SUBTROPICAL WINTER GUESTS, OFFSHORE PORTUGAL

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Abstract: Coccolithophore communities developing off Portugal during November, 1996 were composed of species from both temperate (influenced by ENACWp) and subtropical (influenced by ENACWp) regions. The first group includes Gephyrocapsa muellerae, G. ericsonii and Emiliania huxleyi. Members of the second group include (for 5m water-depth samples) Alisphaera spatula, Calcidiscus leptoporus, Coronosphaera mediterranea, Discosphaera tubifera, Gephyrocapsa oceanica, Polycrater galapagensis, Rhabdosphaera clavigera, Syracosphaera pulchra, S. molischii, Umbilicosphaera sibogae and Umbellosphaera tenuis, some of which are typical of subtropical upper photic zone water-masses. Deeper-water samples (between 75 and 85m water-depth) showed the presence of Algirosphaera quadricornu, Alveosphaera bimurata, Cyclolithus anulus, Florisphaera profunda, Michaelsarsia elegans, Syracosphaera lamina and Turrilithus latericioides; species typical of subtropical middle and lower photic zone water-masses. The presence of these subtropical assemblages during the end of summer - autumn is taken as direct evidence that at least 120 to 220m of the uppermost part of the water-column is sourced from S of the Azores Front and fed into the Portuguese slope poleward current system.

Introduction

The Gulf Stream system is the dominant feature of N Atlantic surface circulation at present and probably has been since the closing up of the Isthmus of Panama at the end of the Early Pliocene. Deflected NE by the eastern N America coast, the tropical waters subdivide before crossing the Mid-Atlantic Ridge to form the N Atlantic Current, N of 46°N, and the less well-defined Azores Current, between 32° and 36°N (Pollard & Pu, 1985; Klein & Siedler, 1989). The Azores Current thermohaline front occurs between 35° and 36°N, in close proximity to a deep chlorophyll maximum, and when it reaches the surface

during winter it can tilt towards the N (Stramma & Müller, 1989). At Central Water depths, eastern N Atlantic waters of subtropical origin (ENACWT), formed along the Azores Front, were shown to occur off the Portuguese coast, over the southward-flowing waters of subpolar origin (ENACWp) (Fiúza, 1984). At the surface, branches of the Azores Front can probably feed warmer and saltier waters into the Iberian slope poleward-flowing current (the Portuguese Coastal Countercurrent - PCC: Fiúza et al., submitted), observed during the winter both by infrared satellite pictures and in situ hydrographic data (Frouin et al., 1990). Between April and September (summer

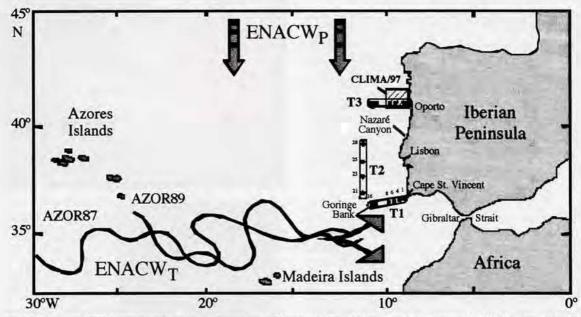


Figure 1: Water and CTD sampling station location map, with Transect 1 (T1, Stations 1 to 19), Transect 2 (T2, Stations 19 to 29) and Transect 3 (T3, Stations 34 to 44) sampled during the CORVET 96 cruise. Dashed square displays the sampling area during the CLIMA/97 cruise. Main oceanographic current patterns in the eastern Atlantic Ocean; ENACWP - eastern N Atlantic Central Waters of subtropical origin; ENACWT - eastern N Atlantic Central Waters of subtropical origin. AZOR 87, AZOR 89 - registered trajectories of the Azores Current during 1987 and 1989 IPIMAR cruises. (Adapted from Rios et al., 1992; Dias et al., 1990).

conditions), upwelling develops off Iberia (Wooster *et al.*, 1976) thus overprinting this pattern.

Material and methods

For the present study, 18 samples were collected during the CORVET (, Corrente da Vertente') cruise of the Instituto Hidrográfico in November, 1996, off the western Portuguese coast (Figure 1). During the first phase of the cruise, from 2nd-5th November, a regional study was conducted during which hydrographic and nephelometric measurements were obtained along an open ocean meridional (N-S) transect at 12°W (T2) and along two zonal transects, E-W from the shelf to open-ocean: one at about 36°N, between Cape St. Vincent and the Gorringe Bank (T1) and the other at 41°30'N (T3). A complementary set of 14 samples was also studied from a second cruise (CLIMA), collected from a more-restricted area over the northern shelf of Portugal (see CLIMA/97 in Figure 1). The CLIMA cruise was conducted during December of 1997, when oceanographic conditions were reflecting a more-typical winter regime. The data were obtained with a Neil Brown MK III-C CTD equipped with a nephelometer. Water samples, both for CTD calibrations and for suspended particulate matter evaluations, were obtained with a 12bottle rosette system. Onboard ship, 2 to 5 litre watersamples were filtered through HA Millipore membrane filters (0.45µm) with a vacuum pump. A direct pressure system was used for surface samples taken at 5m waterdepth. Additional sets of deep-water filters were prepared at stations with water depths over 3 000m. This lower set of samples was collected at the maximum nepheloid layer (around 70 to 80m water-depth). During the CLIMA cruise, an additional set of samples were collected at 30 and 80m. On samples from the CORVET cruise, coccosphere abundances were estimated by 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, coccosphere abundance was determined by SEM on a total area of 0.5mm² (24 photographs with 750x magnification). The raw count values were converted to cells per litre based on area counted and volume of water filtered. A total of 16 major taxa were identified and counted on the petrographic microscope. Subsequent observation of selected samples of the CORVET cruise, and of all samples of the CLIMA cruise, by SEM increased the total number of recognised species to 48 (see Taxonomic Appendix, below).

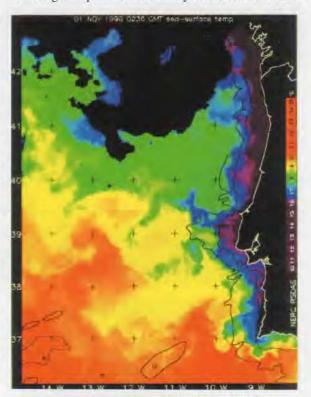
Physical study

Fiúza (1984) showed that there were two main sources for the ENACW off the Atlantic NE coast of Portugal: a) subpolar modal water formed by deep winter convection, N of 50°N, and advected southwards - which we will call the subpolar contribution, ENACWp; and b) eastern N Atlantic water - which we will call the subtropical contribution, ENACWT - formed along the Azores Front during winter and advected eastwards (Figure 1).

During CORVET 96, the study was conducted at the end of a period of almost one month during which a high-

pressure region was located off the western Portuguese coast, extending over Iberia, inducing upwellingfavourable winds. Events of intensification and decay of these upwelling conditions, with a time-scale of several days, were associated with the changing position of the high-pressure region. The expression of these events on the sea-surface temperature was followed before and during the cruise with satellite images kindly provided by the Remote Sensing Data Analysis Service of the Plymouth Marine Laboratory. These images reveal that T1 (Cape St. Vincent-Gorringe Bank transect) was sampled during the decay phase of a 4-5 day upwelling event. The upwelling conditions just before the beginning of the regional study are clearly revealed in the satellite image for the 1st November (Figure 2A), as a band of cold water along the western Iberian coast. At some locations, this coastal band of cold water extends offshore, in the form of upwelling filaments, reaching the continental slope region. Hydrographic fields reconstructed from in situ CTD data also detected the upwelling conditions revealed by satellite images.

Along T2, Stations 21 and 23, located S of 38°30'N, showed strong contributions of ENACW_T, corresponding to the high temperature and salinity branch of the ENACW.



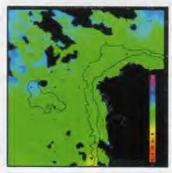


Figure 2A (above): Satellite image during the CORVET cruise. 1st November, 1996

Figure 2B (left):
Satellite image of the sampling area (northern Portuguese shelf: see Fig. 1) during the CLIMA cruise. (Kindly provided by the Remote Sensing Data Analysis Service of the Plymouth Marine Laboratory)

The situation is radically changed at the stations in the northward region (25 and 28), which have a lower contribution from the subtropical branch of ENACW and a greater contribution from the ENACWp branch. A sharp temperature/salinity transition exists at Station 25 between the northern and southern areas. A comparison of the hydrographic data with the corresponding sea-surface temperature field obtained from remote sensing, suggests that this anomalous region probably results from the intrusion of water from the northern area across the warm surface-waters located S of 39°N. A second aspect is the fact that the rapid surface transition observed at Station 25 has a subsurface expression, with a change in watermass characteristics at depths between 100 and 500m. These are depths influenced by the N Atlantic Central Water (NACW).

A region of high salinity (maximum of 36.0% at about 70m depth) is observed in the upper 300m, about 20 to 40km offshore from the shelf edge along T3. This region corresponds to the PCC which Frouin et al. (1990) and Haynes & Barton (1990) have shown to occur along the northern Portuguese coast in winter. Direct current observations over the northern Portuguese slope have revealed that, during upwelling conditions, the surface expression of the PCC was replaced by the equatorward jet associated with the upwelling regime (Vitorino, 1989; Silva, 1992). This seems to be the situation observed during this transect, which took place in weak upwelling conditions.

The CLIMA 97 cruise sampled a restricted area on the northern part of the Portuguese shelf in which general conditions could be characterised as typical winter conditions, in which there was a highly variable wind regime, with sustained periods of winds with a southerly component (Fiúza et al., 1982). During this period there was invasion of the shelf by warm oceanic waters, due to the prevailing downwelling conditions. Offshore waters were almost completely mixed with coastal waters, being those coastal waters largely influenced by local river runoff (low salinity and low temperature values in the upper 25m layer) (Figure 2B).

Coccolithophore Results

CORVET cruise

In the upper water-column layer (5m), mean total coccolithophore standing crops were about 1.8×10^4 cells 1^{-1} , ranging between 3.4×10^2 (Station 43) and 8.4×10^4 cells 1^{-1} (Station 1) (for locations, see Figure 1).

The coccolithophore community present in our samples (members of which are illustrated in Plate 1) included the global and opportunistic species, *Emiliania huxleyi*, with values ranging from <100 to 8.1×10^3 cells Γ^1 (Station 1). Also present in most of the samples are the species *Gephyrocapsa ericsonii* and *Gephyrocapsa muellerae*, with values reaching 30.8×10^3 (Station 1) and 21×10^3 cells Γ^1 (Station 34), respectively, closer to the upwelling inner regions. The latter species has already been recognised in temperate water masses (Jordan *in* Jordan & Kleijne, 1994) and is used as an indicator of the temperate biogeographic coccolithophore zone (Zone 2 of McIntyre & Bé, 1967;

Winter et al., 1994). Helicosphaera carteri was also present but in smaller numbers (<500 cells Γ¹). Coccolithus pelagicus, a species that is commonly found in subarctic cold water-masses and in upwelling areas (Cachão & Moita, in press), was recorded at only one station (Station 1) and in low numbers (<100 cells Γ¹). However, species generally related to warmer (subtropical) water-masses were also found. These included: Umbellosphaera tenuis, Umbilicosphaera sibogae, Discosphaera tubifera, Rhabdosphaera clavigera var. clavigera, R. clavigera var. stylifera, Calcidiscus leptoporus and Gephyrocapsa oceanica. Absolute abundances for these and other species, determined from 5m water-depth samples, are presented in Table 1 (Cachão et al., 1998).

SEM examination of filter samples from Stations 1, 23 and 42 (5m water-depth) confirmed the presence of the previous species, and others such as: Alisphaera spatula, Coronosphaera mediterranea, Polycrater galapagensis, Syracosphaera molischii and Syracosphaera pulchra. Among these species, D. tubifera, P. galapagensis, R. clavigera and U. tenuis are typical of the upper photic zone (UPZ) of subtropical water-masses (R. Jordan, pers. comm., 1999; Jordan, 1988; Winter et al., 1994). SEM observations on filters from Stations 4 (75m water-depth) and 41 (86m water-depth) also showed the presence of Algirosphaera quadricornu, Alveosphaera bimurata, Cyclolithus anulus, Florisphaera profunda var. elongata, Michaelsarsia elegans, Syracosphaera lamina and Turrilithus latericioides. Of these, M. elegans prefers to live in the middle photic zone (MPZ) whereas A. quadricornu, A. bimurata, C. anulus, F. profunda, S. lamina and T. latericioides all tend to live in the lower photic zone (LPZ) of subtropical waters (R. Jordan, pers. comm., 1999; Jordan, 1988; Winter et al., 1994).

CLIMA cruise

The coccolithophore mean average standing crop was maximum at the surface, reaching, at 5m water-depth, 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. Offshore samples (>45km from shore) revealed higher standing crops than coastal ones, although diversity was more or less constant (see Table 2).

The most abundant species found was G. ericsonii, with standing crops ranging from 7.9×10^5 to 0.4×10^3 cells Γ^1 . As in the previous cruise, the opportunistic species, E. huxleyi, was also present in significant numbers $(7.3 \times 10^4)^3$ to 0.4×10^3 cells Γ^1), as well as G. nuellerae $(3.6 \times 10^4)^4$ to 1.1×10^3 cells Γ^1). Subtropical species were also found in significant numbers, such as in the case of G. nuellerae $(3.4 \times 10^4)^4$ to 0.4×10^3 cells Γ^1), nuellerae $(3.6 \times 10^4)^3$ cells Γ^1), nuellerae $(3.6 \times 10^4)^3$ cells nuellerae $(3.6 \times 10^4$

A list of all the identified species in samples taken during CORVET and CLIMA cruises is presented in the Taxonomic Appendix, below.

Station Latitude Longitude Max. depth (m)	1 37°01.3'N 9°03.2'W 96	4 36°57.1'N 9°21.6'W 1530	6 36°53.2°N 9°42.2'W 2050	8 36°48.2'N 10°06.0'W 2720	14 36°33.8°N 11°19.2W 1327	16 36'30.9'N 11'33.8'W 55
Temperature (°C) Salinity (%)	17.28 36.05	19.63 36.38	19.72 36.44	20.87 36.59	20.16 36.46	20.04 36.42
Standing crop	84	9	18	8	10	8
C. leptoporus D. tubifera	*	0.8	0.6	0.4	2.3	1.1
G. ericsonii G. muellerae	31.5 30.8	1.0	7.0 0.2	1.1 0.4	1.3	0.6
G. oceanica	7.4	•	0.1	500		
E. huxleyi H. carteri	8.1	1.6	1	0,2 P		1.8
R. clavigera	0.7	1.0		0.7		
Syracosphaera spp. Ú. sibogae	1.8	0.4	0.9	0.8	1.3	0.3
U. temis	0.7	2.4	4.3	3.1	4.5	1.2

Table 1A: Data sheet of coccolithophore absolute abundances (x10³ cells 1^{-1}) in samples from surface-waters (5m depth) of the S transect. * = free coccoliths only; P = rare occurrences (<100 cells 1^{-1}).

between the temperate and subtropical coccolithophore assemblages was positioned more-or-less parallel to the Nazaré Canyon (See Figure 1). However, Jordan (1988) and Winter et al. (1994) showed that, off Portugal, subtropical coccolithophore assemblages could only be found, in the oceanic domain, S of the Azores Front (i.e. at latitudes lower than 36°N). In Mediterranean waters, several of these subtropical coccolithophore species can also be found (Kleijne, 1993). However, these waters outflow from the Gibraltar Strait at depths (>400m) incompatible with the development of these photosynthetic

Station Latitude Longitude Max. depth(m)	21 37°04.7'N 12°00.5'W 5070	23 37°45.0°N 12°00.0°W 5075	25 38°24.4'N 11°59.4'W 4850	28 39°24,5°N 12°00.0°W 4066
Temperature (°C) Salinity (%)	19,70 36.29	19.45 36.20	18.60 35.98	19.10 36.08
Standing crop	8	18	6	19
C. leptoporus	2.7	1.3	P	0.6
D. tubifera G. ericsonii	0.9	0.5	P 0.7	0.7
G. muellerae	P	0,4	1.6	1.9
G. oceanica		0.1		
E. huxleyi	P	0.6	0.4	0.4
H. carteri		0.1	0.5	0.3
R. clavigera		3.3	0.2	10.8
Syracosphaera spp. U. sibogae	1.4	2.4	0.3	1.4
U. temits	3.8	7,6	0.9	2.2

Table 1B: Data sheet of coccolithophore absolute abundances $(x10^3 \text{ cells } 1^{-1})$ in samples from surface-waters (5m depth) of the N-S transect. * = free coccoliths only; P = rare occurrences (<100 cells 1^{-1}).

species. So, the presence of several UPZ, MPZ and LPZ subtropical species near the Portuguese shelf, during winter, can only be understood if related to the PCC. The presence of this subtropical community close to the Portuguese shelf, at latitudes higher than 41°N (when it is absent from more-offshore oceanic waters even during summer: Jordan, 1988), is direct evidence that, during winter, waters from S of the Azores Front are fed into the Portuguese slope area by the poleward current system. Moreover, the subtropical coccolithophores retain their vertical community structure, with a diverse assemblage of LPZ species being recorded in the deeper samples (A. quadricornu, A. bimurata, C. anulus, F. profunda, S. lamina and T. latericioides). So, at least the uppermost 120 to 220m of the subtropical water-column are driven towards the PCC. Satellite imagery and surface drifter

Station Latitude Longitude Max. depth (m)	34 41°24.6'N 8°49.2'W 38	35 41°24.7'N 8°54.9'W 66	36 41°24.7'N 9°02.0'W 90	37 41°24.3'N 9°14.3'W 800	39 41°24.5'N 9°46.6'W 2618	41 41°24.6'N 10°30.9'W 3585	42 41°24.5°N 10°40.0'W 2410	43 41°24,6'N 10°50,3'W 3061
Temperature (°C') Salinity (‰)	15.09 35.32	15.33 35.46	15.40 35.48	15.82 35.83	17.71 35.89	17.37 35.88	17.69 35.80	17.71 35.82
Standing crop	63	20	9	0	0	10	24	0.3
C. leptoporus	*	*				0.1	0.2	
G. ericsonii	3.0	7.0				2.5	1.8	*
G. muellerae	20.9	6.2	*			1.4	9.5	*
G. oceanica	32.0	5.0	0.7			*	*	
E. huxleyi	*	1.2				0.5	0.3	*
H. carteri	*					0.1	0.3	
Syracosphaera spp.	*	*				0.2	0.2	
Ú. sibogae	*							
U. temis	*	*				*	9.6	

Table 1C: Data sheet of coccolithophore absolute abundances $(x10^3 \text{ cells } 1^3)$ in samples from surface-waters (5m depth) of the N transect. ** = free coccoliths only.

Discussion

The presence of *E. huxleyi* and *G. ericsonii* in waters off Portugal was predictable, given their cosmopolitan distribution. The temperate species, *G. muellerae*, was also expected to be present since this area is under the direct influence of the ENACWP, in which it may codominate with the previous species (Jordan, 1988; Winter *et al.*, 1994). McIntyre & Bé (1967) considered that the transition

studies (Fiúza et al., submitted) have not identified this connection, but this winter coccolithophore community found in offshore Portuguese waters is direct evidence for a link between the Azores Front and the PCC. The presence of the LPZ subtropical community off Portugal at shallower depths (~70-80m) than they usually appear in subtropical waters can be easily understood by the lower light availability during winter, together with lower water

Station Latitude Longitude Depth (m)	82 41°29.9'N 8°50.4'W	80 41°29.7'N 9°02.9'W	77 41°30.0°N 9°15.2°W 800	74 41°29.8°N 9°25.7°W 2031	69 41°29.8°N 10°00.3°W 3100	104 40°41.1°N 8°53.1°W 30	102 41*41.2*N 09*05.2*W 104	100 41°41 3'N 09°19 2°W 430	99 41°41.4°N 09°23.0°W 1075	93 41°41.2'N 09°59.7'W 2886	120 40°51.0°N 08°55.1°W 43	119 41°51.0°N 09°00.1°W 86	117 41°49.3°N 09°10.1°W 120	114 41°48.5′N 09°24.6′W 913
Temp.(°C)	30	- /-	.000	2001	2100		104	420	1012	2000	**		140	717
5	100	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
30 80	-	15.481	15.345	16.366			15 211	15.550	16.245	15.295	7	16.420	16.021	16.445
Salinity														
5	-	35.793		35.879	*	34.215	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	4	35.998	36.003	35.950
Standing crop (x10 ³ cell 1 ³)														
5	102	108	-	967	75	69	278	454		4	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 (x10³ cells 1¹¹) in samples from 5m, 30m and 80m depths, CLIMA 97 cruise.

Station	Sampling Depths (m)	A. brasiliensis	A. ordinata	A. unicornis	C. leptoporus	C. mediterranea	C. pelagicus	D. tubifera	E. huxleyi	G. ericsonii	G. muellerae	G. oceanica	H. carteri	R. clavigera	Scyphosph. spp.	Syracosph. spp.	S. lamina	S. molischii	S. pulchra	U. sibogae
69	30 80							4.8	34.8 37.2	307.2 84.6	14.2 10.2			7.9	3.2 13.5	14.2			1.6	4,8
74	5 30 80	0.4			•	1.6		6.8	73.0 44.3	786.6 543.2	36.6 19.7	4.1 3.2		1.4	2.7 8.2	23 50.9	14.8			28.4 18.0
77	30 80	1.7	1.7		:			1.7	60,9 30.7	198 70.4	15.2	11.8		•	1.7 9.0	8.5			1.7	25.4 18.0
80	5 30 80		1.6		•				20.3 35.6	62.3 74.4	8.1 6.5	9.5 3.2			4.1 0.4	3.2	1.6	1.6		4.1 8.1
82	5 30	1.7					:		18.6 8.1	40.6 1.8	3.4	22.0		0.9		11.8		1.8		1.7
93	30 80				:			*	65.0 28.8	438.6 66.0	18.1	1.8		1.8	5.4 8.5	25.3			3.6	16.3
99	30 80							1.7	42.3 38.9	196.3 294.5	13.5 18.6	:			:	3.4 8.5				11.8 35.5
100	5 30 80		1.7	1.7	•	•		1.7 3.4	67.7 32.2 16.2	282.6 208.2 50.5	35.5 5.1 5.4	5.1		1.7	1.8	16.9 1.7		3.4	3.4	33.3 3.4 12.6
102	5 30 80				:				47.4 27.1 7.2	162.5 49.1 32.5	23.7 6.8 7.2	33.8	:	:	1.7	:		3.4	3.4	3.4 13.: 5.4
104	5 30				0.6				33.8	9.5	5.4	1.3	0.6		0.6	16.2			1.4	2.7
114	5 30 80							1.7	9.3 26.2 25.0	85.9 223.2 123.3	9.3 8.2	2.3		•	1.6	3.1 24.6 1.7	3.3			9.3 13. 28.
117	30 80						3.4	1.7	44.7 16.6	171.9 44.5	1.9	:	:	•	8.6 0.9				1.7	22.
119	30 80							•	37.1 6.8	72.7 20.3	11.4	2.8		•	1.4	2.8	1.4		1.4	12.
120	5 30						:	0.4	25.7 2.4	48.7 0.4	1.4	1.4	0.4		0.4	5.4			1.4	3.6

Table 2B: Data sheet of the coccolithophore absolute abundances (x10³ cells 1⁻¹) in samples from 5m, 30m and 80m depths, CLIMA 97 cruise. * = free coccoliths only.

transparency (mean turbidity values were 0.8mg l⁻¹ for the upper 5m layer off Portugal).

During the CLIMA cruise, the subtropical-dominant species occurring off Portugal were not the same ones that were more abundant during the previous CORVET cruise. While in November of 1996, *U. tenuis* and *C. leptoporus* were the dominant warm-water forms, during December 1997, *U. sibogae* was the most abundant subtropical form. While during the CORVET cruise, there was a clear distinction between two communities (an offshore subtropical assemblage and a coastal temperate community) during the CLIMA cruise these two communities were mixed, reaching their maximum development in more-offshore waters. These differences can be attributed to several causes: (1) the regional oceanographic regime of offshore Portugal (the end of an

upwelling regime during the CORVET cruise and a winter moderate regime during the CLIMA cruise); (2) the developmental history of the subtropical coccolithophore communities transported eastward along the Azores Front; and (3) the physical local conditions of the northern Portuguese shelf, mainly the presence of a stratified, lowsalinity water-body from river runoff.

The presence of a warmer-water coccolithophore community off Portugal, associated with a winter (low to non-upwelling conditions) and not with a summer (moderate to strong upwelling conditions: unpublished data of the CODENET-II cruise, June 1999) oceanographic regime, has implications for the palaeoceanographic interpretations that may be deduced from calcareous nannofossils in the geological record of western Iberia. Following these findings, an increase in these warm-water

species abundances in the geological record must be interpreted as reflecting an increase in the intensity/number of SW winter wind-regime conditions, most of them related to storms, and not necessarily with regional climate warming.

Conclusions

The coccolithophore community developing off Portugal was found to be much richer than expected, with species both from temperate regions (directly influenced by ENACWp) and subtropical regions (directly influenced by ENACWT) dominating particular areas, or intermixing in others. Among the first group, we found G. muellerae, together with G. ericsonii and E. huxleyi. Members of the second group present in the surface-waters (5m waterdepth) included A. spatula, C. leptoporus, C. mediterranea, D. tubifera, G. oceanica, P. galapagensis, R. clavigera, S. pulchra, S. molischii, U. sibogae and U. tenuis, some of which are typical of the UPZ of subtropical water-masses. Deeper-water samples (75 to 85m) contain A. quadricornu, A. bimurata, C. anulus, F. profunda, M. elegans, S. lamina and T. latericioides. The presence of this subtropical community so close to the shelf, and at latitudes higher than 41°N, appears to provide strong evidence that, during winter, waters from S of the Azores Front are fed into the PCC. Indeed, since a subtropical LPZ coccolithophore community structure could be recognised, we can infer that at least the upper 120 to 220m of these subtropical surface-waters are driven towards the PCC.

Acknowledgements

The authors wish to express their thanks to Richard Jordan for helping to make species determinations by SEM, for providing data on coccolithophores from the Azores Front, for fruitful discussions, and for a preliminary review of the manuscript. The manuscript also benefited from the critical reviews of Jeremy Young, Karl Baumman, José-Abel Flores, Paul Bown, Jorge Silva and Aurora Rodrigues, whom the authors also thank. This research was supported by Centro de Geologia of the University of Lisbon (Proxypal) and PRAXIS XXI (FCT). The Museu Nacional de História Natural da Universidade de Lisboa, Instituto Hidrográfico, UCTRA (University of Algarve), and the Plymouth Marine Laboratory also provided logistic support during the present research. This paper is a contribution to the CODENET EC network, and constitutes contribution #A-144 of the DISEPLA Group and contribution #25 of PALEO (Grupo de Paleontologia do Museu Nacional de História Natural).

Taxonomic Appendix

Division: HAPTOPHYTA Cavalier-Smith, 1986 Class: PRYMNESIOPHYCEAE Hibberd, 1976 Order: PRYMNESIALES (Fritsch) Papenfuss, 1955

Family: BRAARUDOSPHAERACEAE Deflandre, 1947

Genus Braarudosphaera Deflandre, 1947

B. bigelowi (Gran & Braarud, 1935) Deflandre, 1947

Family: CALCIOSOLENIACEAE Kamptner, 1937

Genus Anoplosolenia Deflandre, 1952

A. brasiliensis (Lohmann, 1919) Deflandre, 1952

Genus Calciosolenia Gran, 1912 C. cf. C. murrayi Gran, 1912

Family: COCCOLITHACEAE Poche, 1913

Genus Calcidiscus Kamptner, 1950 C. leptoporus (Murray & Blackman, 1898) Loeblich & Tappan, 1978

Genus Coccolithus Schwartz, 1894

C. pelagicus (Wallich, 1877) Schiller, 1930 Cyclolithus Kamptner, 1948 ex Deflandre, 1952

C. anulus Lecal, 1967
Genus Oolithotus Reinhardt, 1968

Jenus Oolithotus Reinhar

O. sp.

Genus

Genus Umbilicosphaera Lohmann, 1902
 U. sibogae var, sibogae (Weber-van Bosse, 1901)
 Gaarder, 1970
 U. sibogae var, foliosa (Kamptner, 1963) Okada & McIntyre, 1973

Family: NOËLAERHABDACEAE Jerković, 1970

Genus Emiliania Hay & Mohler, 1967 E. huxleyi (Lohmann, 1902) Hay & Mohler, 1967

Genus Gephyrocapsa Kamptner, 1943 G. ericsonii McIntyre & Bé, 1967

> G. muellerae Bréhéret, 1978 G. oceanica Kamptner, 1943

G. ornata Heimdal, 1973

Family: HELICOSPHAERACEAE Black, 1971, emend. Jafar & Martini, 1975

Genus Helicosphaera Kamptner, 1954 H. carteri var. carteri (Wallich, 1877) Kamptner, 1954

Family: PONTOSPHAERACEAE Lemmermann, 1908

Genus Scyphosphaera Lohmann, 1902 S. apsteinii var. apsteinii Lohmann, 1902

Family: RHABDOSPHAERACEA Haeckel, 1894

Genus Acanthoica Lohmann, 1903 emend. Schiller, 1913, emend. Kleijne, 1992 A. quattrosphina Lohmann, 1903

Genus Algirosphaera Schlauder, 1945 emend. Norris, 1984 A. quadricornu (Schiller, 1914) Norris, 1984 A. robusta (Lohmann, 1902) Norris, 1984

Genus Discophaera Haeckel, 1894 D. tubifera (Murray & Blackman, 1898) Ostenfeld, 1900

Genus Rhabdosphaera Haeckel, 1894
R. clavigera var. clavigera Murray & Blackman, 1898
R. clavigera var. stylifera (Lohnmann, 1902) Kleijne & Jordan, 1990

Family: SYRACOSPHAERACEAE Lemmermann, 1908

Genus Alisphaera Heimdal, 1973 emend, Jordan & Chamberlain, 1993 A. capulata Heimdal, 1981

A. ordinata (Kamptner, 1941) Heimdal, 1973

A. spatula Steinmetz, 1991

A. unicornis Okada & McIntyre, 1977

Genus Alveosphaera Jordan & Young, 1990
A. bimurata (Okada & McIntyre, 1977) Jordan & Young, 1990

Genus Calciopappus Gaarder & Ramsfjell, 1954 C. caudatus Gaarder & Ramsfjell, 1954

Genus Coronosphaera Gaarder, 1977
C. mediterranea (Lohmann, 1902) Gaarder in Gaarder & Heimdal, 1977

Genus Michaelsarsia Gran, 1912 emend. Manton et al., 1984 M. elegans Gran emend. Manton et al., 1984

Genus Ophiaster Gran. 1912 O. hydroideus (Lohmann) Lohmann emend. Manton & Oates. 1983

Genus Syracosphaera Lohmann, 1902

S. cf. S. borealis Okada & McIntyre, 1977

- S. sp.1 cf. S. epigrosa (Okada & McIntyre, 1977) Kleijne, 1993
- S. epigrosa Okada & McIntyre, 1977
- S. halldalii Gaarder ex Jordan & Green, 1994
- S. lamina Lecal-Schlauder, 1951
- S. molischii Schiller, 1925
- S. nodosa Kamptner, 1941
- S. noroitica Knappertsbusch, 1993 emend. ortog.
- S. orbiculus Okada & McIntyre, 1977
- S. ossa (Lecal) Loeblich & Tappan, 1968
- S. prolongata Gran ex Lohmann, 1913
- S. pulchra Lohmann, 1902
- Genus Umbellosphaera Paasche, 1955
 - U. tenuis (Kamptner, 1937) Paasche, 1955

Family: CALYPTROSPHAERACEAE Boudreaux & Hay, 1969

- Genus Calyptrolithina Heimdal, 1982
 - C. divergens (Halldal & Markali, 1955) Heimdal, 1982
- Genus Syracolithus (Kamptner) Deflandre, 1952
 - S. dalmaticus (Kamptner, 1927) Loeblich & Tappan, 1966

Genera Incertae sedis

- Genus Florisphaera Okada & Honjo, 1973
 - F. profunda var. oblongata Okada & McIntyre, 1980
- F. profunda var. profunda Okada & Honjo, 1973
- Genus Polycrater Manton & Oates, 1980
 - P. galapagensis Manton & Oates, 1980
- Genus Turrilithus Jordan et al., 1991 T. latericioides Jordan et al., 1991
- For bibliographic references on species taxonomy see Perch-Nielsen (1985), Jordan & Kleijne (1994) and Jordan & Green (1994).

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