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**Coccolithophores
calcite production**

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Calcite production by Coccolithophores in the South East Pacific Ocean: from desert to jungle

L. Beaufort¹, M. Couapel¹, N. Buchet¹, and H. Claustre²

¹CEREGE, Universités Aix-Marseille- CNRS, BP80 cedex 4, 13545 Aix en Provence, France

²Laboratoire d'océanographie de Villefranche, CNRS – Université Pierre et Marie Curie-Paris 6, 06230 Villefranche-sur-Mer, France

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Correspondence to: L. Beaufort (beaufort@cerege.fr)

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Abstract

BIOSOPE cruise achieved an oceanographic transect from the Marquise Islands to the Peru-Chili upwelling (PCU) via the centre of the South Pacific Gyre (SPG). Water samples from 6 depths in the euphotic zone were collected at 20 stations. The concentrations of suspended calcite particles, coccolithophores cells and detached coccoliths were estimated together with size and weight using an automatic polarizing microscope, a digital camera, and a collection of softwares performing morphometry and pattern recognition. Some of these softwares are new and described here for the first time. The coccolithophores standing stocks are usually low and reach maxima west of the PCU. The coccoliths of *Emiliania huxleyi*, *Gephyrocapsa* spp. and *Crenalithus* spp. (Order Isochrysidales) represent 50% of all the suspended calcite particles detected in the size range 0.1–46 μm (21% of PIC in term of the calcite weight). The latter species are found to grow preferentially in the Chlorophyll maximum zone. In the SPG their maximum concentrations was found to occur between 150 and 200 m, which is very deep for these taxa. The weight and size of coccoliths and coccospheres are correlated. Large and heavy coccoliths and coccospheres are found in the regions with relative higher fertility in the Marquises Island and in the PCU. Small and light coccoliths and coccospheres are found west of the PCU. This distribution may correspond to that of the concentration of calcium and carbonate ions.

1 Introduction

The coccolithophores represent an important group of unicellular algae. They are found in abundance from high latitudes where they form large blooms which are detected by satellites (Balch et al., 2007; Brown and Yoder, 1994), at low latitudes both in oligotrophic (e.g. Okada and McIntyre, 1979) and upwelling (e.g. Giraudeau and Bailey, 1995) zones. They are responsible for about half of the total oceanic carbonate production (Milliman, 1993). Carbonate precipitation, settling (including ballasting aggre-

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gates containing organic mater), burial, and dissolution are key processes for characterizing the oceanic carbon cycle (e.g., Archer et al., 2000). Yet, despite their major role in the CO₂ cycle, many aspects of calcite production by the coccolithophores are poorly known. In particular the environmental effects on the secretion of coccoliths are poorly understood because of the small number of direct field observations (Balch and Kilpatrick, 1996). Several laboratory and mesocosms experiments have shown a decrease in the production of calcium carbonate by the coccolithophores under increasing CO₂ (e.g. Engel et al., 2005; Riebesell et al., 2000). The increase of CO₂ in the atmosphere will results in a decrease of the pH of oceanic waters, which may have dramatic consequences on oceanic calcifiers (Felly et al., 2004; Orr et al., 2005). It is therefore urgent to analyse in greater detail how coccolithophores are calcifying in Today's Ocean.

The South Pacific Gyre (SPG) is the most oligotrophic zone in Today's Ocean, and it is one of sparsely sampled open ocean area (Claustre and Maritorena, 2003), in particular for coccolithophores. The primary objective of BIOSOPE was to study the South Pacific Gyre along a transect through the central part of the SPG to the Peru-Chili Upwelling (PCU). We document here the variations of the coccolithophore standing stock along this transect, as well as the absolute abundance of detached coccoliths and of other small suspended calcite particles. We also study their size and weight, in order to describe how coccolithophore are calcifying in opposite natural trophic environments. We use methods we developed recently based both on the microscopy automation and the polarizing characteristics of calcite mineral. Some of the softwares used are described here for the first time.

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2 Material and methods

2.1 Setting

The BIOSOPE cruise in the southern Pacific, on board the French Research Vessel l'Atalante (26 October to 11 December 2004) completed a transect of about 8000 km that began in the mesotrophic waters west of the Marqueses archipelago and ended in the eutrophic waters off the coastal waters of Chile (Fig. 1). This represents the largest possible trophic gradient that can be investigated in today's world ocean. The South Pacific Gyre (SPG) is the most oligotrophic region of the world's ocean. Two features may explain why this broad geographic area possess the lowest surface chlorophyll concentration estimated through satellite imagery (0.019 mg Chlam⁻³): First, it has the largest pycnocline depth recorded in the world ocean hydrological database (>200 m); second the flux of atmospheric dust (e.g. iron) is extremely low (Claustre et al., 2007¹). In contrast, the PCU system and the Marquise area (Equatorial ocean upwelling) are bathed by nutrient richer waters.

The sea surface temperature and salinity recorded during the cruise varied from 13 to 28°C and from 34 to 36.5 PSU, respectively, with higher values toward the West and lower values toward the East.

2.2 Sampling

Twenty stations were sampled for biogeochemical parameters (Claustre et al., 2007¹). Samples for the study of the coccolithophorids were taken according to the Depth of the Chlorophyll Maximum (DCM) at every station. At most stations, water samples were taken at 6 water depths: at the surface (actually 5 m), between the surface and the DCM, at the DCM and two samples below the DCM. In most cases 4 litres of sea-water

¹Claustre, H., Sciandra, A., and Vaultot, D.: Introduction to the special section: bio-optical and biogeochemical conditions in the South East Pacific in late 2004 – the BIOSOPE cruise, Biogeosciences Discuss., in preparation, 2007.

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were filtered on a nitrate cellulose membrane with a diameter of 47 mm and a pore size of $0.45\ \mu\text{m}$. At the last 4 stations of the transect (in the PCU) the diameter of the membrane was 23 mm and four litres of water was filtered. In consequence the quantity of particles in these filtrats was extremely high and often the coccoliths could have remained hidden during subsequent analysis. The absolute number given for those stations have therefore large chance to have been underestimated. The membranes were quickly dried and stored at room temperature. Once in the laboratory, a quarter of each membrane was mounted between slide and cover-slip and fixed with Canada Balsam which has the property to render the membrane optically transparent. Additionally a small fragment of the filter was examined using a Hitachi 3000N Scanning Electron Microscope (SEM).

2.3 Grabbing frames

A Polarizing Optical Microscope (LEICA DMRBE) with a 50X oil immersion objective was used for automatic scanning of slides in cross-polarized light. Microscope stage motions and focus were computer-controlled. For each sample, forty fields of view were grabbed by a 2 Megapixel Spot Insight camera. Each frame is $240 \times 180\ \mu\text{m}^2$ with a pixel area of $0.0225\ \mu\text{m}^2$. The amount of light going through the sample was precisely controlled.

2.4 Analyzing calcite particles

We developed a new software using LabView (National Instruments) which automatically detects and measures all birefringent particles from grabbed frames, hereafter called "*Particle Analyser VI*". It takes advantage of the fact that only birefringent crystals are illuminated in cross-polarized light; the other crystals and the background remains dark. There is a relation between the thickness and the brightness of crystals, and this can be calibrated for a transfer function (Beaufort, 2005). The *Particle Analyser VI* opens all the frames in a sample and counts the number of objects brighter

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than background, and measures their surface. We placed a lower threshold at 3 pixels ($0.07 \mu\text{m}^2$) to get rid off background noise; and an arbitrarily chosen upper threshold at 74 000 pixels ($1683 \mu\text{m}^2$ equivalent to circular particles having a $46 \mu\text{m}$ diameter as for example foraminifera). This upper-threshold is large enough to analyse all particles in the nanoplankton size range including aggregates. Knowing the volume filtered in millilitre (V_f), the surface of the membrane (S_m), the number (N_f) and the surface (S_f) of the frames grabbed, and the total number of particle analysed by sample (N_t), the number of particles per millilitre N is:

$$N = N_t \times S_m / (N_f \times S_f \times V_f)$$

The *Particle Analyser VI* automatically measures the “lightness” (L) of all the frames as the sum of all Grey Levels pixel values. A transfer function has been established following the protocol established in (Beaufort, 2005), but applied to samples prepared with cellulosic membranes instead of smear slides. In recalibrating we poured different amounts (precisely weighted) of pure calcite powder into known volumes of water. These suspensions were filtered on membranes of the same type as used during the BIOSOPE transect, and processed as described above. The relation between Grey Levels and weight on the membrane now may serve as a transfer function (Fig. 2).

$$w = 0.0013 \times GL$$

where w is the weight in pg per pixel ($0.0225 \mu\text{m}^2$); GL is the Grey Level measured per pixel (average of all the frames divided by the number of pixel per frame)

The calcite weight per millilitre (W) is calculated as following:

$$W = w \times N_p \times S_m / (N_f \times S_f \times V_f)$$

Where N_p is the number of pixel per frame ($=2 \times 10^6$). The values are given in pg ml^{-1} . Particulate Inorganic Carbon (PIC) is often given in $\text{mmol CaCO}_3 \text{ m}^{-3}$. PIC values for the fraction smaller than $46 \mu\text{m}$ ($\text{PIC}_{<46\mu}$) in this unit are obtained by dividing W by 10^5 .

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2.5 Automated analysis of coccoliths and coccospheres: taxonomic recognition and size analysis

Coccoliths and coccospheres were automatically detected by SYRACO, a software developed in C++ at CEREGE (Beaufort and Dollfus, 2004; Dollfus and Beaufort, 1999).

5 Based on Artificial Neural Network (ANN) SYRACO is adapted to pattern recognition. In this study the ANN has been trained by the SYRACO learning algorithm, on a training set composed of two classes: (1) elliptical placoliths (essentially *Emiliana huxleyi* and *Gephyrocapsa oceanica*), and (2) spherical coccospheres smaller than 10 μm in diameter. The training set is a sample from the Southern Indian Ocean in which all the
10 coccospheres are of *E. huxleyi*, but because of the large generalisation capability of the ANN the coccosphere recognition used here is not species specific. But coccospheres from other orders (Syracosphaerales, Zygodiscales and Coccolithales) are generally not recognised by this ANN.

All the frames have been computed with SYRACO; when an object belonging to one of the 2 classes is detected, its image is saved in a class specific output frame.
15 These output frames are used to perform morphometry and to check the reliability of the recognition. We verified the reproducibility of our technique by counting manually the number of coccospheres in all the frames in 20 samples. The results obtained by the automated and the manual approaches are extremely similar and often identical. In only two samples the number of coccospheres was higher as determined by
20 manual counts. This was due the presence of aggregates of coccospheres in densely populated membranes.

For the coccolith however the number specimen recognized by SYRACO was lower than those determined by human counts. This is not the case when sample are prepared on smear slides (Beaufort and Dollfus, 2004). In the present case, the samples
25 were prepared with membranes that cannot be mounted absolutely flat on the slides, and thus significant portions of the fields of view are out of focus (e.g. Fig. 3a), also coccoliths are often tilted on the mesh of the membrane, often coccoliths are in contact,

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or forming small aggregates which are not recognized by SYRACO.

Because of the large generalisation capability of the ANN, a significant amount of objects that more or less resemble the targeted pattern are included in the specific output frames. In the case of coccospheres, these “invading” objects are “manually”
5 erased from the frame. For the coccoliths, they are automatically withdrawn from the analysis by another new software developed in LabView.

This software, hereafter called “*Coccolith Analyser VI*”, automatically measures coccoliths and coccospheres. It reads the specific output frames and analyses all objects. In the case of coccoliths it first looks for four landmarks characteristic of the coccoliths.
10 If these are not found, the analysis of this object ends. This pre-processing eliminates all non-coccoliths objects that were wrongly recognized by SYRACO. However we found that this process withdraws from the analysis up to 25% of the coccoliths. In the case of coccospheres, all the objects are analysed (incorrectly identified coccospheres were erase manually, see above). The *Coccolith Analyser VI* measures the
15 grey level of the objects, their diameter and their surface, and tabulates the results. There is a bias in the measurement of the diameter of the small and dim objects, such as coccolith of $-0.6 \mu\text{m}$. This due to the fact that we apply a Grey Level threshold below which is defined background. This threshold erodes 2 pixels in the periphery of the dim objects. The pixel size being $0.15 \mu\text{m}$ and 4 pixels being eroded in total when
20 the length is measured, we added $0.6 \mu\text{m}$ to the coccolith length results. By comparing optical measurement with SEM measurement, it appears that for small placolith like *E. huxleyi* the entire distal shield is not detected in cross-polarized light. The measures have to be multiplied by a 1.25 factor. When these corrections are applied the correspondence between SEM and optical measurements on small placoliths are in good
25 agreement. No correction was applied to coccospheres for which SEM and optical measurements are matching.

It should be noted that in a theoretical case of a pure *E. huxleyi* sample, the size distribution estimated by SYRACO and the *Coccolith Analyser VI* will narrower that that estimated with the *Calcite Analyser VI* because SYRACO detects only well preserved,

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well oriented and isolated coccoliths whereas the *Calcite Analyser VI* will measure all particles, including aggregated, broken, out of focus and tilted coccoliths.

2.6 Importance and composition of the Isochrysidales

Emiliana huxleyi and several species belonging to the genus *Gephyrocapsa* and *Crenalithus* represent all the calcifying taxa of the marine Isochrysidales Order (de Vargas et al. in press). We will call this complex “EGC” (for *Emiliana*, *Gephyrocapsa* and *Crenalithus* ranked in order of abundance). SYRACO has been trained to recognize the EGC complex and is therefore the focus of this paper. The specific composition of EGC varied significantly in the BIOSPE sample. We therefore analyse with a Scanning Electron Microscope the samples. This analysis reveals that East of Easter Island (about 110° W) the EGC dominates the coccolithophore community with relative abundance ranging from 60 to 100%. West of Easter Island the coccolithophore concentration diminishes and EGC represents 40% on average of the coccolithophore community. *Gephyrocapsa oceanica* dominates in the Marqueses area. Between 130° W and 100° W the relative abundances of *Gephyrocapsa* and *Emiliana* are variable with a low dominance of *Emiliana*. From 100° to the CPU, *Emiliana* and *Crenalithus* spp dominate the communities. *Emiliana* represent in some samples about 100% of the coccolithophores. A complete analysis of the species distribution in BIOSOPE cruise is in preparation (Couapel et al., 2007²).

²Couapel, M. and Beaufort, L.: Variations of Coccolithophores assemblages along a strong nutrient gradients in the Southeast Pacific, in preparation, 2007.

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3 Results

3.1 Spatial distribution of calcite particles

The concentrations of suspended calcite particles, detached coccoliths and coccospheres show very similar patterns of distribution in the BIOSOPE transect (Fig. 4):
5 Maximum concentrations are found between 80° and 100° W, associated with the subtropical front (Claustre et al., 2007¹).

The concentration in coccospheres is generally very low (average of 9/ml with a maximum of 150/ml). That of detached coccoliths ranges from 11 to 1200 coccoliths per millilitre with an average of 150. The amount of suspended calcite particles and the
10 total weight of calcite per millilitre were in average 733 particles/ml and 11 200 pg/ml (or $\text{PIC}_{<46\mu} = 0.11 \text{ mmol CaCO}_3 \text{ m}^{-3}$) respectively. The corrected total weight of the EGC detached coccoliths and coccospheres is 2431 pg/ml (or 0.024 mmol CaCO₃/m³), which represent 21% of the $\text{PIC}_{<46\mu}$. Large aggregates that may be rich in coccoliths composed a large part of remaining 79%.

15 The spatial distributions of detached coccoliths and suspended calcite particles present two larger scatters of higher concentrations around 95° W (between 50 and 100 m depth) and around 85° W at about 30 m depth. Coccospheres are found in great abundance only in the second scatter. SEM examination of samples in the former scatter confirms the presence of numerous coccoliths of *E. huxleyi*, with very rare coccospheres. This “cloud” of detached coccoliths may correspond to a recent bloom of
20 *E. huxleyi*.

The observed pattern of density distribution of calcite particles is confirmed by the study of in situ optical properties described in Twardowski et al. (2007a)³ (i.e. the ratio of backscattering to scattering) is dependant on size distribution of particle assemblage

³Twardowski, M. S., Claustre, H., Freeman, S. A., Babin, M., Sciandra, A., Beaufort, L., Groundwater, H., and Stramski, D.: Optical scattering and its relationship with particle biogeochemistry in the Southeast Pacific, Biogeosciences Discuss., in preparation, 2007a.

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(high when dominated by small particles and reciprocally) and on refractive index (high for particles with high refractive index, like calcite). for particle density. This ratio approximately scales with the number of suspended calcite particle and the PIC estimated by the “*Calcite Analyser VI*” (Twardowski et al., 2007a³); more particularly it exhibits the two prominent scatters of coccoliths at the exact same position than the present analysis and confirms the relative “patchy” distribution of these biogenic particles.

3.2 Grain size distribution of suspended calcite particles, detached coccoliths and coccospheres

Ninety five percent of the 416 000 suspended calcite particles analysed in the BIOSOPE samples have a surface inferior to $20 \mu\text{m}^2$ or a diameter inferior to $5 \mu\text{m}$ (in the $0.1\text{--}46 \mu\text{m}$ range). The distribution is unimodal and slightly skewed toward larger particles, with a mode at $3.2 \mu\text{m}^2$ (Fig. 5a). The distribution of detached coccoliths and coccospheres are unimodals with modes at $3.2 \mu\text{m}^2$ and $40 \mu\text{m}^2$, respectively (Fig. 5a). Interestingly, the mode of the suspended calcite particles is the same than that of the detached EGC coccoliths. The number of detached coccoliths (mostly *E. huxleyi* plus some *Gephyrocapsa*) represents 1/5 of all suspended calcitic particles.

Sample ST18 at 30 m is almost monospecific (*E. huxleyi* represents more 95% of the coccolith assemblage). In the size range ($1\text{--}10 \mu\text{m}^2$) of *E. huxleyi*, we observed very few particles in the view fields that were not of this species (e.g. Figs. 3a, b). The number of coccoliths detected by SYRACO and the *Coccolith Analyser VI* represents only 40% of the suspended calcite particles in the same size range (Fig. 5b). That means our system missed 60% of coccolith because they were out of focus, tilted, broken or aggregated. Applying a correcting factor of 2.5 to the entire suite of samples, we can now estimates that the EGC coccoliths represent 50% of all the suspended calcite particles detected in the range $0.1\text{--}46 \mu\text{m}$.

The correlation of $r=0.93$ (Fig. 6) existing between the numbers of calcite particles detected by the *Calcite Analyser VI* and the number of coccoliths detected and measured by SYRACO and the *Coccolith Analyser VI* shows the importance of the EGC

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coccolithophores as calcite producers in the Pacific. The correlation indicates that *E. huxleyi* is the main source of fine suspended calcite particles in the open ocean (*E. huxleyi* dominates assemblages where the coccolith density is high).

3.3 Size and weight distribution

5 The diameter and weight of the coccoliths and coccospheres show the same spatial distribution (Fig. 4). These parameters have in general higher values in eutrophic (PCU) or mesotrophic (Marquesas) zones and lowest values between 80 and 100° W (Fig. 7). In oligotrophic area, these values are larger in the deep photic zone. There are significant correlations (Fig. 8) between the station average diameter of coccoliths and coccospheres ($r=0.87$). The same is true for their weights ($r=0.88$). Also there are significant correlation between station average of the weight and the diameter of the coccoliths ($r=0.97$) and of the coccosphere ($r=0.94$).

3.4 Depth profiles

15 Morphometric and abundance data show depth profiles which are similar to that of the chlorophyll concentration (Fig. 9), implying that maxima of the coccolithophores parameters are found most often at the chlorophyll maximum. In consequence, the concentrations in coccolithophores and coccoliths, their weight and their size, are highest at shallow depth in the upwelling area, and deep in oligotrophic area. For example in the centre of the gyre *E. huxleyi* is most abundant between 150 and 200 m.

20 3.5 Number of coccoliths per coccosphere

Assuming that, the detached coccoliths have the same morphological characteristic than the coccoliths in situ on the coccosphere, then the number of coccoliths per coccosphere is obtained by dividing the average weight of coccospheres by the average weight of the coccoliths. Doing so, we found an average of 15 coccoliths per coccospheres with standard deviation of 5. No clear pattern was found in the spatial

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distribution of that number.

4 Discussion

4.1 Abundance distribution

The EGC coccospheres stocks estimated in the South East Pacific are low with a median value of 4000 cell per litre. The lowest values are found at Station GYR at the centre of the South Pacific Gyre. However in the centre of the gyre at all stations coccolithophores were continuously present down to 300 m. The average stock at Station GYR2 was 1250 cell per litres. This is equivalent to 375×10^6 cells m^{-2} in a 300 m thick water column and this represents only the stock of marine Isochrysidales (EGC) which represent only a small fraction (1/3) of the coccolithophores in that area. The stocks of EGC estimated in this study are in the same range as previously reported for the tropical Pacific, 1–240 cell/ml (Hagino and Okada, 2006), 0–60 cell/ml (Balch and Kilpatrick, 1996), 1–100 cell/ml (Ohkouchi et al., 1999; Okada and Honjo, 1973). 0–60 cell/ml (Giraudeau and Beaufort, 2007). The highest cell density of *E. huxleyi* (240 cell/ml) in the South Equatorial Pacific was reported in the Peru Upwelling ($\sim 85^\circ W$ – $\sim 2^\circ S$) (Hagino and Okada, 2006). This is equivalent to what is found in BIOSOPE, where up to 150 cell/ml were observed west of the CPU. The *E. huxleyi* abundance drops from this 150 cell/ml outside the CPU to 9 cell/ml at maximum in the CPU. This is very different from what has been observed in other upwelling systems. For example higher numbers of coccospheres of *E. huxleyi* were observed at the centre rather than outside the Benguela upwelling (~ 250 cell/ml) (Giraudeau and Bailley, 1995). In the case of BIOSOPE experiment, the abundance of coccospheres decreases sharply from the edge to the centre of PCU (a caution note should be given here because smaller filters has been used in the PCU; see the material and method section).

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4.2 *Emiliana huxleyi*: important calcite producer:

The BIOSOPE PIC values are in the same range (0.05–0.35 mmol/m³) than previously published for the Equatorial Pacific (Balch and Kilpatrick, 1996) if we exclude one value from the latter study of 1.33 mmol in the open ocean upwelling. One of the important finding of the present study is a strong relation between the numbers of coccoliths of *E. huxleyi* and the number of suspended calcite particles (and therefore, the PIC). *Emiliana* has been seen as one of the most important calcite producers (e.g. Westbroek et al., 1993) or at the opposite, it has been considered to represent only an insignificant share of the oceanic calcite production (Paasche, 2002; Ziveri et al., 2007), because this species secrete one of the lightest coccoliths (Beaufort and Heussner, 1999; Young and Ziveri, 2000). We show here that most of the fine calcite particles in the BIOSOPE transect have to be attributed to EGC coccoliths (essentially of *E. huxleyi*) production. Calcification in the Tropical Pacific is very high, (equal the rate of photosynthesis) and the turnover times of calcite in the euphotic zone ranges from 3 to 10 days (Balch and Kilpatrick, 1996). These high turnover rates of calcite induce a high ballasting of organic matter by carbonate particles and a high depletion of Ca⁺⁺ ion in the euphotic zone (Balch et al., 2007). Because of the high abundance of detached coccoliths, and coccospheres, the ballasting due to *E. huxleyi* coccolith must have been particularly efficient around 90° W–30° S.

4.3 Weight and size relation between coccolith and coccosphere

An interesting aspect of this study, is the fact that there is a close (r=relationship between the diameter of the coccoliths and of the coccospheres in the EGC complex. A factor of ~1.9 can be used to estimate the diameter of a coccosphere from the length of a coccolith. Also the number of coccoliths per coccosphere is 15 in average without changes through the BIOSOPE transect. These values could be used in paleoceanographic studies for estimating the number and the size of the cells of marine Isochrysidales from the number and length of their coccoliths.

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4.4 Calcification, cell diameter and carbonate chemistry:

The most calcified EGC are found in the Marquises area and Peru-Chili Upwelling (PCU). This could results from the high fertility of these areas, if we rely on the recent culturing experiments showing that *E. huxleyi* is more calcified in waters rich in P and N in batch cultures (Beaufort et al., 2007) or after addition of nutriments in mesocosms (Engel et al., 2005). The problem is that in these studies the number of cell was also elevated. In BIOSOPE, the highest number of coccospheres was found between 80 and 100° W and it is also in the same samples that the least calcified Isochrysidales were found. The number of coccospheres in the PCU may have been underestimated, but not in the Marquise area. There is no relation between the number of coccospheres and their weight of CaCO₃. In a comparison of numerical simulation and observed data from seasonal blooms in the Bering Sea, it has been shown that the *E. huxleyi* production benefits greatly from an increase in the concentration of carbonate ion in the surface water resulting from the increase in phytoplankton production (Merico et al., 2006). These authors hypothesised that in a zone of seasonal blooms, *E. huxleyi* would calcify more after a spring bloom in response to the increase in carbonate ion concentration. This hypothesis could explain why the heaviest coccospheres are observed in the eutrophic and mesotrophic areas of the BIOSOPE experiment. At the reverse, the least calcified Isochrysidales are found at the subtropical front in the highest coccosphere abundance zone of the BIOSOPE experiment. Because it is not a highly productive area, the production of coccoliths may have decreased the carbonate ion concentration, making calcification more difficult for *E. huxleyi*. Also (Balch et al., 2007) recently suggested that high PIC turnover such as those recorded in the tropical Pacific, would induce a depletion of calcium ion in the photic zone as a response of losses of PIC ballasted particles.

Finally we observed a strong negative correlation between surface oxygen concentration recorded during the cruise (Goyet et al., 2007) and carbonate weight of the coccospheres ($r=0.93$). (Shiraiwa, 2003) described a negative effect of oxygen con-

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centration on calcification and photosynthesis of coccolithophores. But because of the high number of coccospheres in that zone, a direct relation with oxygen (Warburg effect) is not considered here. The low oxygen content is seen as an oceanographic signature of the distinct ocean chemistry of this area which has a strong impact on the coccolithophore calcification. We did not find strong correlation between salinity (and temperature) and any morphological parameter we measured on the coccolithophores. Recently some relation between the length of *E. huxleyi* coccoliths and salinity has been suggested (Bollmann and Herrle, 2007). We do not find this relation here ($r < 0.5$): Although the smallest coccoliths are found in relatively low salinity waters, the longest coccoliths were found in the CPU also with low salinity. Our data suggest that the shape (size and weight) of coccoliths and coccospheres is dependant on the carbonate chemistry and productivity of the water in which they are secreted.

4.5 Deep production of marine Isochrysidales

In the South Pacific Gyre, coccolithophores are growing at great depths. For example at Station STB11, *Florisphaera profunda* is found between 200 and 300 m (maximum abundance at 250 m) (Fig. 10a) and at Station GYR2 it is found at 170 m and possibly bellow whereas the maximum abundances of Isochrysidales was found at 150–170 m (Fig. 10b). Station STB11 is one of the rare case in which maximum abundance of EGC was found above the Deep Chlorophyll Maximum (DCM) (Fig. 10a). Except at Station STB11, maximum abundance occurs at about 120 m, i.e., deeper than usually found for coccoliths in oligotrophic area (e.g. Okada and Honjo, 1973; Okada and McIntyre, 1979). A possibility is that these coccospheres were not of living cells but the sinking remains of coccolithophores that grew at shallower depths. Several lines of evidence argue against this: 1) the maximum abundances of coccospheres are in the Deep Chlorophyll Maxima (DCM). 2) the production in the upper photic zone is too low to fuel the coccosphere maxima where coccosphere abundance is 3 times larger than above. This is particularly true for *Florisphaera profunda* which is found only below 200 m. 3) the community vertical structure is typical of oligotrophic area, 4) It is interesting to note

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that the DCM is not only the place of maximum abundance of EGC, but also an area in which they secrete heavier coccoliths and have larger cells. If those morphological parameters are related to carbonate chemistry of the water as it has been proposed above, this could be the depletion carbonate and calcium ion would be more easily compensated by diffusion from deeper water through the thermocline. The “carbonate stress” would be weaker at greater depth.

In conclusion, the system investigated can be considered as an endmember of oligotrophic systems with the deepest chlorophyll maximum and the clearest waters ever reported (Morel et al., 2007). The coccolithophore assemblage is typically adapted to these conditions with maximum cell density being in general closely associated with the deep Chlorophyll maximum. Furthermore from pigment signature is it very clear that below the chlorophyll maximum and up to depth of 250 and above, the dominating (sometime the only one) carotenoids is 19'-hexnoyloxyfucoxanthin, the marker of prymnesiophyceae (Ras et al., 2007⁴). This observation had to be put in line with the layer of high backscattering ratio (the calcite marker) that is recorded at ~240 m (Twardowski et al., 2007b) at the GYR station.

4.6 Implication of deep production for alkenone paleothermometry and satellite calcite detection

When the temperature difference between the surface and the level of maximum abundance of the EGC, the represent of the marine Isochrysidales, is calculated, it appears that for 1/3 of the stations, the difference is above 2°C (Fig. 11). The Isochrysidales are the producers of alkenones used in paleoceanography as sea surface temperature (SST) proxy. Ohkouchi et al. (1999) described some discrepancies between SST estimates from North Pacific surface sediments and the observed SST at the same location, that could be attributed to the fact that alkenones were produced in the DCM.

⁴Ras, J., Uitz, J., and Claustre, H.: Spatial variability of phytoplankton pigment distribution in the South East Pacific, Biogeosciences Discuss., submitted, 2007.

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Also Conte et al. (2006) found some differences between the alkenone calibration curve based on surface sediment (Muller et al., 1998) and their calibration based on mixed-layer water measurements. But those differences were essentially recorded in high latitudes in absence of DCM. Our results would indicate that it is may be excessive to infer SST from an alkenone record core taken below the South Pacific Gyre because alkenone would have been produced far below the surface (there is no suitable sediments to establish such a record in the Central Southern Pacific, Rea et al., 2006). But it has been shown that alkenones are produced exclusively in the mix layer depth, and above the DCM in ALOHA Station in the oligotrophic North Pacific Gyre (Prahl et al., 2005). Either Station ALOHA was similar to Station STB11 where *E. huxleyi* was abundant above DCM (Fig. 10), or the secretion of alkenones by *E. huxleyi* is light dependent. In that case the deep production of Isochrysidales observed in SPG would not temper the SST reconstruction based on alkenones.

From the 115 samples analysed in BIOSOPE, 62% of the coccoliths were found at depth below 30 m, and therefore undetectable by satellite. This indicates that a large part of the calcite production from huge oceanic areas cannot be inferred by remote detection. It is interesting to note that coccolith blooms detected by satellite are always in regions of shallow organic production (high latitudes, continental shelves, and upwelling zones) (Balch et al., 2007; Brown and Yoder, 1994).

5 Conclusions

In the South Pacific Gyre coccolithophores grow in low abundance and calcify. The production is spread on a 300 m water column. When integrated to that entire depth, the stock of marine Isochrysidales, which represent a 1/3 of the coccolith community in that area, is 375 million cells per m².

As found in other coccolithophores study of the Tropical Pacific, the stocks observed during BIOSOPE are low. However, EGC coccoliths compose a significant fraction of Particulate Inorganic Carbone (PIC) (around 50% in term of number of particles and

21% in term of weight). Broken coccoliths and aggregates of these same taxa may represent a large part of the remaining PIC.

Therefore a large amount of the fine calcite particles in the BIOSOPE transect have to be attributed to EGC coccoliths and essentially to *E. huxleyi* production. Calcification in the Tropical Pacific is very high, (equal the rate of photosynthesis) which induce a high ballasting of organic matter by carbonate particles and a high depletion of Ca^{++} ion in the euphotic zone (Balch et al., 2007). Because of the high abundance of detached coccoliths, and coccospheres, the ballasting due to *E. huxleyi* coccolith must have been particularly efficient especially around 90°W – 30°S where *E. huxleyi* is found in great abundance.

There is a close relationship between the diameter of the coccoliths and of the coccospheres in the EGC complex. The most calcified EGC are found in the Marqueses area and Peru-Chili Upwelling (PCU). This could results from the high fertility of these areas: high phytoplankton production can induce an increase in the concentration of carbonate ion in the surface water which will benefit for the coccosphere calcification. At the reverse, the least calcified EGC are found west of the PCU in the highest coccosphere abundance zone of the BIOSOPE experiment. Because it is not a highly productive area, the production of coccoliths may have decreased the carbonate and calcium ion concentrations, making calcification more difficult for *E. huxleyi*.

In the South Pacific Gyre, coccolithophores are growing at great depths: the maximum abundances of EGC were found between 150 and 170 m. The Deep Chlorophyll maximum is not only the place of maximum abundance of EGC, but also an area in which they secrete heavier coccoliths and have larger cells.

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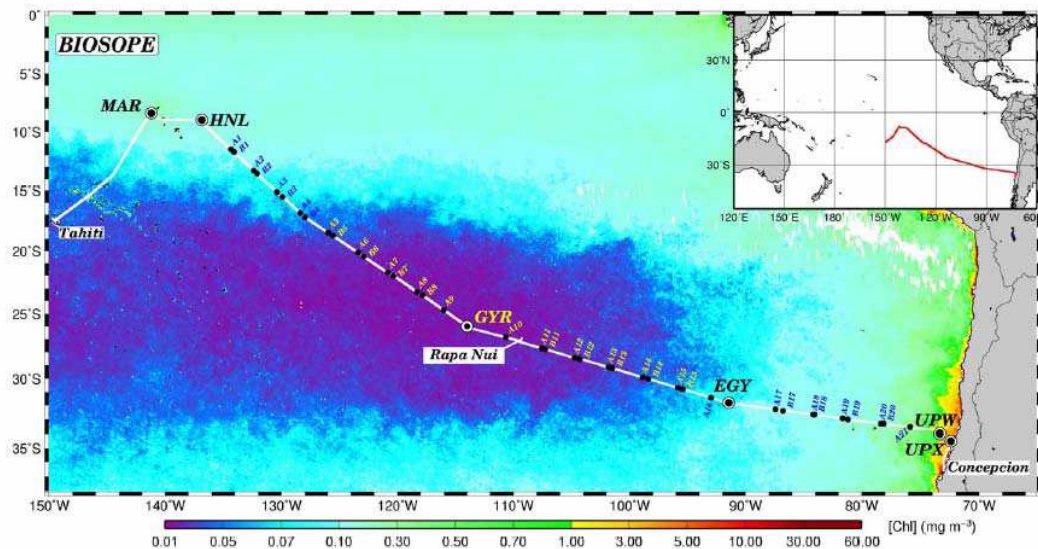


Fig. 1. Map showing the position of the station and the ocean surface Chlorophyll concentration estimated from satellite imagery.

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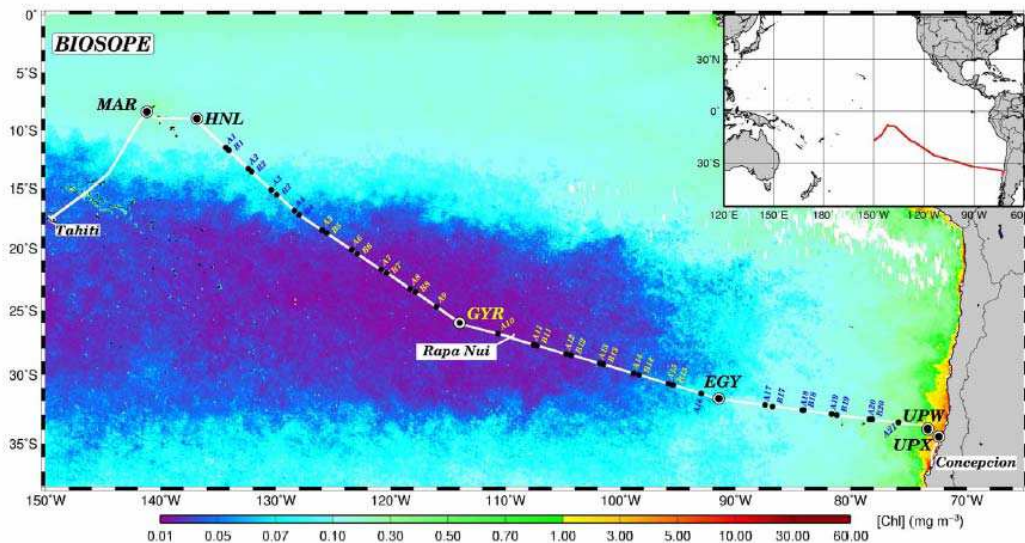


Fig. 2. Transfer function of Grey Levels into weight of calcite in picogram. The x-axis gives the weight of calcite put onto the membrane per surface unit (here the area of one pixel). The y-axis represents the Grey Level value measure in average of one pixel. The line represent de best regression going through the origin.

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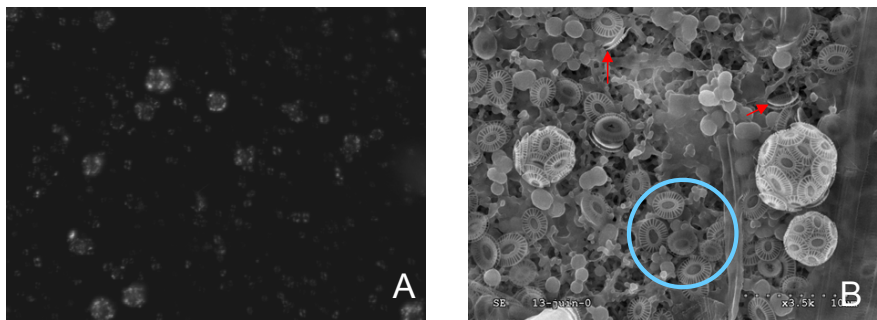


Fig. 3. Images of view field of sample taken at 30 m at Station 18 taken on a Polarizing Microscope **(a)** and a Scanning Electron Microscope **(b)**. The upper right portion of **(a)** is not in focus. In **(b)**, some not well oriented coccoliths are indicated by a red arrow, and some patches of coccoliths are encircled in blue. All coccoliths in these photos are *E. huxleyi*.

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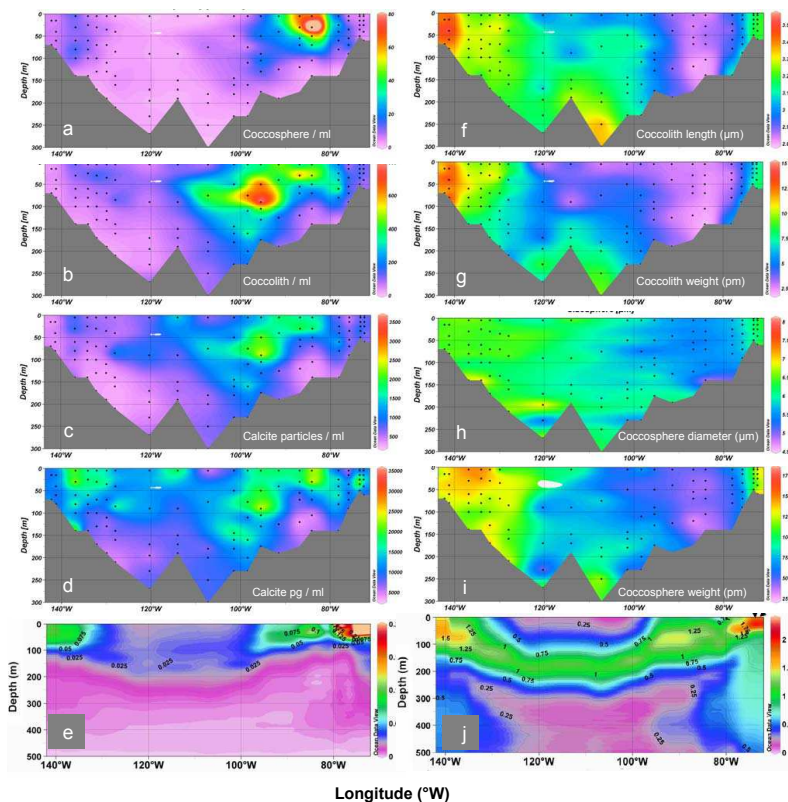


Fig. 4. Density distribution of coccospheres per millilitre **(a)**, detached coccoliths per millilitre **(b)**, Suspended calcite particles per millilitre **(c)**, Total weigh of suspended calcite particles in pg/ml **(d)**, attenuation coefficient, cp (m^{-1}) **(e)**. The attenuation coefficient data have been processed as described in Claustre et al. (2007). Average length of detached coccolith (μm) **(f)**; Average weight of detached coccoliths (pg) **(g)**; Average diameter of coccospheres (μm) **(h)**, Average weight of coccospheres (pg), and concentration in Chlorophyll a from Claustre et al. (2007).

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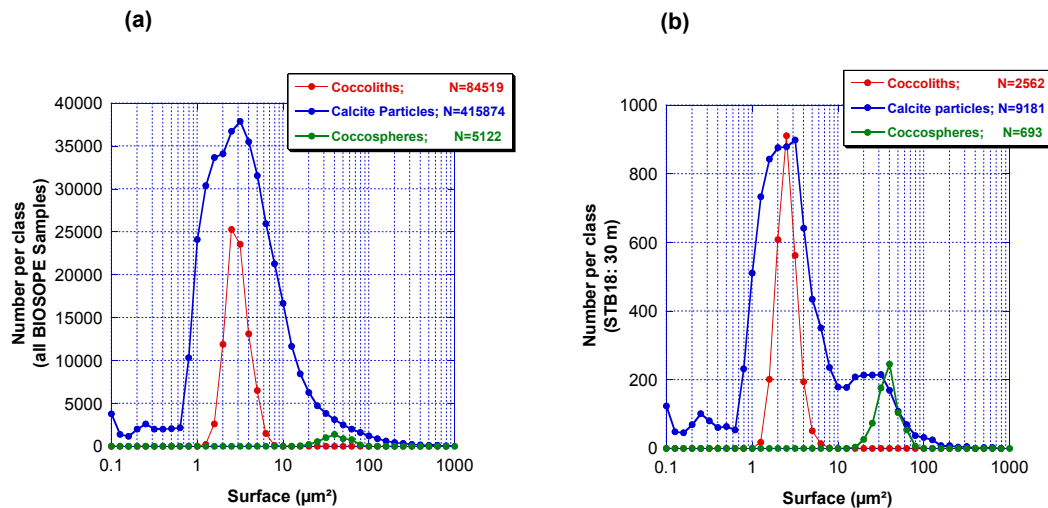


Fig. 5. Distribution of area of coccoliths (red), coccospheres (green) and calcite particles (blue) in all samples **(a)** and in sample taken at 30 m at Station 18 **(b)**.

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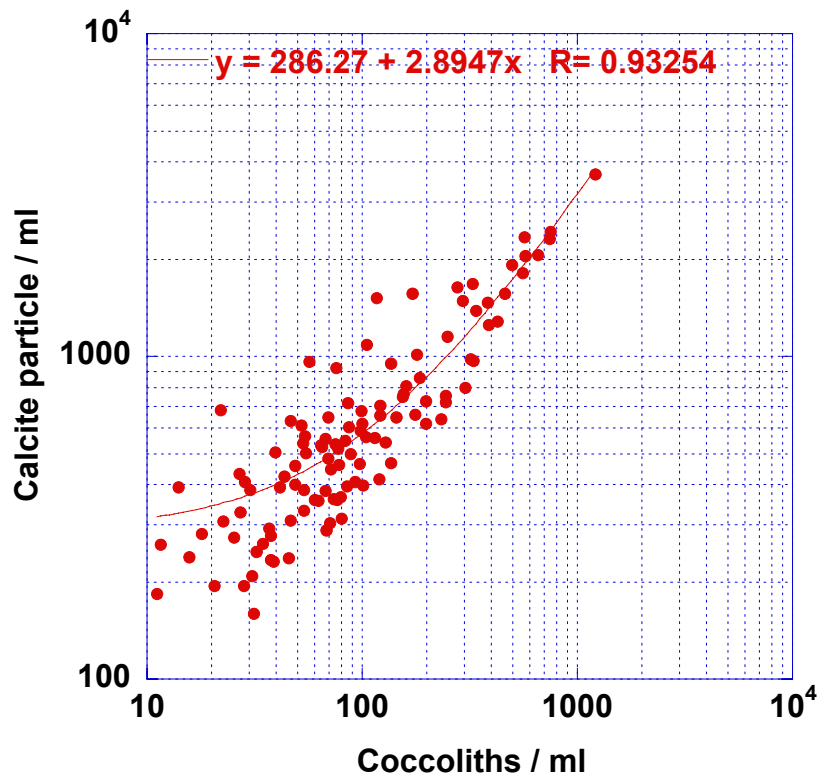


Fig. 6. Correlation between concentrations of suspended calcite particles and of detached coccoliths.

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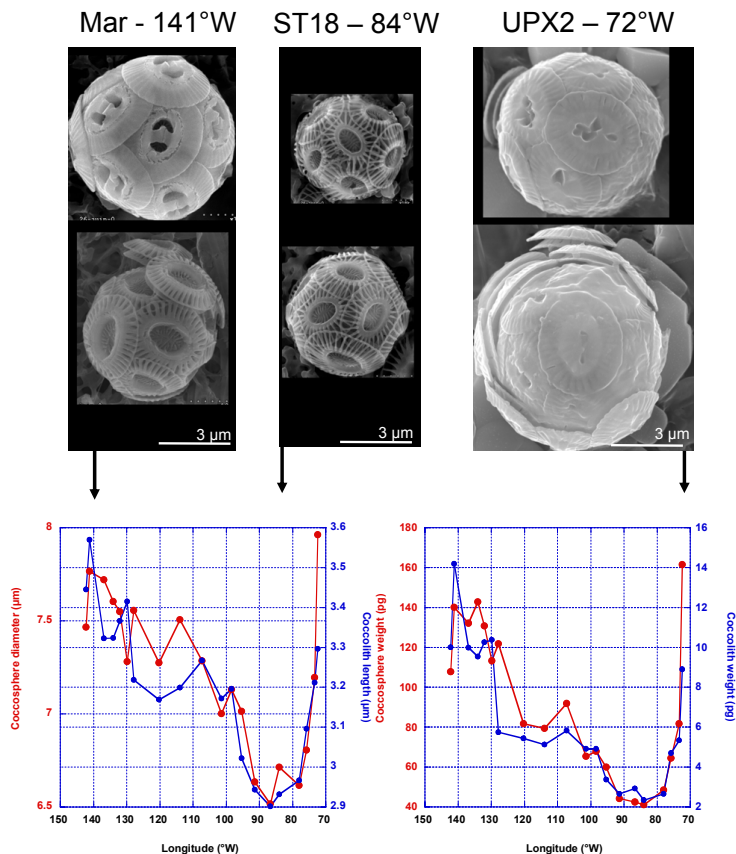


Fig. 7. Bottom left: Variability of Isochrysidales coccosphere diameter (red) and coccolith length (blue) in μm averaged for every BIOSOPE station (average weighted by the concentration at each depth). Bottom right: variability of coccosphere (red) and coccolith (blue) weight in pg averaged for every BIOSOPE station (average weighted by the concentration at each depth). Top: 6 SEM photos (scale bar represents $3\ \mu\text{m}$: same scale in every photo) of typical Isochrysidales in 3 BIOSOPE stations. 3295

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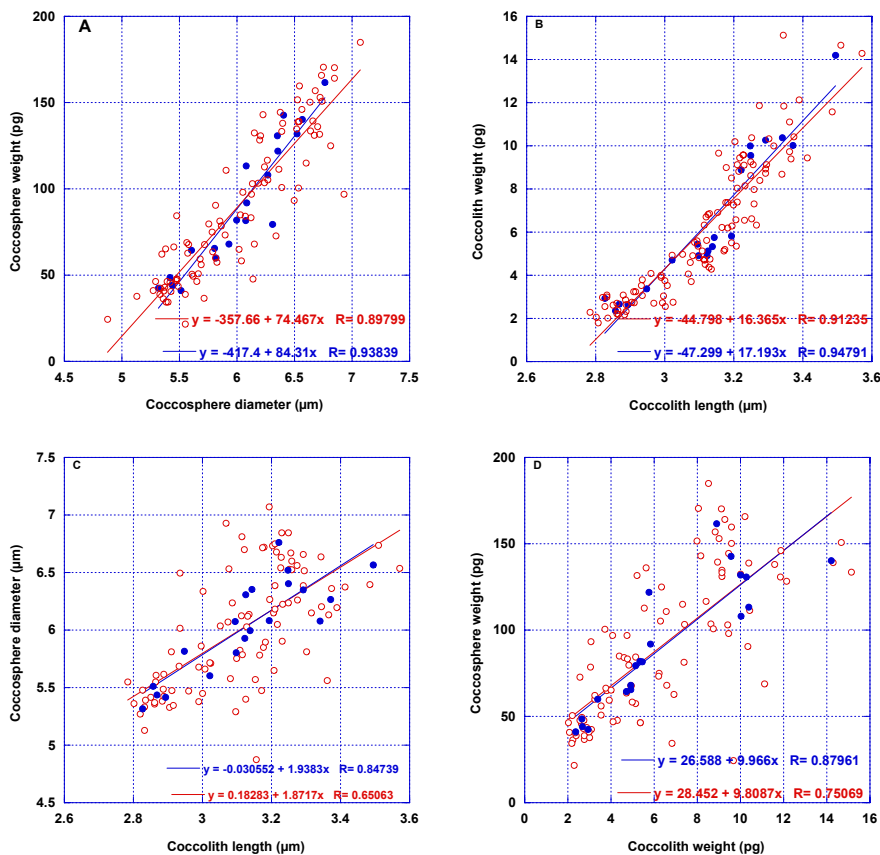


Fig. 8. Correlation between coccosphere diameter and weight **(A)**, coccolith length and weight **(B)**, coccolith length and coccosphere diameter **(C)** weight of coccolith and coccosphere **(D)** of EGC (Isochrysidales) in BIOSOPE samples (open red circles) and weighted average in BIOSOPE stations (filled blue circles).

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Coccolithophores calcite production

L. Beaufort et al.

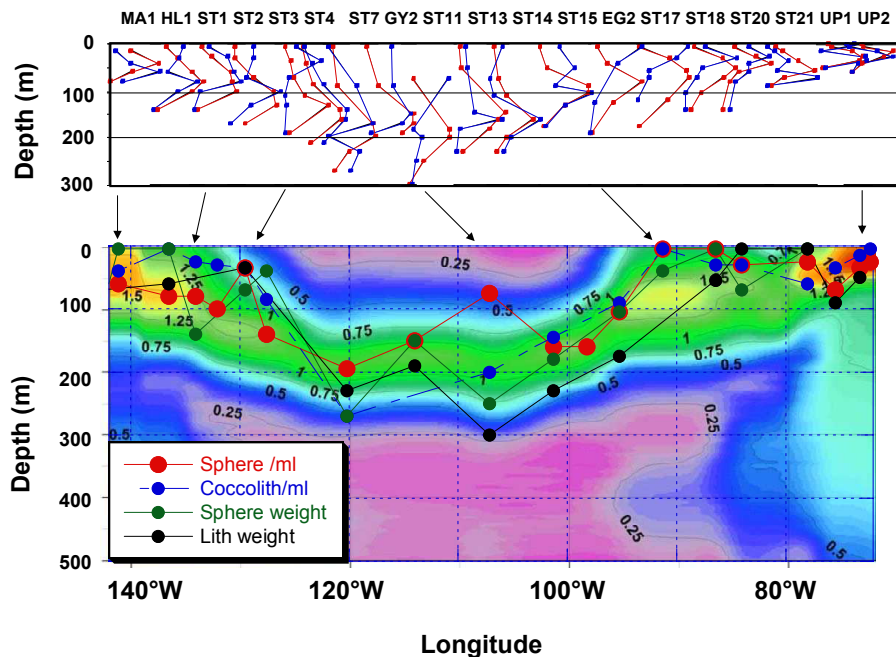


Fig. 9. Top Chlorophyll concentration (red) and EGC (Isochrysidales) coccosphere abundance (blue). The scales have been adjusted at each station. Bottom on top of the chlorophyll a profile, a dot is plotted at the maximum depth of coccosphere density (red), detached coccolith density (blue), weight of coccosphere (green), weight of coccoliths (black).

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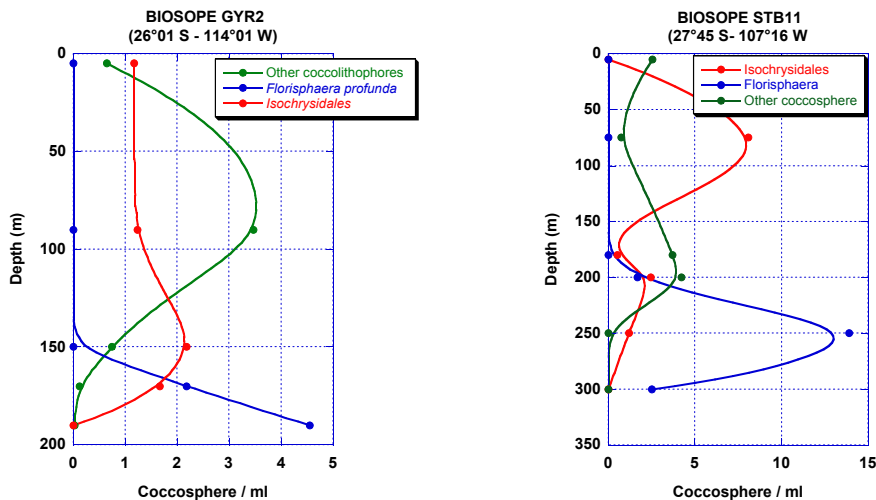


Fig. 10. Density in cells/ml of EGC (Isochrysidales) (red), *Florispheera profunda* (blue) and other coccolithophores (green) at station STB11 (right) and GYR2 (left).

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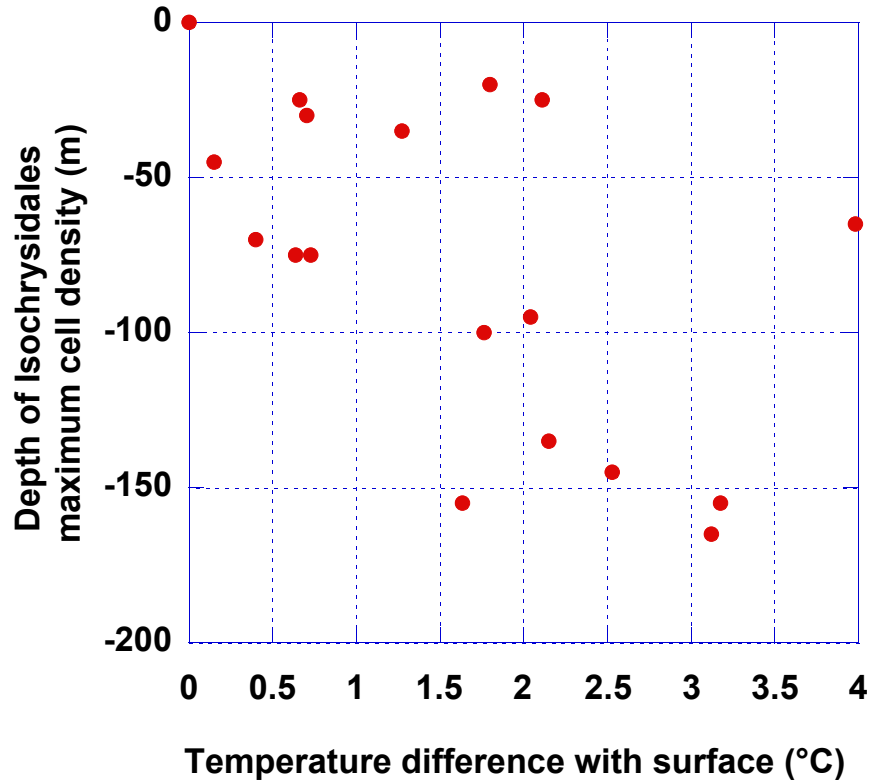


Fig. 11. Temperature difference between the depth of the maximum EGC (Isochrysidales) cell density and surface.

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