

## In vivo measurements of the seasonal photosynthetic fluorescence of the Mediterranean coral *Cladocora caespitosa* (L.)

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**SUMMARY:** In situ photosynthetic fluorescence of the zooxanthellate Mediterranean coral *Cladocora caespitosa* (L.) was measured seasonally on colonies from 5 to 27 m depth using an INF-300 Integrating Natural Fluorometer (Biospherical Instrument Inc.). This oceanographic instrument, used to measure the in vivo phytoplankton chlorophyll *a* (Chl *a*) fluorescence, was adapted to record the natural fluorescence of *C. caespitosa* by SCUBA divers. The resulting curves of natural fluorescence of Chl *a* vs photosynthetically active radiation (PAR 400-700 nm) showed that: (1) natural fluorescence was limited by light availability in both deep and shallow colonies in all seasons; (2) photosynthesis occurred in *C. caespitosa* also in winter, when temperature is low and seawater turbidity contributes significantly to PAR attenuation; and (3) the efficiency of the Chl *a* fluorescence increased from summer to winter. This last finding outlines the winter coupling between zooxanthellae activity and calcification processes and is consistent with the formation of the high density band in the coral skeleton.

**Keywords:** coral, Mediterranean Sea, in vivo fluorescence, photosynthesis.

**RESUMEN:** MEDIDAS IN VIVO DE LA FLUORESCENCIA FOTOSINTÉTICA ESTACIONAL EN EL CORAL MEDITERRÁNEO *CLADOCORA CAESPITOSA* (L.). – La fluorescencia fotosintética in situ, de las zooxantelas del coral mediterráneo *Cladocora caespitosa* (L.), se determinó estacionalmente sobre colonias desde 5 a 26 m de profundidad a través de un fluorímetro integrador INF-300 (Biospherical Instrument Inc.). Este instrumento oceanográfico, utilizado para medir la fluorescencia de la clorofila *a* del fitoplancton in vivo, se ha adaptado para determinar la fluorescencia natural de *C. caespitosa* por los buceadores. Las curvas resultantes de la fluorescencia natural de la clorofila *a* vs la radiación (PAR 400-700 nm) fotosintéticamente activa mostraban que: la fluorescencia natural estaba limitada por la disponibilidad de luz en ambas colonias de profundidad y de aguas poco profundas en todas las estaciones del año, (2) la fotosíntesis producida en *C. caespitosa* tenía lugar también en invierno, cuando la temperatura es baja y la turbidez del agua contribuyen de forma significativa a la atenuación de PAR, (3) la eficiencia de la fluorescencia de la clorofila *a* incrementaba desde verano a invierno. Este último hallazgo pone de manifiesto el acoplamiento entre la actividad de las zooxantelas y los procesos de calcificación y es consistente con la formación de la banda de alta densidad en el esqueleto coralino.

**Palabras clave:** coral, mar Mediterráneo, fluorescencia in vivo, fotosíntesis.

## INTRODUCTION

*Cladocora caespitosa* (L.) is a scleractinian coral living in the Mediterranean Sea from 5 to 40 m depth in turbid environments (Laborel, 1961; Zibrowius, 1980). Large fossil *C. caespitosa* formations have been dated since the Late Pliocene and

characterised the warmer climatic phases of the Pleistocene when this coral formed true reefs in both the eastern and western Mediterranean Sea (Peirano *et al.*, 2004). Today *C. caespitosa* forms extensive shallow-water 'beds' of colonies with densities up to 4 col m<sup>-2</sup> or massive banks covering several square metres (Peirano *et al.*, 2001; Kružić and Požar-Domac, 2004).

The coral has a phaceloid form with separated corallites growing upward. Sclerochronology studies revealed that *C. caespitosa* deposits two bands per year with annual growth rates ranging from 1.36 to 4.42 mm yr<sup>-1</sup> and no differences were found in either the timing of band deposition or growth rates between shallow and deep colonies (Peirano *et al.*, 1999). The low-density band is deposited during the dry, hot summer (June-September). In autumn (October-November) the coral begins the deposition of the high density band, which is fully developed in March, at the end of the winter, a season characterised by rain, low sea water temperature and rough sea (Peirano *et al.*, 2005).

In winter *C. caespitosa* lives in such a turbid environment (less than 6 m water transparency measured with the Secchi disk) that it is hard to believe that, both in shallow water and at depth, photosynthesis can even occur, let alone contribute to the coral's growth.

Although some tropical species react to cooler water temperature and lower PAR with the enhancement of chl contents and zooxanthellatae densities (Warner *et al.*, 2002), *Cladocora caespitosa* did not show seasonal variation of the photosynthetic apparatus (Schiller, 1993; Rodolfo-Metalpa *et al.*, 2006).

In the present work the seasonal, photosynthetic activity of the coral was verified through measurements of in vivo natural fluorescence, as the fluorescent flux from the chlorophyll *a* stimulated by the available sunlight. Natural fluorescence of Chl *a*, which was proved to be related to Chl *a* content, was measured on shallow and deep colonies and compared within seasons and depths and with the band deposition pattern of the coral.

## MATERIAL AND METHODS

Dives between 5 and 27 m were carried out along the eastern Ligurian coast (northwestern Mediterranean), where beds and banks of *Cladocora caespitosa* are common (Peirano *et al.*, 1999). Two sampling sites were located in front of the Magra River (FM), at 5 m depth, and 1 km apart at Punta Bianca (PB), at 10 m depth. Three more sites were positioned at 10, 20 and 40 km to the west of the Magra River, down current: 1) Cala Grande (CG), where *C. caespitosa* colonies are limited to 20 m depth; 2) Capo di Montenero (MN), with one deep bank at 27 m depth and rare,

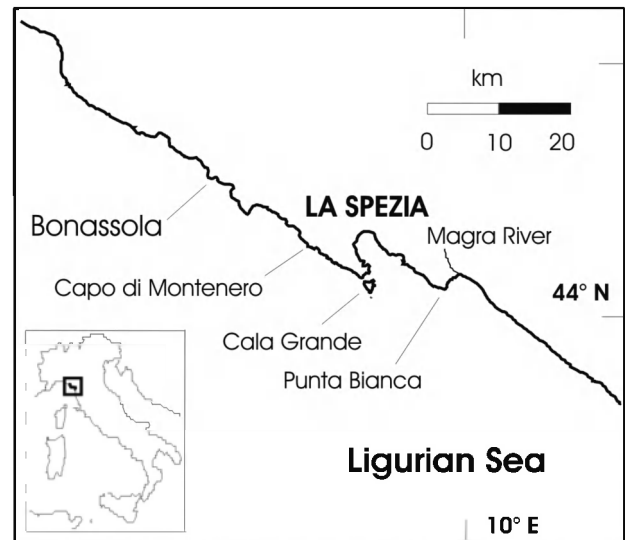


FIG. 1. – Coastal region of La Spezia and sampling sites: Bonassola (BO), Capo di Montenero (MN), Cala Grande (CG), Punta Bianca (PB) and the mouth of the Magra River (FM).

sparse colonies at 17 m; and 3) Bonassola (BO), with shallow coral beds at 7 and 9 m depth and one deep bank at 27 m depth (Fig. 1).

Natural chlorophyll *a* (Chl *a*) fluorescence was measured using an INF-300 Integrating Natural Fluorometer (Biospherical Instrument Inc.), a device used to measure in vivo phytoplankton fluorescence (Chamberlin *et al.*, 1990). The system has a detector arranged to record natural upwelling radiance of a water mass, filtering the emission spectra of Chl *a* and rejecting wavelengths of less than 650 nm. The INF-300 also measures the scalar irradiance of underwater photosynthetically active radiation (PAR, 400 to 700 nm), depth and water temperature and has an internal memory that allows continuous recording of data at a rate of up to 1 record per second.

To adjust the probe to measure Chl *a* fluorescence of *C. caespitosa* the sensitivity of the Chl *a* sensor was first tested in aquaria at constant temperature and light ( $T = 20^{\circ}\text{C}$ ,  $\text{PAR} = 60 \mu\text{E m}^{-2} \text{sec}^{-1}$ ). Measurements were made both on phytoplankton monoculture of *Dunaliella* sp. and on one *C. caespitosa* colony positioned at a distance of 10 cm below the fluorescence sensor. The in vivo phytoplankton fluorescence measurements showed a highly significant positive correlation with increasing Chl *a* contents from a minimum of  $0.88 \mu\text{g l}^{-1}$  Chl *a* ( $N = 14$ ,  $R^2 = 0.989$ ,  $P < 0.0001$ ). The in vivo measurements of *C. caespitosa* fluorescence performed on *C. caespitosa* showed that the measurements were significantly related to the

increasing number of corallites ( $N = 8$ ,  $R^2 = 0.995$ ,  $P < 0.0001$ ) from a minimum of 23 corallites, corresponding to a surface of  $9 \text{ cm}^2$ .

To normalise underwater fluorescence measurements to a preset surface area, a black panel with one circular window with a radius of  $4.1 \text{ cm}$  ( $52.8 \text{ cm}^2$ ) was fixed at a distance of  $10 \text{ cm}$  below the fluorescence sensor. The coefficient of attenuation of the exciting irradiance ( $k$ ), i.e. the attenuation of the fluorescence signal vs the distance from the window sensor was  $k = 1.12$ .

Underwater measurements on *C. caespitosa* were carried out on days with clear sky and flat sea between 11.00 am and 1.00 pm GMT. Sampling was performed in autumn 1999 (October–November), in summer 2000 (August–September), and in winter 2001 (February). Above water, downwelling PAR irradiance was recorded with a ThetaLog Delta-T device connected to a flat sensor. During diving operations the INF-300 was positioned on top of coral colonies or on different areas of coral banks to record the total natural fluorescence ( $F_n$ ). After each recording sequence the diver closed the window with a mobile black sheet to measure the natural fluorescence of the water mass between the sensor and the colony ( $F_w$ ). Hence the fluorescence of the coral ( $F_c$ ) in  $\mu\text{mol cm}^{-2}$  was obtained from the relationship  $F_c = (F_n - F_w) * k$ . The fluorescence per polyp ( $F_p$ ) in  $\mu\text{mol polyp}^{-1}$  was calculated as  $F_p = F_c / N_p$ , where  $N_p$  was the total number of polyps counted in the window.

$F_p$  differences between colonies and differences between seasonal curves of  $F_p$  versus underwater PAR irradiance were analysed through analysis of covariance (ANCOVA), with PAR as a covariate, and Tukey post-hoc comparisons of means. Homogeneity of variances was checked with Levene's test.

## RESULTS

During underwater measurements atmospheric PAR irradiance varied between a minimum of  $200 - 500 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in October–February to a maximum of  $1100 - 1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in August–September. Sea water temperature in autumn and winter was uniform from shallow to  $30 \text{ m}$  depth ( $22^\circ\text{C}$  in October and November,  $14^\circ\text{C}$  in February). In summer, when stratification occurs, water temperatures varied from  $26^\circ\text{C}$  at surface to  $20^\circ\text{C}$  at  $30 \text{ m}$  depth.

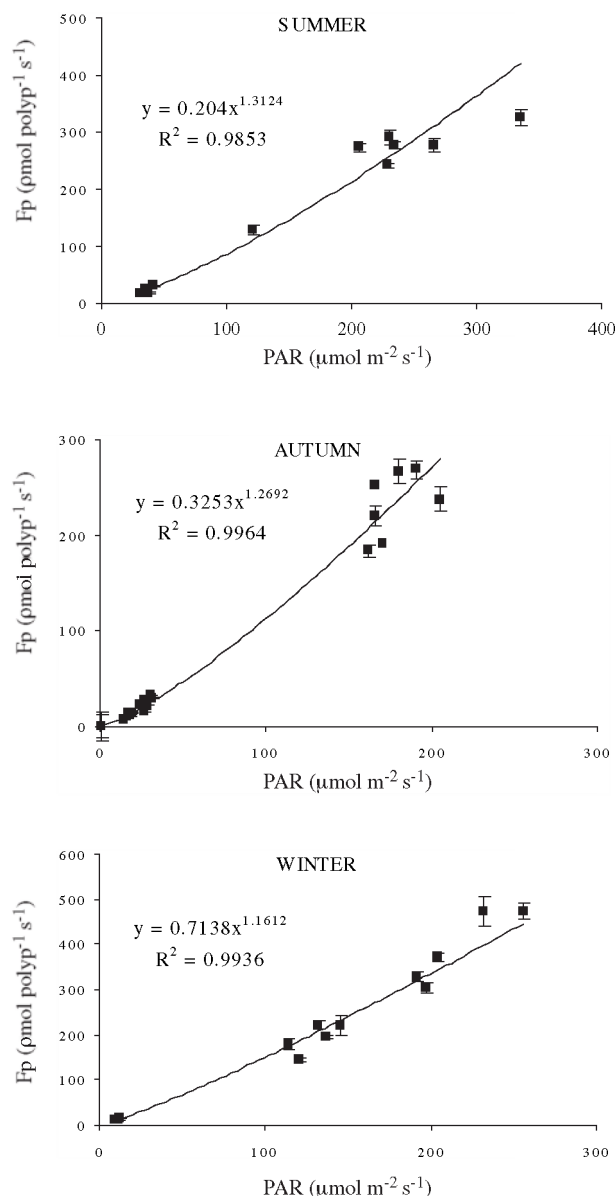


FIG. 2. – *Cladocora caespitosa*. Seasonal natural Chl *a* fluorescence per polyp ( $F_p$ ) vs underwater PAR irradiance.

In the three seasons investigated *C. caespitosa* showed polyp fluorescence ( $F_p$ ) exponentially related to PAR ( $R^2 > 0.988$ ;  $P > 0.05$ ) (Fig. 2).

Differences observed in each season between and within sites were related to water turbidity that, in some cases, limited light availability considerably. For example,  $F_p$  measurements made in autumn (Table 1) on *C. caespitosa* colonies living near the river mouth, at  $9 \text{ m}$  depth (PB14–PB18) ranged from  $15.7$  to  $32.5 \mu\text{mol polyp}^{-1}$ , values comparable with those measured on the same day, at  $20 \text{ m}$  depth, on Cala Grande colonies CG1–CG5 ( $6.6 - 21.9 \mu\text{mol polyp}^{-1}$ ). Again, the comparison of  $F_p$

TABLE 1. – Mean values of in vivo natural fluorescence of chlorophyll *a* per polyp (Fp) (maximum and minimum in parenthesis) and mean photosynthetically active radiation (PAR) measured with INF-300 probe on *Cladocora caespitosa* colonies in the three seasons (sd = standard deviation). Sites: CG = Cala Grande; PB = Punta Bianca; FM = Magra River; Mn = Capo di Montenero; BO = Bonassola.

Season	Colony	Depth (m)	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	PAR (sd)	Fp ( $\mu\text{mol pol}^{-1}$ )	Fp (sd)	n
Summer	CG1	20	31.0	3.9	18.4 (15.7-22)	2.1	55
	CG2	20	31.5	1.4	17.2 (15.3-18.7)	0.9	55
	CG3	20	41.4	1.9	30.1 (27-32.8)	1.7	60
	CG4	20	35.8	4.7	25.5 (21.1-29.8)	3.1	56
	CG5	20	37.8	1.4	18.5 (16.7-20.4)	1.1	63
	PB1	9	206.0	3.2	273.6 (262.4-292.5)	7.8	50
	PB2	9	228.8	4.9	242.3 (232.5-253.9)	4.6	77
	PB3	9	234.5	4.1	276.8 (257.8-290.5)	5.9	78
	PB4	9	265.7	6.5	277.2 (250.5-302.6)	11.7	87
	PB5	9	230.0	9.9	290.6 (238.7-319.6)	13.6	124
	MN1	27	121.3	3.4	128.6 (104.3-142.6)	8.5	135
	MN2	17	334.0	25.0	325.4 (293.9-372.9)	15.1	77
Autumn	CG1	20	17.3	0.7	14.0 (13.7-14.5)	0.2	44
	CG2	20	14.6	0.8	6.6 (5.6-8.3)	0.7	69
	CG3	20	19.3	0.7	14.2 (12.9-15)	0.5	61
	CG4	20	18.4	0.4	11.2 (10.4-11.8)	0.4	71
	CG5	20	24.3	0.5	21.9 (21-22.5)	0.5	37
	CG6	20	0.6	0.03	0.2 (0.1-0.2)	0.02	79
	CG7	20	0.6	0.03	0.2 (0.1-0.2)	0.02	113
	CG8	20	0.6	0.02	0.2 (0.1-0.2)	0.01	90
	CG9	20	0.6	0.03	0.2 (0.1-0.2)	0.01	104
	CG10	20	0.5	0.02	0.1 (0.1-0.2)	0.01	90
	PB14	9	31.1	0.7	32.5 (31.1-33.7)	0.6	40
	PB15	9	31.9	0.5	29.4 (28.1-30.4)	0.6	52
	PB16	9	26.8	0.3	15.7 (14.2-16.5)	0.5	51
	PB17	9	28.5	0.7	21.9 (19-23.7)	1.1	63
	PB18	9	27.2	0.7	26.9 (25.3-28.5)	0.8	57
	FM7	5	204.8	5.6	237.7 (210.7-254.2)	11.3	69
	FM8	5	161.5	8.6	183.2 (150.3-205.1)	15.8	42
	FM9	5	190.7	2.0	268.5 (235.7-291.7)	13.2	52
	FM10	5	180.2	2.3	266.7 (252.7-272.6)	5.1	59
	FM11	5	166.2	3.1	219.9 (192.5-237.1)	10.1	54
	FM12	5	170.4	4.6	191.4 (160.5-219.6)	13.5	58
Winter	FM13	5	166.3	4.3	252.8 (210.2-262.6)	10.4	61
	BO1	27	9.9	0.1	10.5 (10.1-11)	0.2	32
	BO2	27	10.1	0.3	10.5 (8.6-12)	1.0	67
	BO3	27	11.1	0.2	10.1 (9.6-10.5)	0.2	57
	BO4	27	12.3	0.2	15.8 (14.2-16.5)	0.4	80
	BO5	9	145.7	3.0	220.5 (179.8-253.1)	22.9	65
	BO6	9	137.5	1.9	194.5 (188.8-199.9)	2.8	67
	BO7	9	132.3	2.0	222.1 (204.1-235.7)	10.2	54
	BO8	9	114.4	2.6	178.8 (160.1-195.7)	11.4	54
	BO9	9	120.7	1.2	144.1 (138.4-147.7)	2.5	42
	BO10	7	204.1	3.9	372.1 (347.2-386.4)	9.0	77
	BO11	7	191.3	4.7	328.0 (303.8-343.4)	11.3	35
	BO12	7	231.8	0.7	473.2 (432-519.8)	32.9	28
	BO13	7	255.6	19.5	474.1 (433.4-516.6)	17.2	47
	BO14	7	197.3	2.7	302.8 (283.7-319.9)	10.2	54

measurements made in autumn at Cala Grande on two different days (CG1-CG5 vs CG6-CG10) showed significant differences ( $P < 0.05$ ) due to sea-water turbidity, which one day severely reduced underwater irradiance and caused a fall in chlorophyll fluorescence in CG6-CG10 colonies (Table 1).

In general western colonies (Montenero and Bonassola) proved to live in an environment characterised by less turbidity than eastern ones (Cala Grande, Punta Bianca and Foce Magra). This was also true in summer, when fluorescence measured on colonies CG1-CG5 at Cala Grande at 20 m depth

(17.2-30.1  $\mu\text{mol polyp}^{-1}$ ) was significantly lower ( $P < 0.0001$ ) than Fp values recorded at 27 m (MN1; 128.6  $\mu\text{mol polyp}^{-1}$ ) and 17 m (MN2; 325.4  $\mu\text{mol polyp}^{-1}$ ) depth at Punta di Montenero.

The continuous recording of natural fluorescence throughout a day performed in September on the MN1 bank of Punta di Montenero (Fig. 3) was used to calculate the exponential curve  $Fp = 0.9088 \text{ PAR}^{1.0644}$  ( $R^2 = 0.999$ ;  $P > 0.05$ ). The curve did not differ from the autumn curve of Figure 2 ( $P > 0.05$ ), showing that deep colonies of *Cladocora caespitosa* have the same fluorescence activity as shallow ones.

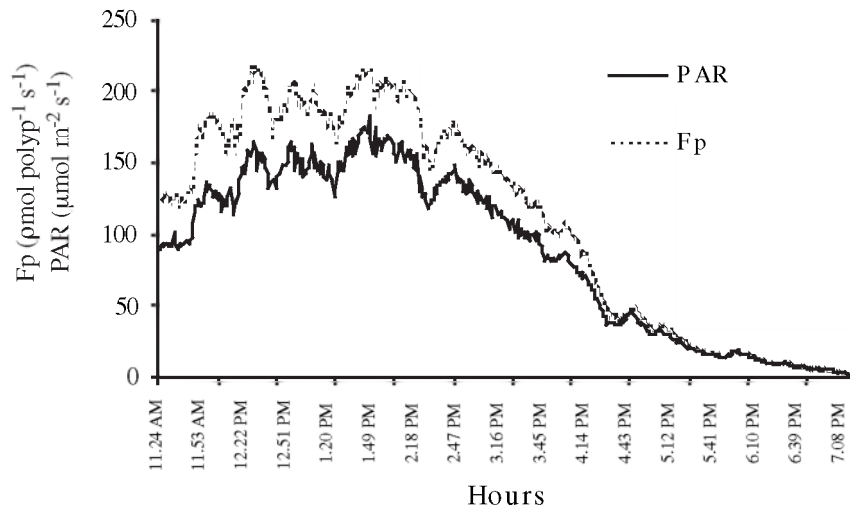


FIG. 3. – *Cladocora caespitosa*. Continuous recording of in vivo Chl *a* fluorescence per polyp (Fp) vs underwater PAR irradiance at Capo di Montenero (MN1, 27 m depth, September).

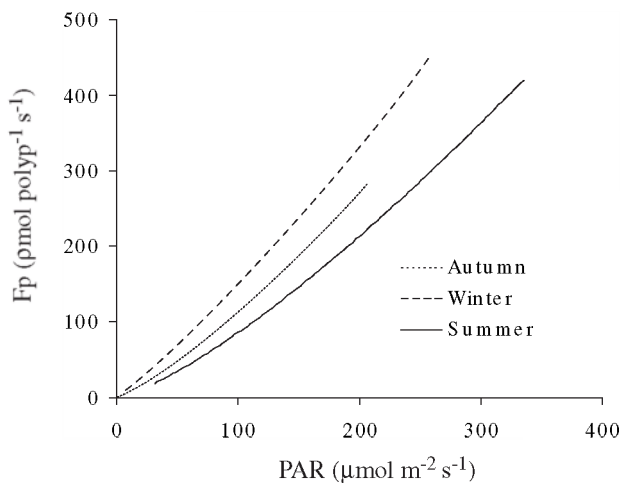


FIG. 4. – *Cladocora caespitosa*. Comparison between seasonal curve of Chl *a* fluorescence per polyp vs underwater PAR irradiance.

The comparison of the three seasonal curves of Fp vs PAR showed that the Chl *a* natural fluorescence of *C. caespitosa* differed significantly ( $P < 0.0001$ ) from summer to winter (Fig. 4), with an increase in efficiency in autumn and winter, seasons characterised by rough sea, low temperature and low light availability.

## DISCUSSION

The INF-300 was used to perform non-intrusive measurements of active photosynthesis in extreme, natural dim conditions without sample manipulation or incubation which, as pointed out by Sakshaug *et al.* (1997), may affect final data. Though the evalu-

ation of true photosynthetic yield from INF-300 measurements proved to be very difficult (Chamberlin *et al.*, 1990; Maritonema *et al.*, 1990), the measurements on *Cladocora caespitosa* confirmed that photosynthesis occurs in the coral even in winter months, when turbidity may reduce light penetration to a minimum.

*C. caespitosa* showed natural fluorescence that was variable in both depth and season, and no photoinhibition effects were observed. The findings allow us to assume that colonies of *C. caespitosa* have photosynthetic Chl *a* fluorescence limited seasonally only by light availability. Chl *a* fluorescence was light-limited in deep colonies and the efficiency of fluorescence increased from summer to winter, when available light is lower. Though the true photosynthetic yield of *C. caespitosa* could not be calculated from INF-300 fluorescence measurements, such findings are in accordance with oxygen-flux measurements conducted by Schiller (1993) on colonies kept at constant temperatures, with the seasonal fluctuations of the photosynthetic capacity of Indo-Pacific corals found by Brown *et al.* (1999), and with higher values of photosynthetic yield measured in periods of cooler water temperature and lower PAR on the Caribbean species of *Montastrea* (Warner *et al.*, 2002).

The increase of natural fluorescence efficiency in autumn and winter supports the hypothesis of the active coupling of zooxanthellae and polyp metabolism toward the enhancement of the calcification processes. This is consistent with the formation of the high-density (HD) band in more than 50% of *C. caespitosa* colonies in autumn and in all the colonies in



winter (Peirano *et al.*, 1999). On the other hand, the lowest values of natural fluorescence recorded in summer are in agreement with the formation of the low-density bands (LD). The summer is indeed a season when *C. caespitosa* is subjected to stress due to periods of high irradiance, high temperature and starvation that may cause the onset of tissue necrosis (Peirano *et al.*, 2005; Rodolfo-Metalpa *et al.*, 2005).

Though the photosynthetic fluorescence of deep colonies is lower than that of shallow ones throughout the year, the absence of differences in growth rates between shallow and deep colonies found by Peirano *et al.* (1999) remains difficult to explain. Whereas in tropical corals this homogeneity is achieved through the increase in zooxanthellae and/or chlorophyll contents in deeper colonies (Stimson, 1997; Brown *et al.*, 1999; Titlyanov *et al.*, 2001; Warner *et al.* 2002), in *C. caespitosa* zooxanthellae contents do not change significantly between shallow and deep colonies and during the year (Schiller, 1993). Some specific biochemical adaptations could be hypothesised in deep colonies to explain growth rates similar to shallow water colonies as being due to the enhanced utilization of carbon sources, a reduction of respiration to photosynthesis ratio or changes in enzyme activities (Barnes and Chalker, 1990; Muscatine, 1990; Warner *et al.*, 2002). Colonies in a shaded environment may balance photosynthesis limitations, enhancing the polyp's active feeding, which—as Houlbrèque *et al.* (2003) demonstrated on the tropical coral *Stylophora pistillata*—contributes to the improvement of calcification processes. In *C. caespitosa* this strategy is consistent with the winter availability of POM and DOM from resuspended sediments (Peirano *et al.*, 2005) and with the parallel increase in plankton, which attains its maximum in this season in the northwestern Mediterranean (Goffart *et al.*, 2002).

Hence, *C. caespitosa* allows one to hypothesise complex environmental adaptations that explain its past and current success in colonising the Mediterranean. Though further research is needed, the results show that a great part of the coral's 'flexibility' is due to its photosynthetic apparatus, which is adapted to react to the extreme variability of underwater irradiance of the Mediterranean. In tropical corals light limitation may severely reduce the photosynthetic yield of zooxanthellae-coral complex (Yentsch *et al.*, 2002) and related reactions, as the increase in density of zooxanthellae and/or pho-

topigments require hours or days to be achieved (Falkowski *et al.*, 1990; Dunne and Brown, 2001). On the other hand, *C. caespitosa* shows a constant chlorophyll content and number of zooxanthellae (Schiller, 1993; Rodolfo-Metalpa *et al.*, 2006), allowing one to hypothesise the enhancement of the PSII system efficiency as the quickest way to adapt to underwater irradiance variability.

## ACKNOWLEDGEMENTS

I am grateful to M. Abbate and R. Rodolfo Metalpa for their help in laboratory measurements and to S. Cocito and anonymous referees for the critical reading of the manuscript. I also wish to thank my colleagues S. Sgorbini, C.N. Bianchi, and D. Ferrari of the "Punta Mesco" Diving Centre for their assistance during diving operations.

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Scient. ed.: P.J. López-González.

Received March 7, 2006. Accepted May 22, 2007.

Published online September 3, 2007.