

(COCCO)LITHS VERSUS (COCCO)SPHERES: APPROACHING THE ECOLOGICAL PERFORMANCE OF COCCOLITHOPHORES

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Abstract: By establishing a per species comparison between the abundance of liths (considered as the 'memory' of the system) versus spheres, a better interpretation of the ecological behaviour, and/or the biostratonomic status, of some of the major coccolithophore species dwelling off Portugal is hoped to be achieved. By comparing the relative position of the liths against the spheres of a certain species in factor diagrams, it may be deduced how the species was ecologically performing. Similar factor loadings for the spheres and the liths of a certain species (close to each other in the factor diagram) may indicate steady and continuous development of the species during a more-or-less extended period of time prior to sampling. Higher factor loadings for spheres relative to liths (spheres located on the extremes of the diagram axes apart from the liths, which are located closer to the origin of the factors) may indicate new (exponential) growth of cells of the species, meaning favourable conditions for its development. In these circumstances, the physical-chemical properties of the water-masses reflect the species ecological optima. Higher factor loadings for liths relative to spheres may indicate decay of the species population, with certain biostratonomic processes (e.g. dispersion, contamination, resuspension, etc. of the liths) being more important than ecological ones. In these circumstances, the physical-chemical properties of the water-masses may reflect a low degree of, or no, relationship with the ecological preferences of the species.

Introduction

Most of the micropalaentologically-oriented works performed upon coccolithophore communities developing in the upper layers of the ocean water-column routinely include counts of coccospheres (hereafter referred to as spheres, for simplicity) and heterococcoliths (hereafter simply referred to as liths), both structures found together on the filters. Subsequently, the liths are generally converted to (virtual) cells by defining a certain number (constant) of liths per cell (sphere) per species. By doing so, a meaningful and probably very important part of the coccolithophore ecosystem information may be lost.

In most of the biological research applied to phytoplankton in general, and to coccolithophores in particular, an important aspect is to recognise ecological performance, i.e. when a particular species is blooming, when it is in a steady developing state, or when it is in a decay process. But how can we address this type of question if most of the data are gathered along transects in which a station is rarely sampled twice, or at least within a time interval of the same order of magnitude of the developmental processes of these microalgae?

Coccolithophores have the unique feature of producing several complex structures (the liths) which may be released or extruded by the cells in certain developmental conditions (growth, cell division or grazing processes) or may be liberated from faecal pellets ('free-coccoliths'; Steinmetz, 1991 in Steinmetz, 1994). Due to their small dimensions (generally 2 to 15µm) and their resilient (calcite) nature, liths may persist for some time in the upper layers of the water-column. In these circumstances, the number of liths present in the water-column, related to the number of cells, may be considered as an additional source of information - a sort of short-term 'memory' of the coccolithophore developmental system. In the present work, we explore this approach by keeping liths data distinct from spheres data.

Material and methods

For the present study, 18 samples were collected during the CORVET ('Corrente da Vertente') cruise, carried out off the western Portuguese coast in November, 1996, by the Portuguese Hydrographic Institute (Figure 1). Hydrographic and nephelometric measurements were obtained along an open-ocean meridional (N-S) transect at 12°W (T2), and along two other (E-W) transects from the shelf to open-ocean, one at about 36°N, offshore Cape St. Vincent (T1) and the other at 41°30'N, offshore Oporto (T3). A complementary set of 14 samples was also studied from a second cruise (CLIMA cruise), collected from a more-restricted area over the northern shelf of Portugal (see

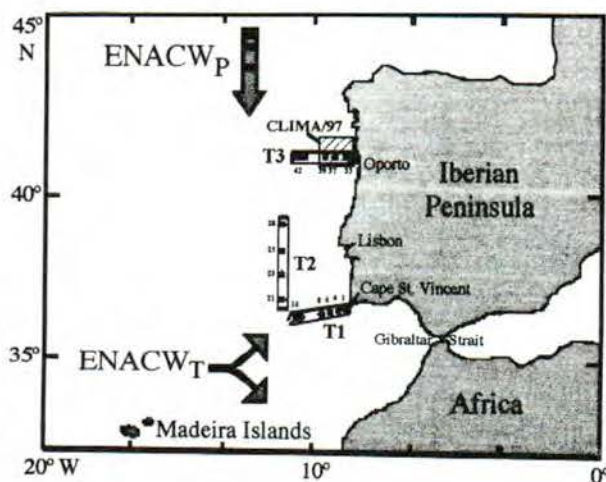


Figure 1: Water sampling location map, with Transect 1 (T1, Stations 1 to 19), Transect 2 (T2, Stations 19 to 29) and Transect 3 (T3, Stations 34 to 44) sampled during the CORVET 96 cruise. Dashed square displays the sampling location area during the CLIMA/97 cruise. ENACWP = eastern N Atlantic Central Waters of subpolar origin; ENACWT = eastern N Atlantic Central Waters of subtropical origin.

CLIMA/97 in Figure 1). The CLIMA cruise was conducted during December, 1997, when oceanographic conditions were reflecting a more-typical winter regime. Physical-chemical data were obtained with a Neil Brown MK III-C CTD equipped with a nephelometer. Surface (5m water-depth) samples were obtained by means of a direct pressure system. During the CLIMA cruise, the samples were collected at 30m and 80m with a 12-bottle rosette system. Onboard ship, 2 to 5 litre water-samples were filtered through HA Millipore membrane filters (0.45µm) with a vacuum pump.

On samples from the CORVET cruise, lith and sphere abundances were estimated using an optical petrographic microscope (1250x magnification) on a total observed area between 1.5 and 4mm² of each filter, depending on the general abundance. On samples from the CLIMA cruise, lith and sphere abundance was determined by SEM on a total area of 0.5mm² (24 photographs with 750x magnification). Raw counts were converted to cells per litre based on the observed filter area and on the volume of water that was filtered. Only loose liths (*i.e.* liths not closely related to spheres in the filter) were considered in the counts. Fields of view with high particle concentrations, such as marine snow or faecal pellets, were rejected due to the difficulty in quantifying the number of single liths.

The data used in the present study was gathered during two consecutive winters. In the winter regime, upwelling is suppressed and an Iberian poleward slope-current develops (the Portuguese Coastal Countercurrent - PCC) bringing northwards subtropical coccolithophore assemblages which normally dwell in waters S of the Azores Front (Cachão *et al.*, 1998, 2000).

Coccolithophore data

During the CORVET cruise, the upper water-column layer (5m) yielded mean total coccolithophore standing crops of 1.8×10^4 cells l⁻¹, ranging between 3.4×10^2 (Station 43) and 8.4×10^4 cells l⁻¹ (Station 1). During the CLIMA cruise, mean total coccolithophore standing crops were maximum at the surface (5m water-depth), reaching 2.7×10^5 cells l⁻¹, decreasing to 2.5×10^5 cells l⁻¹ at 30m, and to less than half of the upper surface values (1.3×10^5 cells l⁻¹) at 80m water-depth.

The coccolithophore community present in our samples included the global and opportunistic species, *Emiliania huxleyi* and *Gephyrocapsa ericsonii*. Also present in most of the samples were the species *Gephyrocapsa muelleriae* and *Helicosphaera carteri*. Species generally related to warmer (subtropical and tropical) water-masses (Winter *et al.*, 1994) were also found. These included *Umbellosphaera tenuis*, *Umbilicosphaera sibogae*, *Discosphaera tubifera*, *Rhabdosphaera clavigera* var. *clavigera*, *R. clavigera* var. *stylifera*, *Polycrater galapagensis* and *Turrillites latericioides*, among other species (Cachão *et al.*, 2000). For taxonomic references, see Jordan & Green (1994).

Only the most abundant taxa with both significant lith and sphere counts were used in the present study. For each one of the two sets of samples (CORVET and CLIMA), a data matrix was computed using per species absolute concentrations of both spheres and liths (Tables 1 and 2).

Factor Analysis was applied to these matrices to obtain the factor loadings for the liths and for the spheres of each taxon (Figure 2). In each factor diagram, representing the main factor space (Factor 1 versus Factor 2), the relative position between spheres and liths, for a particular taxon, is related to the degree of correlation between these two datasets: the closer the liths and spheres are, the higher is their correlation. Arrows have been drawn in, pointing from the spheres position to the liths position, to better illustrate this correlation. For instance, in Figure 2A (CORVET sample set), both liths and spheres of *Calcidiscus leptoporus*, *Syracosphaera* spp., *U. tenuis* and *Gephyrocapsa oceanica* are highly correlated to each other (small arrows). In Figure 2B (CLIMA sample set), only *G. oceanica* and *U. sibogae* display such high correlation. On the other hand, in Figure 2A, *G. muelleriae* and *G. ericsonii* reveal long factor distances (long arrows) between their spheres and liths. This shows that the correlation between them is low. *E. huxleyi* displays an intermediate distance, meaning moderate correlation. In addition, spheres of these species all show higher factor loadings, along Factor 1, than the liths, which means that spheres have higher variance (variability) than their liths. In Figure 2B, *E. huxleyi*, *G. muelleriae* and *Syracosphaera* spp. all have long factor distances between their spheres and liths but in this case the liths have higher variance than the spheres. We will discuss these distributions and their implications in the following section.

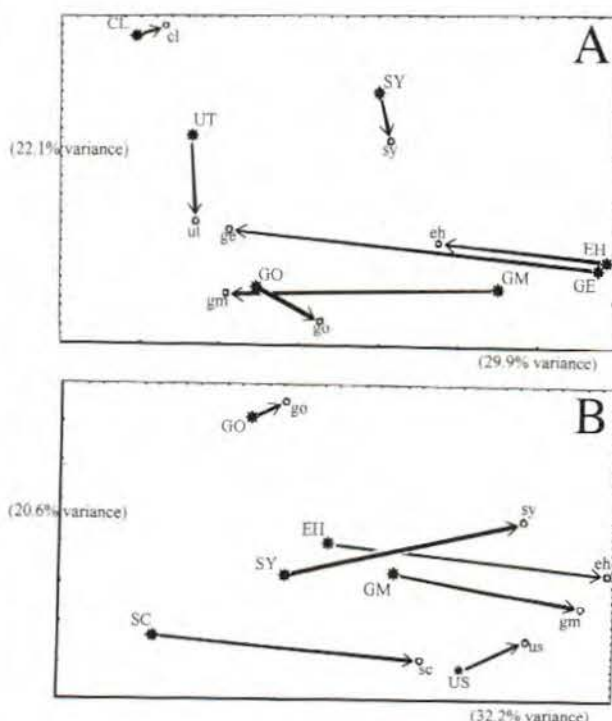


Figure 2: Diagrams of the main factor fields (Factor 1 versus Factor 2) of spheres and liths for: (A) the CORVET sample set; (B) the CLIMA sample set. Taxa codes: CL/cl - *Calcidiscus leptoporus*; EH/eh - *Emiliania huxleyi*; GE/ge - *Gephyrocapsa ericsonii*; GM/gm - *Gephyrocapsa muelleriae*; GO/go - *Gephyrocapsa oceanica*; SC/sc - *Scyphosphaera apsteinii*; SY/sy - *Syracosphaera* spp.; US/us - *Umbilicosphaera sibogae*; UT/ut - *Umbellosphaera tenuis*. Symbol codes: black stars - factor location of the spheres; open circles - factor location of the liths; arrows display the factor distance from the spheres to the liths for a particular taxon.

Discussion

Most authors consider that the proportion of liths of a particular species in the water-column should more-or-less follow the number of spheres, considering they were detached during sampling or during any other physical processes by which the cells released their entire content of liths to the water-column just before sampling. Following this assumption, lith counts are subsequently converted to 'virtual' cells by means of a species-dependent conversion ratio. It does not consider other possibilities, such as liths being detached during (1) growth or reproduction, (2) grazing, or (3) *post mortem* biostratonomical processes such as dispersion. In the first two cases, the previous conversion procedure will tend to maximise the number of cells present in the water-column, while in the second and third cases, it will tend to minimise the original number of cells due to a more-or-less significant loss of liths in the upper layers of the water-column.

From the comparison between the number of spheres and isolated liths present on the same filter, our data shows that the degree of correlation between these pairs of values sometimes changes significantly, depending on the time period, area, or species that are being considered. There are reasons underlying this fact which may hold interesting ecological and/or biostratonomical information. For instance, each of our single filter samples was collected at one particular moment and so the spheres data only reflects the coccolithophore community at that particular instant, not giving any information on the 'health' of the system or on its previous status. Intuitively, we tend to consider high sphere concentrations in a single-time sample as reflecting a bloom when, in fact, we cannot invoke this unless we can demonstrate an increase in number of cells with time. In other words, with single-time sampling we cannot define exactly how species were performing and developing (blooming, decaying, or in a steady crop situation) by only determining sphere (cell) concentrations.

According to our data, some species do in fact show high sphere-lith correlation (*C. leptoporus*, *G. oceanica*, *Syracosphaera* spp. and *U. tenuis* - Figure 2A; *G. oceanica* and *U. sibogae* - Figure 2B), while others do not. Why? This may be due to the influence of distinct factors acting on some species and not on others, at the exact moment when the water-sample was collected. Some of these factors may be ecological, acting mainly on the spheres (cells), while others may be *post mortem* (biostratonomical processes such as dispersion, transport, sedimentation, resuspension, etc.) acting mainly on the liths. In our case, only *G. oceanica* showed high correlation between its liths and spheres during both cruises (CORVET and CLIMA). Our interpretation is that this species was the only one which, in both situations, was developing more-or-less constantly for a more-or-less extended period of time prior to the moment of sampling. In these circumstances, detached liths are being added to the water in a gradual and continuous process, replacing those that are dispersed and lost. Higher lith concentrations closely follow high cell concentrations and *vice versa*. *C. leptoporus*, *Syracosphaera* spp. and *U. tenuis* displayed this same behaviour during the CORVET cruise, while *U. sibogae* displayed it during the CLIMA cruise. This can be useful

in showing distinct ecological, physical-chemical and/or oceanological mechanisms acting on each of the two cruises (see Cachão *et al.*, 2000), which lead to distinct responses by these species.

During the CORVET cruise, *G. ericsonii*, *G. muelleriae* and *E. huxleyi* (the latter to a lesser degree), revealed low correlation between their liths and spheres, with the spheres having higher variability (high factor loadings along Factor 1) than the liths (located closer to the zero position of Factor 1) (Figure 1A). This is interpreted as being due to a relatively recent development of cells of these species and, consequently, few of their loose liths were present in the surrounding waters. Cell concentrations do not follow detached lith concentrations, having higher variance along the dataset because they are being newly added, by the exponential growth phase, to some areas and not to others.

During the CLIMA cruise, *E. huxleyi*, *G. muelleriae* and *Syracosphaera* spp. revealed low correlation between their liths and spheres, with the liths having higher variability (high factor loadings along Factor 1) than the spheres (located closer to the zero position of Factor 1) (Figure 1B). This is interpreted as being due to a decrease in the production of new cells of these species (decay phase of the developmental process). Consequently, the relatively old liths that are present in the surrounding waters were already acted upon or modified by several *post mortem* mechanisms. Lith concentrations tend not to follow cell concentrations, and have higher variance (along the dataset) because they are being dispersed/concentrated or sunk/resuspended in the upper layers of the water-column at a much higher rate than new cells are being added.

During the CLIMA cruise, *Scyphosphaera apsteinii* displayed a distinct factor pattern. Its spheres and liths are located on the negative side and positive side of Factor 1, respectively (Figure 2B). This means that they are negatively correlated, *i.e.* samples with several spheres have almost no loose liths and *vice versa*. This may be due to a more efficient removal of its liths from the areas where cells are developing.

Following these interpretations, measured chemical (nutrients, salinity) and physical (temperature, density, turbulence) properties of the water-column can be used, or not, to describe the most suitable ecological parameters for some species to develop in. Measured properties during both cruises could be used to describe normal developmental conditions (steady growth phase) for *G. oceanica*. Measured properties during the CORVET cruise can also be used to describe this situation for *C. leptoporus*, *Syracosphaera* spp. and *U. tenuis*, while those measured during the CLIMA cruise can describe the continuous development of *U. sibogae*. On the other hand, measured properties during the CORVET cruise can be used to define exponential growth development conditions for *E. huxleyi*, *G. ericsonii* and *G. muelleriae*. Since, during the CLIMA cruise, *E. huxleyi*, *G. muelleriae* and *Syracosphaera* spp. were most probably in a declining growth phase, the measured water-properties should not be used to characterise their optimum ecological conditions.

Station	1		4		6		8		14		16	
Latitude	37°01.3'N		36°57.1'N		35°53.2'N		36°48.2'N		36°33.8'N		36°30.9'N	
Longitude	9°03.2'W		9°21.6'W		9°42.2'W		10°06.0'W		11°19.2'W		11°33.8'W	
Depth (m)	96		1530		2050		2720		1327		55	
Taxa	sph	liths	sph	liths	sph	liths	sph	liths	sph	liths	sph	liths
<i>C. leptoporus</i>	0	1.8	0.8	3.2	0.6	7.2	0.4	7.3	2.3	15.4	1.1	8.0
<i>G. ericsonii</i>	30.8	34.5	0.2	12.2	7.0	64.4	0.3	1.2	1.3	43.5	0.6	1.0
<i>G. muelleriae</i>	30.8	269.2	0.8	16.8	0.2	30.7	0.4	0.7	0	1.4	0	0.07
<i>G. oceanica</i>	7.4	147.8	0	1.2	0.1	17.3	0	0	0	2.1	0	0.07
<i>E. huxleyi</i>	8.1	377.0	1.6	70.3	1.4	53.6	0.2	13.1	0	4.8	1.8	17.0
<i>H. carteri</i>	0	1.4	0	0.2	0	0.2	0.07	0.3	0	0.1	0	0
<i>R. clavigera</i>	0.7	1.0	1.0	5.8	0	0.1	0.7	3.2	0	0	0	0
<i>Syracosph. spp</i>	1.8	19.3	0.4	5.6	0.9	7.4	0.8	11.1	1.3	9.2	0.3	0.5
<i>U. tenuis</i>	0.7	4.6	2.4	55.9	4.3	54.8	3.1	40.1	4.5	77.6	1.1	6.3

Table 1A: Data sheet for the main coccolithophore species in samples (5m depth) from the S transect (Section S) during the CORVET cruise. Spheres and liths abundances $\times 10^3 \text{ l}^{-1}$.

It should be stressed that the conclusions retrieved from these datasets for the above-mentioned taxa cannot be extrapolated for other situations, but the methodology can be used to test other cases.

Conclusions

Coccolithophores have the unique capability, among marine algal groups, of releasing considerable amounts of mineralised, resilient structures (the liths) into the water-column. By keeping lith data independent from sphere data in per species counts, better descriptions of the ecological and/or the biostratonomical status of the major

Station	21		23		25		28	
Latitude	37°04.7'N		37°45.0'N		38°24.4'N		39°24.5'N	
Longitude	12°00.5'W		12°00.0'W		11°59.4'W		12°00.0'W	
Depth (m)	5070		5075		4850		4066	
Taxa	sph	liths	sph	liths	sph	liths	sph	liths
<i>C. leptoporus</i>	2.7	15.5	1.3	9.4	0.1	0.7	0.6	5.0
<i>G. ericsonii</i>	0.09	13.2	0.4	6.9	0.2	1.8	0.7	12.2
<i>G. muelleriae</i>	0.09	5.4	0.4	16.9	1.6	7.5	1.9	57.8
<i>G. oceanica</i>	0	1.5	0.1	2.8	0	0.1	0	0.2
<i>E. huxleyi</i>	0.09	12.0	0.6	22.8	0.4	2.9	0.4	5.4
<i>R. clavigera</i>	0	0	3.3	8.8	0.2	0.2	10.8	71.5
<i>Syracosph. spp</i>	0	1.9	2.4	13.4	0.3	0.2	1.4	9.8
<i>U. tenuis</i>	3.8	69.4	7.6	94.7	0.9	8.2	2.2	58.8

Table 1B: Data sheet for the main coccolithophore species identified in samples (5m depth) from the N-S transect (Section N-S) during the CORVET cruise. Spheres and liths abundances $\times 10^3 \text{ l}^{-1}$.

Station	34		35		36		41		42		43	
Latitude	41°24.6'N		41°24.7'N		41°24.72'N		41°24.6'N		41°24.5'N		41°24.6'N	
Longitude	8°49.2'W		8°54.9'W		9°02.0'W		10°30.9'W		10°40.0'W		10°50.3'W	
Depth (m)	38		66		90		3585		2410		3061	
Taxa	sph	liths	sph	liths	sph	liths	sph	liths	sph	liths	sph	liths
<i>C. leptoporus</i>	0	0.7	0	0.2	0	0	0.1	0	0.2	1.1	0	0
<i>G. ericsonii</i>	3.0	185.6	6.9	101.6	0	0	2.5	4.3	1.8	31.2	0	0.03
<i>G. muelleriae</i>	20.9	459.3	6.2	110.6	0	0.08	1.4	11.6	9.4	174	0	0.03
<i>G. oceanica</i>	32.0	409.3	5.0	50.1	0.7	0.8	0	0.4	0	2.1	0	0
<i>E. huxleyi</i>	0	284.0	1.2	93.2	0	0	0.6	2.1	0.3	40.5	0	0.03
<i>Syracos. spp.</i>	0	20.1	0.2	1.0	0	0.08	0.2	0.1	0.2	5.8	0	0
<i>U. tenuis</i>	0	0	0	0.2	0	0	0	0.8	9.6	193	0	0

Table 1C: Data sheet for the main coccolithophore species identified in samples (5m depth) from the N transect (Section N) during the CORVET cruise. Spheres and liths abundances $\times 10^3 \text{ l}^{-1}$.

coccolithophore species dwelling off Portugal can be obtained. This information is particularly important when sampling is not repeated in time but rather consists of a series of samples collected sequentially over a more-or-less extended area or transect. In these circumstances:

1. high sphere-lith correlations are obtained when the species are developing more-or-less constantly for an extended period of time prior to the moment of sampling (*C. leptoporus*, *G. oceanica*, *Syracosphaera* spp. and *U. tenuis* during the CORVET cruise; *G. oceanica* and *U. sibogae* during the CLIMA cruise). In these circumstances, detached liths are being added to the water in a gradual and continuous process, replacing those that are dispersed and lost. Higher lith concentrations closely follow high cell concentrations and *vice versa*;

2. low sphere-lith correlations, with the spheres having higher variability (higher factor loadings) than the liths,

are interpreted as being due to a relatively recent development of cells and, consequently, few loose liths being present in the surrounding waters. Cell concentrations do not follow detached lith concentrations and have high variance along the dataset because they are being newly added, by exponential growth, to some areas and not to others; and

3. low sphere-lith correlations, with the liths having higher variability (higher factor loadings) than the spheres, are interpreted as being due to a decrease in the production of new cells of these species (decay phase of the developmental process). Consequently, the relatively old liths present in the surrounding waters had already been acted upon by several *post mortem* (biostratonomical) mechanisms. Lith concentrations tend not to follow cell concentrations and have higher variance (along the dataset) because they are being dispersed/concentrated

Station	82	80	77	74	69	104	102	100	99	93	120	119	117	114
Latitude	41°29.9'N	41°29.7'N	41°30.0'N	41°29.8'N	41°29.8'N	40°41.1'N	41°41.2'N	41°41.3'N	41°41.4'N	41°41.2'N	40°51.0'N	41°51.0'N	41°49.3'N	41°48.5'N
Longitude	8°50.4'W	9°02.9'W	9°15.2'W	9°25.7'W	10°00.3'W	8°53.1'W	09°03.2'W	09°19.2'W	09°23.0'W	09°59.7'W	08°55.1'W	09°00.1'W	09°10.1'W	09°24.6'W
Depth (m)	30	94	800	2031	3100	30	104	430	1075	2886	43	86	120	913
Temp (°C)														
5	-	16.726	-	16.469	-	15.179	15.630	16.197	16.463	16.226	14.863	15.194	16.257	16.421
30	-	16.801	16.707	16.517	-	16.541	17.046	16.728	16.501	16.242	16.692	16.296	16.744	16.418
80	-	15.481	15.345	16.366	-	-	15.211	15.550	16.245	15.295	-	16.420	16.021	16.445
Salinity														
5	-	35.793	-	35.879	-	34.213	34.427	35.639	35.798	35.867	32.813	33.551	35.430	35.849
30	-	35.889	35.940	35.931	-	35.629	35.924	35.853	35.833	35.897	35.765	35.178	35.813	35.850
80	-	36.024	36.007	35.942	-	-	36.015	36.004	35.944	35.970	-	35.998	36.003	35.950
Standing crop (x10 ³ cell l ⁻¹)														
5	102	108	-	967	-	69	278	454	-	-	84	-	-	120
30	20	136	330	709	393	8	103	256	274	576	9	148	254	300
80	-	30	128	200	156	-	52	88	398	120	-	32	89	180

Table 2A: Data sheet of the location, temperature, salinity and total coccolithophore standing crops (x 10³ cells l⁻¹) in samples from 5m, 30m and 80m water-depth, CLIMA 97 cruise.

Station (5m)	82	80	74	104	102	100	120	114
Taxa	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths
<i>E. huxleyi</i>	18.6 770.0	20.3 750.0	73.0 736.5	33.8 503.6	47.4 1072.9	67.7 2335.4	25.7 173.3	9.3 697.0
<i>G. muelleriae</i>	3.4 37.2	8.1 33.8	36.6 48.7	5.4 8.1	23.7 40.6	35.5 150.6	1.4 19.0	9.3 35.6
<i>G. oceanica</i>	22.0 245.4	9.5 83.9	4.1 12.2	- 90.7	33.8 257.2	5.1 52.5	1.4 54.2	2.3 14.7
<i>S. apsteinii</i>	- -	4.1 2.7	2.7 8.1	- -	- -	- 10.2	- 2.7	- 3.9
<i>Syracosph. spp.</i>	13.5 54.1	- 19	23.0 25.7	17.6 25.7	6.8 30.4	23.7 42.3	6.8 4.1	3.1 18.6
<i>U. sibogae var. sib.</i>	1.7 79.5	4.1 440.0	28.4 62.3	2.7 82.6	3.4 71.1	33.8 1098.3	- 82.6	9.3 604.2

Table 2B: Data sheet of main coccolithophore species identified in samples of 5m water-depth, CLIMA cruise. Spheres and liths abundance x 10³ l⁻¹.

Station (30m)	82	80	77	74	69	104	102	100	99	93
Taxa	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths
<i>E. huxleyi</i>	8.1 256.3	35.6 594.9	60.9 1106.8	44.3 320.0	34.8 861.4	2.5 73.5	27.1 981.5	32.2 1100.0	42.3 1287.8	65.0 2061.5
<i>G. muelleriae</i>	2.7 4.5	6.5 33.9	15.2 101.5	19.7 8.2	14.2 57.0	- 0.6	6.8 60.9	5.1 106.6	13.5 110.0	18.1 164.3
<i>G. oceanica</i>	2.7 69.5	3.2 32.3	11.8 25.4	3.2 4.9	- -	1.3 8.2	5.1 69.4	- 20.3	- 16.9	1.8 21.7
<i>S. apsteinii</i>	- 1.8	0.4 3.3	1.7 13.5	8.2 4.9	3.2 9.5	0.6 0.6	1.7 10.2	- 10.2	- 6.8	5.4 32.5
<i>Syracosph. spp.</i>	0.9 10.6	6.4 35.5	10.2 20.5	65.7 23.0	15.8 30.0	- 3.2	- 37.2	1.7 22.0	3.4 15.3	28.9 28.8
<i>U. sibogae var. sib.</i>	2.7 15.3	8.1 86.8	25.4 252.2	18.0 27.9	4.8 72.8	1.3 30.4	13.5 134.7	3.4 181.1	11.8 323.2	16.2 391.7

Station (30m)	120	119	117	114
Taxa	sph. liths	sph. liths	sph. liths	sph. liths
<i>E. huxleyi</i>	2.4 46.2	37.1 818.0	44.7 761.6	26.2 1399.8
<i>G. muelleriae</i>	1.2 1.6	11.4 45.6	1.7 39.5	8.2 134.6
<i>G. oceanica</i>	0.4 9.6	2.8 68.4	- 18.9	- 11.5
<i>S. apsteinii</i>	0.4 1.2	1.4 -	8.6 12.0	1.6 -
<i>Syracosph. spp.</i>	- 1.6	5.6 24.2	1.7 8.6	27.9 41.0
<i>U. sibogae var. sib.</i>	3.6 43.8	12.8 69.8	22.3 199.4	13.1 283.9

Table 2C: Data sheet of the main coccolithophore species identified in samples of 30m water-depth, CLIMA cruise. Spheres and liths abundance x 10³ l⁻¹.

Station (80m)	80	77	74	69	102	100	99	93
Taxa	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths	sph. liths
<i>E. huxleyi</i>	3.2 429.3	30.7 350.2	43.4 738.8	37.2 660.0	7.2 1469.4	16.2 449.5	38.9 1827.7	28.8 575.4
<i>G. muelleriae</i>	1.6 25.3	- 39.7	11.7 63.5	10.2 16.9	7.2 93.9	5.4 30.7	18.6 162.5	- 23.7
<i>G. oceanica</i>	7.9 68.0	- 34.3	- -	- 10.2	- 162.5	1.8 12.6	- 1.7	- 11.8
<i>S. apsteinii</i>	- 12.6	9.0 9.0	8.4 35.1	13.5 10.2	- 7.2	1.8 16.2	- 37.2	8.5 32.2
<i>Syracosph. spp.</i>	2.4 13.5	- 27.0	1.7 15.1	- 3.4	- 66.7	- 9.0	8.5 37.2	- 18.6
<i>U. sibogae var. sib.</i>	12.6 110.7	18.0 236.5	36.8 267.4	3.4 57.5	5.4 196.8	12.6 281.6	35.5 648.2	16.9 297.8

Station (80m)	119	117	114
Taxa	sph. liths	sph. liths	sph. liths
<i>E. huxleyi</i>	6.8 681.4	16.6 612.3	25.0 1114.7
<i>G. muelleriae</i>	1.1 56.4	5.2 33.2	- 95.0
<i>G. oceanica</i>	1.1 116.2	- 31.4	- 10.0
<i>S. apsteinii</i>	- 3.4	0.9 10.5	- 8.3
<i>Syracosph. spp.</i>	- 51.9	- 10.5	1.7 23.3
<i>U. sibogae var. sib.</i>	2.2 155.7	20.1 166.8	28.3 445.6

Table 2D: Data sheet of the main coccolithophore species identified in samples of 80m water-depth, CLIMA cruise. Spheres and liths abundance x 10³ l⁻¹.

or sunk/resuspended in the upper layers of the water-column at a much higher rate than new cells are being added.

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References

- Cachão, M., Oliveira, A. & Vitorino, J. 1998. Coccolithophore assemblages from offshore Portugal. *CODENET Report*: 50-58.
- Cachão, M., Oliveira, A. & Vitorino, J. 2000. Subtropical winter guests, offshore Portugal. *Journal of Nannoplankton Research*, **22**(1): this volume.
- Jordan, R.W. & Green, J.C. 1994. A Check-list of the extant Haptophyta of the world. *J. Mar. Biol. Ass., UK*, **74**: 149-174.
- Steinmetz, J.C. 1991. Calcareous nannoplankton biocoenosis: sediment trap studies in the Equatorial Atlantic, Central Atlantic, and Panama Basin. In: S. Honjo (Ed.). *Ocean Biocoenosis Series No. 1*. Woods Hole Oceanographic Institute Press: 85pp.
- Steinmetz, J.C. 1994. Sedimentation of Coccolithophores. In: A. Winter & W. Siesser (Eds). *Coccolithophores*. Cambridge University Press: 179-197.
- Winter, A., Jordan, R. & Roth, P. 1994. Biogeography of living Coccolithophores in ocean waters. In: A. Winter & W. Siesser (Eds). *Coccolithophores*. Cambridge University Press: 13-37.