sea, pp 33–57. Ed. by P. G. Falkowski. New York, London: Plenum Press 1980

Jerlov, N. G.: Marine optics, 231 pp. Amsterdam, Oxford, New York: Elsevier Scientific Publishing Company 1976

Littler, M. M. and D. S. Littler: Deepest known plant life discovered on an uncharted seamount. Science, N.Y. 227, 57–59 (1985)

Loya, Y.: Community structure and species diversity of hermatypic corals of Eilat, Red Sea. Mar. Biol. *13,* 100–123 (1972)

McCloskey, L. R. and L. Muscatine: Production and respiration in the Red Sea coral *Stylophora pistillata* as a function of depth. Proc. R. Soc. London B *222,* 215–230 (1984)

Mergner, H. and H. Schuhmacher: Morphologie, Ökologie und Zonierung von Korallenriffen bei Aqaba (Golf von Aqaba, Rotes Meer). Helgoländer wiss. Meeresunters. *26,* 238–358 (1974)

Muscatine, L., P. G. Falkowski and Z. Dubinsky: Carbon budgets in symbiotic associations, pp 649–658. *In:* Endocytobiology, vol. II. Berlin, New York: Walter de Gruyter & Co 1983

Muscatine, L., P. G. Falkowski, J. W. Porter and Z. Dubinsky: Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata.* Proc. R. Soc. London. B *222,* 181–202 (1984)

Porter, J. W., L. Muscatine, Z. Dubinsky and P. G. Falkowski: Primary production and photoadaption in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata.* Proc. R. Soc. Lond. B *222,* 161–180 (1984)

Schlichter, D., W. Weber and H. W. Fricke: A chromatophore system in the hermatypic, deep-water coral *Leptoseris fragilis* (Anthozoa: Hexacorallia). Mar. Biol. *89,* 143–147 (1985)

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