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Skeleton growth and density pattern of the temperate, zooxanthellate scleractinian *Cladocora caespitosa* from the Ligurian Sea (NW Mediterranean)

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ABSTRACT: X-radiographs of corallites of the zooxanthellate coral *Cladocora caespitosa* (L.), collected in the Ligurian Sea between 3 and 27 m depth, were examined. *C. caespitosa* deposits 2 bands yr⁻¹; the high density band is deposited during winter (November to March) while the low density band is deposited in summer. Average growth rates ranged from 1.36 ± 0.58 to 4.42 ± 1.61 mm yr⁻¹. No differences in the timing of band deposition were found between shallow and deep colonies. A comparison of the band pattern with monthly temperature–irradiance measurements from the Ligurian Sea, and with literature data on the photosynthetic efficiency of zooxanthellae, led us to hypothesise a mechanism of growth with a low dependency on autotrophy.

KEY WORDS: Coral · *Cladocora caespitosa* · Growth · Mediterranean Sea

INTRODUCTION

Many papers have been published on coral growth since X-radiography was first used to demonstrate the annual banding pattern (Knutson et al. 1972, Budde-meier et al. 1974). Despite some problems in the interpretation of density band patterns related to the 3-dimensional development of corallites (Barnes & Lough 1989, Lough & Barnes 1990, Barnes & Taylor 1993, Le Tissier et al. 1994) and a few exceptions (Charuchinda & Chansang 1985, Brown et al. 1986), the deposition of 1 high density (HD) and 1 low density (LD) band per year has been widely accepted. Coral banding has been related to both cyclic variation of environmental parameters (Knutson et al. 1972, Budde-meier et al. 1974, Lough & Barnes 1997) and anthropogenic disturbance (Hudson et al. 1994). Both influence the packing of skeletal elements (Oliver et al. 1983, Barnes & Devereux 1988, Barnes & Lough 1993).

Comparing banding patterns of hermatypic corals, Highsmith (1979) proposed a model whereby the banding pattern changes with latitude. He hypothesised that in 'high latitude' (temperate) corals, HD bands form during periods of low temperature and low light intensity, whereas LD bands form during periods of high temperature and high light intensity. This assumption was confirmed by observations on *Porites* species living in shallow water in the Red Sea (Klein & Loya 1991, Klein et al. 1992). In deep samples of the same genus, however, Klein et al. (1993) highlighted a shift to an opposite, depth-related deposition pattern and outlined the importance of investigating the nature and timing of band deposition in extreme conditions.

Cladocora caespitosa (L.) is the only colonial and zooxanthellate coral native to the Mediterranean (Zibrowius 1980) and belongs to the Faviidae, a family among the most important reef builders in tropical areas. It lives between the surface and 50 m depth and has Recent and Pleistocene records (Bernasconi et al. 1997, Aguirre & Jiménez 1998). Where abundant, it

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forms 'beds' of globose to hemispherical colonies or banks up to more than 1 m high and covering several square metres (Laborel 1961, Kühlmann et al. 1991, Schiller 1993a, Morri et al. 1994, Kühlmann 1996). The colonies of *C. caespitosa* are phaceloid, i.e. the corallites develop vertically, each having its own walls independent of the others. The occurrence of an alternating dense and less dense banding on X-radiographs, as in the most studied tropical relatives, has been demonstrated only recently (Peirano et al. 1998).

In the present paper, we report for the first time on the corallite structure and sclerochronological data of *Cladocora caespitosa* from the Ligurian Sea (NW Mediterranean). The timing of HD and LD band deposition was reconstructed by comparing samples from different periods of the year, and then related to seasonal change in water temperature and irradiation. The annual growth was calculated from colonies at different sites and depths.

METHODS

In 1994, 24 colonies of *Cladocora caespitosa* were collected at 3 sites in the La Spezia region, Italy (Fig. 1): Punta Bianca (March and November, 3 m depth), Capo di Montenero (July, 10 m) and Cala Grande (July, 20 m). One further sample was taken at Bonassola (March, 27 m depth) from a large bank (Morri et al. 1994).

In the laboratory, the colonies were measured and as many long, rectilinear, isoplanar (i.e. developed in 1 plane) and unbored corallites as possible were carefully isolated. Cleared of living or subfossil epibionts,

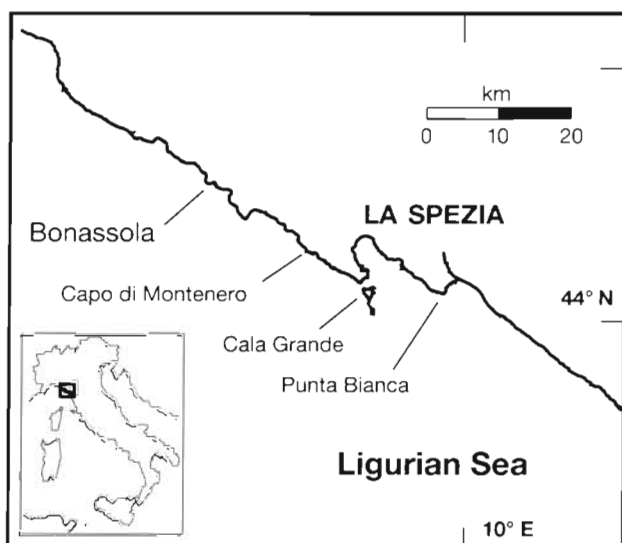


Fig. 1. Coastal region of La Spezia, Italy, and sampling sites

the corallites were immersed in a 1:1 peroxide solution to remove organic remains and dried at 70°C. Skeletal features of the corallite were observed by stereomicroscopy and scanning electron microscope on sagittal sections obtained with a grinding machine.

To measure growth rates and timing of band deposition, the corallites were X-rayed with a medical unit Senograph 500t-CGR mammography machine (exposure conditions of 31 kV, 25 mA at a distance of 30 cm). Contact prints obtained from X-ray films on high contrast paper were scanned and the computer images of corallites were analysed with the public domain NIH-Image programme for Macintosh. The software gave a value of optical density (OD) to each pixel of the scanned images, ranging from 0 (white) to 255 (black) (Fig. 2). Image analysis, performed along the corallite axis, produced a plot of computed mean optical density that allowed the HD density peaks to be recognised and the distances between them to be measured (Fig. 2). Annual mean growth rates were computed for each colony and related to colony morphology. Colony morphology was described as the degree of sphericity using the *Is*-index of Riegl (1995): $Is = \text{maximal height} / \text{maximal diameter}$. Data were analysed using the SYSTAT (SPSS Inc., Chicago) statistical package for PC.

Timing of band deposition was compared with monthly water temperature of the Ligurian Sea (Picco 1990) and monthly photosynthetically active radiation (PAR) at 3, 10, 20 and 27 m depth. PAR irradiances at the sea surface were calculated with the formula: $E(\text{PAR}) = 0.43E(\text{G})$ (Innamorati 1990), where $E(\text{G})$ was the monthly irradiance of global terrestrial irradiation measured with a pyranometer for the years 1958 to 1977 (Osservatorio Meteorologico di Genova 1985). Values in watts per square metre were multiplied by 4.6 to convert into micro-Einsteins per second per square metre (McCree 1972). To compute PAR monthly irradiance at the 4 depths, we used the 2 equations:

$$Kc = 1.7Sd^{-1} \text{ and } I_z = e^{-Kc \cdot z}$$

where Kc is the light extinction coefficient, Sd is the water transparency measured by Secchi-disk, and I_z is the light intensity (as % of surface irradiance) at each depth z (in metres). Secchi-disk water transparency for the studied zone has a mean value of 11.6 m (Della Croce et al. 1992).

RESULTS

Corallite structure

Ground, sagittal sections of corallites showed the typical scleractinian architecture described by Zibrowius (1980) and Veron (1993). Primary septa form

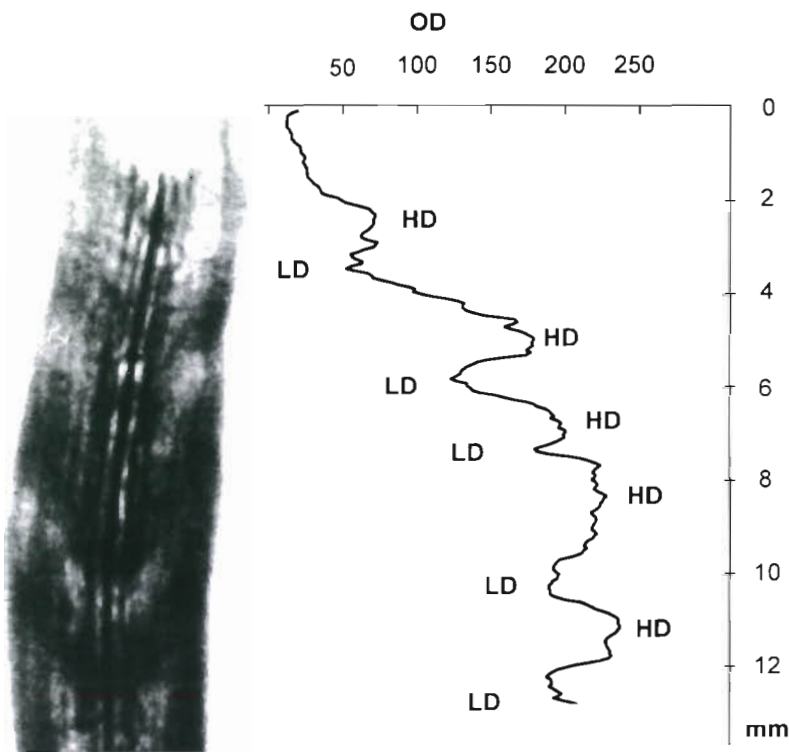


Fig. 2. *Cladocora caespitosa*. Left: Positive X-ray image of a corallite with dark bands or high density zones (HD) and white bands or low density zones (LD). Right: Resulting image-analysis plot with mean optical density (OD) versus corallite length (mm)

paliform lobes, or pali, at the centre of the calyx; both septa and pali have spikes on their distal margins (Fig. 3). Dissepimental layers were evident and regularly spaced along the growth axis. In the inner part of the corallite, the fusion of spikes, septa and pali produces the columella, presenting alternate zones with thick and less thick trabecular matrices along the growth axis. On X-radiographs, these zones corresponded to HD and LD bands (Figs. 2 & 3).

Timing of band deposition

Identification of the density of the uppermost band on X-ray negatives of corallites sampled on different dates showed that *Cladocora caespitosa* deposits 2 bands yr^{-1} . This coral deposits the HD band during the winter season both in shallow and in deep (>10 m) water (Table 1, Fig. 4). In November, more than 50% of corallites had started dense band deposition as a ring at the top of the septa; by March, the HD band was fully developed.

The LD band developed in summer (July) and was complete in November. In most instances (see examples shown in Figs. 2 & 3), both linear growth and density of skeletal deposition were greater during winter months compared to the summer months. No differences were shown in the timing of band deposition between shallow and deeper sites.

Corallite growth

Annual growth was measured between HD peaks starting from the last completely formed HD band at the apex of each corallite, which corresponded to the year 1993. Subsequent distances between HD bands were measured using a computer measurement procedure. For each colony the annual mean growth rates were thus computed, ranging from $1.30 \pm 0.64 \text{ mm yr}^{-1}$ (CL 13) to $4.03 \pm 1.42 \text{ mm yr}^{-1}$ (PBm 8) (Table 2). Significant differences were found between colonies (1-way Model II ANOVA, $p < 0.01$). The computation of variance components showed that differences

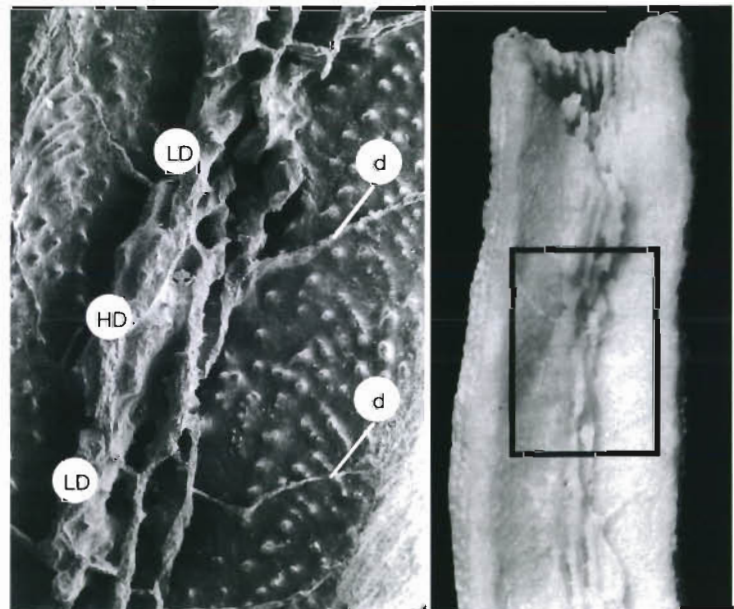


Fig. 3. *Cladocora caespitosa*. Right: Ground section of the same corallite as in Fig. 2. Left: scanning electron photomicrograph ($\times 30$) of the rectangular zone shown. The photomicrograph shows dissepiments (d), low density bands (LD), and a high density band (HD) with pali and spines fused together

Table 1 *Cladocora caespitosa*. Results of outermost band observation. Percent number of corallites (\pm confidence limit 95%) ending with a high (HD) or low (LD) density band, in shallow or deep (>10 m) waters. Values in parentheses are actual numbers of corallites. No deep samples were available for November. Data show that most corallites end with a fully developed HD band in March, and with a LD band in July; November represents an intermediate situation

	November	March	July
HD shallow	51.8 \pm 5.9 (141)	71.1 \pm 4.1 (342)	17.2 \pm 6.9 (20)
LD shallow	48.2 \pm 3.0 (131)	28.9 \pm 2.07 (139)	82.8 \pm 5.2 (96)
HD deep	–	71.4 \pm 9.7 (60)	14.3 \pm 8.2 (10)
LD deep	–	28.6 \pm 4.9 (24)	85.7 \pm 4.2 (60)

within colonies accounted for the largest part of the variability (62%).

The differences within each colony might be due to variability in growth among individual corallites or years. This was investigated by a 2-way Model II ANOVA applied for the period 1989 to 1993. Differences between corallites were highly significant in the colonies BO ($p < 0.001$), PBn 13 ($p = 0.001$) and MN 13 ($p = 0.001$), and significant in the colonies PBm 5 ($p = 0.019$), PBm 6 ($p = 0.027$), MN 5 ($p = 0.022$) and MN 18 ($p = 0.039$). Differences between years were found only in the colonies PBm 2 ($p = 0.001$) and CL 20 ($p = 0.012$).

Differences in growth between colonies were tested for 1993 with a 1-way Model II ANOVA and Tukey's

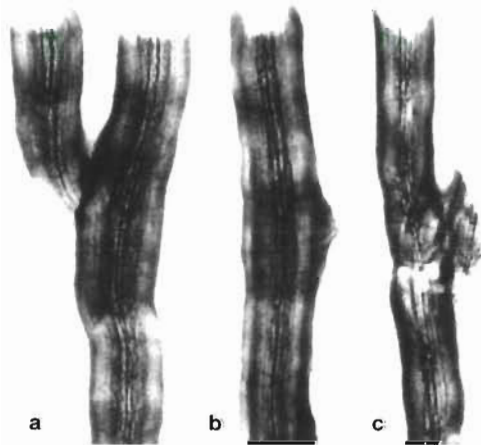


Fig. 4. *Cladocora caespitosa*. Positive contact prints of X-ray images of apices of corallites collected in different months, all in shallow waters (see Table 2 for sample names): (a) November (PBn13); (b) March (PBm8); (c) July (MN19). Terminal dark (= high density) banding is apparent in November and fully developed in March

Table 2. *Cladocora caespitosa*. Size (d : maximal diameter; h : maximal height of colonies), mean annual growth rates and standard deviation (SD) of the colonies (BO: corallites from Bonassola bank; CL: colonies from Cala Grande; PBm and PBn: colonies collected at Punta Bianca in March and November, respectively; MN: colonies from Capo di Montenero). Differences between means are significant (1-way Model II ANOVA, $p < 0.01$; see 'Results: Corallite growth' for further explanation)

Sample	d	h	Mean	SD	Years (n)
BO	–	–	2.58	0.96	63
CL 7	11	15	2.15	0.60	13
CL 13	8	3	1.30	0.64	37
CL 18	12	7	1.63	0.50	12
CL 20	12	7	1.62	0.90	40
PBm 1	20	8	2.74	0.93	18
PBm 2	15	12	2.90	1.05	10
PBm 3	12	8	3.18	1.20	8
PBm 4	12	9	4.00	1.56	9
PBm 5	12	8	2.38	1.37	14
PBm 6	20	14	3.20	1.21	11
PBm 8	24	13	4.03	1.42	21
PBn1	15	7	1.79	1.09	17
PBn 3	8	5	3.60	1.04	8
PBn 7	12	12	3.54	1.28	11
PBn 13	17	15	3.31	1.25	14
PBn 16	8	9	1.78	1.24	26
PBn 17	17	9	1.88	1.38	27
MN 1	10	7	1.75	0.49	10
MN 5	–	–	3.60	1.33	11
MN 11	–	–	3.10	1.28	6
MN 13	–	–	3.11	0.94	13
MN 18	7	4	2.76	0.84	5
MN 19	–	–	3.33	1.22	9

HSD multiple comparison procedure. The matrix of pairwise comparison probabilities showed that colonies could be divided into 5 different groups (Fig. 5). The first group (a in Fig. 5) included 2 slow-growing (1.36 and 1.63 mm yr^{-1}) colonies coming from 20 m depth; the second group (b) included all the remaining deep (>10 m) colonies and 3 shallow ones (MN 1, PBn 1, PBn 16) with mean corallite growth between 1.58 and 2.19 mm yr^{-1} . The third (c) and fourth (d) groups included shallow colonies with corallite growth between 2.55 and 3.23 mm yr^{-1} , and between 3.30 and 3.90 mm yr^{-1} , respectively. Finally, the fifth group (e) included the 2 fast-growing colonies (4.29 and 4.42 mm yr^{-1}). This grouping pattern did not appear site-related, since colonies from different sampling stations were intermixed in the 5 clusters. Deep colonies tended to grow less than most of the shallow ones, but the results above suggest that the depth-related difference is not significant, since 3 shallow-water colonies were grouped with deep ones.

Different growth rates and colony morphology were compared plotting the Is -index of Riegl (1995) versus mean growth rates. Comparisons did not show any correlation ($R = 0.263$, $p = 0.277$).

Sample	Year 1993			ANOVA 1 Tukey Test Groups identified with multiple comparison procedure
	mean	SD	n	
CL 13	1.36	0.58	27	a
CL 20	1.63	0.78	27	
PBn1	1.58	0.78	10	
MN 1	1.68	0.47	10	
BO	2.19	0.96	81	
CL 18	2.05	0.59	11	b
PBn16	2.16	0.33	13	
CL 7	1.99	0.28	8	
PBm 1	2.82	1.02	54	c
PBm 5	2.55	1.33	20	
MN 18	2.82	0.86	18	
MN 11	2.74	1.52	14	
PBn 13	3.21	1.25	143	
PBn 7	3.23	1.10	55	d
MN 13	3.14	0.94	22	
PBn17	2.81	1.27	9	
PBm 6	3.30	1.38	33	
PBm 3	3.37	1.49	30	
MN 19	3.31	1.19	19	e
PBm 2	3.78	0.83	16	
MN 5	3.87	1.29	37	
PBn 3	3.90	0.90	11	
PBm 8	4.29	1.30	178	
PBm 4	4.42	1.61	60	

Fig. 5. *Cladocora caespitosa*. Mean growth rates of colonies in 1993 (SD: standard deviation; n: number of corallites) and groups resulting from 1-way Model II ANOVA and Tukey's HSD multiple comparison test. The dendrogram derives from the matrix of pairwise comparison probabilities, using Euclidean distance and complete linkage. Bold letters indicate significant groupings ($p > 0.05$)

DISCUSSION

Corallite structure

Our observations suggest that *Cladocora caespitosa* conforms to a growth model involving 2 processes, as already observed in *Porites* (Barnes & Lough 1993, and references therein): (1) lengthening of the calyx wall and (2) internal fusion of skeletal elements.

The first process principally concerns septa and corallite walls. It seems to follow a very regular pattern, as suggested by the relatively constant distance observed between successive dissepimental layers. At no stage did any corallite show a dissepiment near the apex of the calyx. This suggests that the formation of a new dissepiment is started only when the calyx has reached a sufficient height to provide the polyp with the same volume. The above process is consistent with (1) the phaceloid form that allows a continuous development of corallites without restriction of the surface to volume ratio, a potential cause of variation in thickness of the tissue layer in massive corals (Barnes & Lough 1992); (2) the unlimited life of the polyp; and (3) the direct relationship between corallite diameter and polyp biomass (Schiller 1993a).

The second process (fusion of skeletal elements) is clearly observed in the columella structure and is determined by continuous linear growth during which septa fuse deep in the axis. During the winter season (November to March) the greater density of skeletal deposition influences the architecture and thickness of the columella, with spikes and lobes more closely assembled and fused in HD bands than in LD bands, a process also observed in many tropical corals (Barnes & Devereux 1988, Barnes & Lough 1993). In the West Atlantic species *Montastrea annularis*, HD banding was seen as primarily due to thickening of exothecal elements by Dodge et al. (1992). This cannot be the case for *Cladocora caespitosa*, however, due to its phaceloid form.

Timing of band deposition

The banding pattern of the temperate coral *Cladocora caespitosa* is consistent with Highsmith's (1979) model for 'high latitude' hermatypic species, with the deposition of a denser band in winter and a less dense band during spring to summer. In particular, the deposition pattern of *C. caespitosa* at latitude 44° N resembles

that of *Porites* at 29° N in the Red Sea (Klein & Loya 1991) and that of hermatypic corals near Bermuda (32° N) (Dodge & Thomson 1974), where the HD band deposition coincides with the period of lowest water temperature.

We found no differences in banding pattern between shallow and deep colonies despite clearly different temperature regimes (Fig. 6). This suggests that density banding in *C. caespitosa* cannot be interpreted as a temperature effect alone. Schiller (1993b) found that the photosynthetic efficiency of symbiotic zooxanthellae within *C. caespitosa* depends not only on water temperature but also on radiation intensity. This dependence also regulates the rate of carbon utilised for the skeleton.

The deposition in *Cladocora caespitosa* of a denser band in winter and a less dense band in summer is consistent with Schiller's (1993b) findings on the variable translocation rate of zooxanthella products to the polyp, decreasing from 70% in winter to 40% in summer. Differing photosynthetic efficiency of the zooxanthellae in deeper colonies, however, cannot explain the similarity in timing of band deposition since Schiller (1993b) showed that zooxanthella densities and chlorophyll content did not differ from shallow to deep sites.

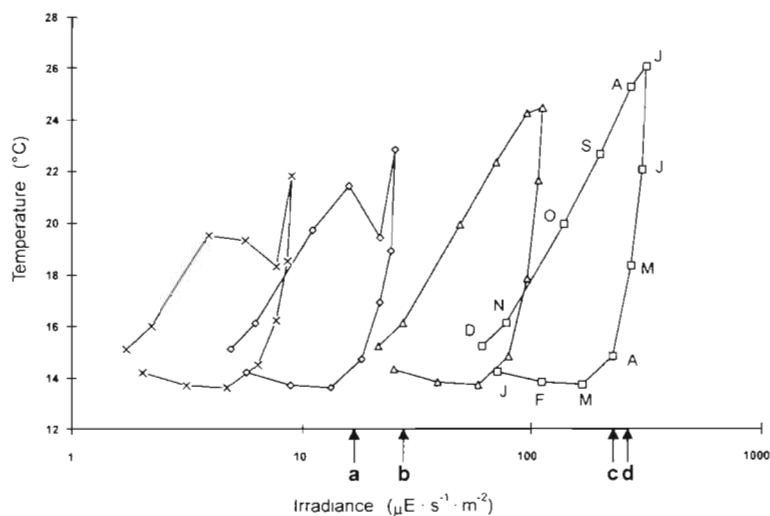


Fig. 6. Monthly temperature-PAR irradiance annual diagrams for the Ligurian Sea at 3 (□), 10 (Δ), 20 (◇) and 27 m (×) depth. Arrows along the x-axis indicate the zooxanthella compensation (I_c) and the photosynthesis inhibition (P_i) irradiance levels, according to Schiller (1993b): a = I_c at 17°C sea-water temperature; b = I_c at 21°C; c = P_i at 15°C; d = P_i at 21°C. Photosynthesis of *Cladocora caespitosa* at 3 m depth is likely to be inhibited from April to August. Deeper than 20 m, colonies live at irradiance values below compensation level all year around

In the Ligurian Sea, PAR irradiance levels were optimal for photosynthesis in shallow waters, but below 20 m depth they were never higher than $26 \mu\text{E s}^{-1} \text{m}^{-2}$ (Fig. 6), a value below the zooxanthella compensation irradiance level measured by Schiller (1993b). From May to August, the irradiance could exceed 230 to $250 \mu\text{E s}^{-1} \text{m}^{-2}$ in shallow waters, values above which Schiller (1993b) recorded photosynthesis inhibition.

The fact that the deep colonies grow at low irradiance levels throughout the year confirms the importance of 'dark calcification' in zooxanthellate corals (Marshall 1996). It also suggests that growth processes in *Cladocora caespitosa* are not only related to autotrophy, as hypothesised by Schiller (1993b), but more likely to a combination of autotrophy and heterotrophy, as also observed in the temperate coral *Oculina arbuscula* (Miller 1995). The relative importance of the 2 contrasting feeding modes in corals has been subject to lengthy debate (Goreau et al. 1971), and differences may exist according to individual species (Risk et al. 1994). Among heterotrophic mechanisms, mucus nets are used by many corals either as a primary or accessory way of feeding (Sorokin 1993, Schlichter & Brendelberger 1998). Mucus production in *C. caespitosa* is extremely high. Since the species often lives in turbid environments (Peirano et al. 1998), this mucus production might essentially be a cleaning mechanism (Telesnicki & Goldberg 1995), but Herndl & Velimirov (1986) observed that the mucus released by *C. caespitosa* is nutritionally rich. Whether it is utilised as a food

source, however, is still to be verified. Another aspect needing further investigation is the role of zooxanthellae in deeper colonies: they might primarily act in recycling nutrients rather than directly participating in the food balance.

Corallite growth

The rectilinear continuous growth of corallites in *Cladocora caespitosa* facilitates the measurement of the annual growth rate by avoiding problems related to the 3-dimensional development of corallites of tropical coral species, with massive growth forms.

C. caespitosa growth rates (1.3 to 4.3 mm yr^{-1}) in Liguria are similar to those measured with the alizarin method (2.9 to 5.2 mm yr^{-1}) on colonies in the Adriatic Sea (Schiller 1993a). The growth rates measured in the Adriatic are within the range of the Ligurian data, despite the lower winter and summer temperatures (from

8.9°C in January to 19 – 21°C in August and September) and the greater exposure to storm events at Schiller's (1993a) Adriatic site.

Acknowledgements. We thank F. Spairani and S. Sgorbini for their support in field and laboratory work, G. Calzetta and the staff of the Sarzana Hospital for X-radiographs and S. Furia for her help with image processing. E. Schiano (La Spezia) provided advice on irradiance measures, H. Zibrowius (Marseille), M. Pichon (Perpignan) and M. Le Tissier (Newcastle-upon-Tyne) critically read the manuscript. Suggestions by anonymous referees significantly improved the manuscript.

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