Coccolith size increase of *Calcidiscus leptoporus* offshore Morocco during the Last Glacial Maximum: an expression of enhanced glacial productivity?

Jorijntje Henderiks

Geological Institute, ETH-Z, Sonneggstrasse 5, CH-8092 Zürich, Switzerland. Present address: Inst. för Geologi och Geokemi, Stockholm Universitet, S-106 91 Stockholm, Sweden; jorijntje.henderiks@geo.su.se

Sabrina Renaud

Geological Institute, ETH-Z, Sonneggstrasse 5, CH-8092 Zürich, Switzerland. Present address: S.R. Lab. Paléoenvironnements et Paléobiosphère, UMR 5125 CNRS UCB Lyon I, F-69622 Villeurbanne, France

Abstract In recent years, the morphological variability of the coccolithophore species *Calcidiscus leptoporus* has been studied from a global set of Holocene sediment samples and along seasonal variations in both plankton and sediment trap studies. These studies show inverse morphological trends with temperature. A direct application of morphological changes in fossil assemblages to reconstruct palaeoenvironmental conditions has remained limited, although the seasonal investigations have offered additional insight in other ecological factors than temperature controlling the dynamics and distribution of *C. leptoporus*, such as nutrient availability and hydrographic conditions. In this pilot study, we explore the possible causes of glacial-interglacial variability in its coccolith morphology in the Canary Basin, by comparing our observations to the seasonal variations reported in the literature.

Size-measurements of *C. leptoporus* coccoliths in Holocene sediments from the NE Atlantic show smallest mean size at low temperatures. In contrast, mean *C. leptoporus* coccolith-sizes in sediment samples corresponding to the Last Glacial Maximum (LGM) were significantly larger than their Holocene counterparts in the Canary Islands region (NE Atlantic). We argue that this may be an expression of a change in productivity during the LGM, in favour of the production of *C. leptoporus* with large (>8μm) coccoliths.

Seasonal plankton samples off Bermuda (North Atlantic) revealed that during the nutrient-rich winter season the production of large coccoliths was highest, whereas coccolith size was significantly decreased during summer. Very recently, similar observations in sediment traps from the NE Atlantic have been reported, with the largest *C. leptoporus* coccoliths encountered during spring blooms, under elevated nutrient conditions and lowered sea-surface temperatures.

During the LGM, coastal upwelling was generally enhanced offshore Morocco due to the increased strength of the trade winds. Consequently, it is proposed that overall increased yearly nutrient input, together with cooler glacial sea-surface waters, resulted in the dominant production of large 'winter/bloom'-type coccoliths of *C. leptoporus*, especially in the regions near the coastal upwelling zone.

Keywords Coccolith morphology, *Calcidiscus leptoporus*, glacial-interglacial variability, Last Glacial Maximum, Atlantic, Canary Basin

1. Introduction

In few cases have coccolith assemblage studies of surface sediments, and their relative changes down-core, been used to infer temperature conditions and circulation patterns (*e.g.* Roth & Coulbourn, 1982; Okada & Wells, 1997; Wells & Okada, 1997; Takahashi & Okada, 2000), or productivity fluctuations (Molfino & McIntyre, 1990; Beaufort *et al.*, 1997, 2001). However, the process of species-selective dissolution limits studies focusing on coccolith assemblages alone. Carbonate dissolution takes place both during settling of coccoliths out of the photic zone and progressively within the sediments. To avoid this potential bias, several studies have focused on the morphological variability (mainly size) of a single, or a group, of species that are abundant in sediment samples

and are regarded as dissolution-resistant. Such studies have revealed great morphological variability, which could be related to specific environmental parameters and may be the result of either genetic variability or ecophenotypy (*e.g.* Baumann, 1990, 1993; Young & Westbroek, 1991; Bollmann, 1997; Knappertsbusch *et al.*, 1997). Very recently, a new palaeotemperature proxy has been developed, based on the morphology of the coccolithophore genus *Gephyrocapsa* (Bollmann *et al.*, 2002). Its application was validated off NW Africa, successfully reconstructing sea-surface temperatures during the Last Glacial Maximum (LGM; Henderiks & Bollmann, in review).

Calcidiscus leptoporus (Murray & Blackman, 1898) Loeblich & Tappan, 1978 is a cosmopolitan species, today

ranging from equatorial to polar waters (McIntyre & Bé, 1967; Geitzenauer *et al.*, 1977). Its fossil record dates back to the Early Miocene (Young, 1998). Although *C. leptoporus* never reaches high abundances in surface-waters, it can dominate coccolith assemblages in sediments due to its resistance to dissolution (McIntyre & McIntyre, 1970). It is therefore regarded as a promising species for palaeoceanographic reconstructions.

C. leptoporus has been shown to have a wide morphological variability in a global set of Holocene sediment samples (Knappertsbusch *et al.*, 1997), in sediment trap time-series (Baumann & Sprengel, 2000; Renaud *et al.*, 2002), and through seasonal variations in plankton samples (Renaud & Klaas, 2001). These studies show inverse morphological trends with temperature. Knappertsbusch *et al.* (1997) identified three morphotypes of *C. leptoporus* ('small' - coccolith diameter ≤5μm, 'intermediate' - 5-8μm and 'large' - ≥8μm) within the living plankton, which can be found down to Holocene sediments in various mixtures. They found that the relative frequency of large coccoliths (≥8μm) within Holocene surface sediments is positively correlated to mean annual sea-surface temperature, with the largest coccoliths in tropical regions (Knappertsbusch *et al.*, 1997). However, in seasonal samples, the individual responses of the three different *C. leptoporus* morphotypes show more complex patterns with environmental parameters, both in their abundance and average intra-morphotype size-variations (Renaud *et al.*, 2002). Fine, qualitative morphological characters, like the shape of the suture lines and the central opening, were proposed by Kleijne (1993) to discriminate between morphotypes. These characters are not normally targeted by morphometric work. The most recent work, with data emerging from life-cycle studies (Geisen *et al.*, 2002) and molecular biology (Saez *et al.*, in press), conclusively demonstrates the species character of *Calcidiscus* morphotypes and the taxonomy has been changed accordingly.

In the following pilot study, the objective was to test the palaeoceanographical application of morphological variability in *C. leptoporus*, by selecting three sites from the Canary Basin for a Holocene-LGM comparison. Today, seasonal coastal upwelling offshore Morocco results in an E-W fertility-gradient north of the Canary Islands, including productive, upwelling-influenced surface-waters nearshore and oligotrophic surface-waters of the subtropical NE Atlantic gyre further offshore. Annual mean sea-surface temperatures (MSST) range from 17˚C to 23˚C. During the LGM, atmospheric circulation was enhanced over NW Africa (*e.g.* Sarnthein *et al.*, 1981; Hooghiemstra *et al.*, 1987), which led to more intense coastal upwelling in the studied area (see also Henderiks *et al.*, 2002 and references therein). Sea-surface temperatures were 4˚C to 6˚C lower than today (CLIMAP, 1981; Henderiks & Bollmann, in review).

2. Material and methods

Four sites were selected from the Canary Basin for our Holocene-LGM comparison (Figure 1a). Their locations are given in Table 1, as well as all additional sediment samples, representative of the Holocene and LGM time periods, which were included in this pilot study. Gravity cores and corresponding multi-cores from the Canary Basin were taken during two CANIGO cruises with R/V *Meteor* in 1996 and 1998 (M38/1 and M42/4; Wefer *et al.*, 1997, 1999). Time control is based on oxygen isotope stratigraphy and radiocarbon dating (Moreno *et al.*, 2001 - GeoB 5559; Freudenthal *et al.*, 2002 - GeoB 4216; Henderiks *et al.*, 2002 - GeoB 4241, 4242). Coccolith assemblages and their accumulation rates in the same cores are described in Henderiks (2001). In the Canary Basin, relative abundances of *Coccolithus leptoporus* are between 3% and 6%, both during the Holocene and the LGM, and only minor glacial-interglacial variation in accumulation rates was found for this species (Henderiks, 2001).
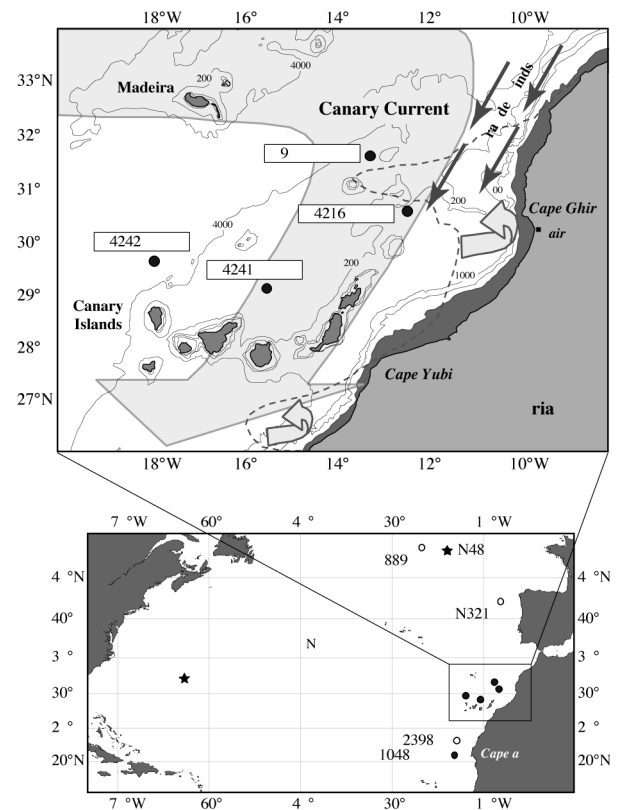

Figure 1: **A)** Detail of Canary Islands region, showing locations of gravity cores used and present day oceanographic and atmospheric circulation patterns. Seasonal coastal upwelling, driven by NE trade-winds during summer, occurs off Capes Ghir and Yubi. Dashed line depicts extent of high pigment concentrations in surface-waters, most likely related to upwelling, as observed by satellite (Davenport *et al.*, 1999). Note dark grey area outside today's coastline, showing presumed exposed shelf area, and glacial coastline, during glacial sea-level lows. **B)** Location of additional sediment samples representing Holocene (open symbols) and LGM (filled symbols) time-slices, as well as the BATS Hydrostation-S time-series and NABE-48 sediment trap deployments (stars) considered in this study. For sample location details, see Tables 1a-1b

Core	Lat.	Long.	Water depth	MSST	Chloro-phyll
(GeoB)	(North)	(West)	(m)	(°C)	(μmole/l)
T88-9P	48°23.2'	25°05.6'	3193	13.78	0.537
N3KF-21	42°09.0'	12°10.0'	4560	15.91	0.304
GeoB 4216	30°37.8'	12°23.8'	2324	19.31	0.313
GeoB 4242	29°40.5'	17°53.3'	4286	20.78	0.214
GeoB 5559	31°38.7'	13°11.2'	3177	19.54	0.263
V23-98	23°07.2'	19°18.0'	3506	21.06	1.050

Table 1a: Holocene surface sediment samples used in this study. Modern annual MSSTs and chlorophyll concentrations given per location from World Ocean Atlas (Levitus *et al*., 1998). Sample identification includes ship, cruise and core number. T = R/V *Tyro*, APNAP-II (van Kreveld *et al*., 1996); N = NORESTLANTE III, Instituto Hidrografico of Portugal; V = VEMA, Lamont-Doherty Geological Observatory; GeoB = *Meteor* cores from the University of Bremen

Core	Lat.	Long.	Water depth	Sample depth	Age	Reference
(GeoB)	(North)	(West)	(m)	(cm)	(kyr)	(Age Model)
GeoB 4242	29°40.5'	17°53.3'	4286	93	20.2	Henderiks *et al*. (2002)
GeoB 4241	29°10.0'	15°27.1'	3609	43	18.7	Henderiks *et al*. (2002)
GeoB 5559	31°38.7'	13°11.2'	3177	48	19-21	Moreno *et al*. (2001)
GeoB 4216	30°37.8'	12°23.8'	2324	78	17.9	Freudenthal *et al*. (2002)
GeoB 1048	20°54.8'	19°43.2'	3635	78	17.8	Henderiks & Bollmann (subm.)

Table 1b: Selected gravity cores used for the analysis of *C. leptoporus* morphology during the LGM

Additional Holocene sediment samples (see Figure 1b), taken to the north of the main area of investigation, were kindly supplied by the Instituto Hidrografico of Portugal (N3KF21) and the Vrije Universiteit, Amsterdam (T88-9P; see van Kreveld *et al*., 1996). Relative abundances of *C. leptoporus* in these samples are highest, with 17% and 12%, respectively (Henderiks, 2001). To the south, two sites offshore Cape Blanc, within today's centre of perennial coastal upwelling off NW Africa, were analysed for the Holocene (V23-98; Bollmann, 1997) and LGM (GeoB 1048) time-slices.

We compare the glacial-interglacial variability in coccolith morphology to modern seasonal changes observed in plankton samples from the Bermuda time-series (BATS) Hydrostation-S (Renaud & Klaas, 2001). Samples used are representative for summer (17th July, 1991) and winter (29th January, 1992), both taken from about 25m depth (Haidar & Thierstein, 2001). In addition, two samples from the NABE-48 sediment trap were included, representing the (1) post-bloom summer (25th July, 1989) and (2) spring bloom (26th March, 1990) seasons (data from Renaud *et al*., 2002; Figure 1b).

2.1 Sample preparation and morphometric measurements

Coccolith analyses of sediment samples were conducted with a Hitachi S2300 Scanning Electron Microscope (SEM), at ETH-Z. A subsample of fine-fraction sediment (<38μm) was put in suspension with denaturated alcohol and sprayed on a coverglass (after Bollmann *et al*., 1999). After drying, the coverglass was mounted on an aluminium sample-holder and sputtered with gold prior to SEM analysis.

Morphometric measurements of *Calcidiscus leptoporus* coccoliths in these samples were carried out following Knappertsbusch *et al*. (1997), using the method described by Bollmann (1997), with minor modifications. Slowscan SEM images were digitised using *analySIS* software (version 3.00), resulting in 768x576 pixel images. All specimens were analysed at a magnification of 8000x, which resulted in a pixel-size of 0.0241μm. Using a mouse-driven cursor, the diameter of every placolith was measured, and the number of radial elements counted, on digitised SEM images of at least 30 specimens.

Plankton samples (collected on 47μm *Millipore* filters with 0.45mm pore-size) were analysed using a Phillips XL30SIS SEM, at ETH-Z. Full details of the plankton sampling method are given in Haidar *et al*. (2000). Images of *C. leptoporus* coccospheres, and any additional loose coccoliths, were recorded digitally at a magnification of 3000x or 6000x (see Renaud & Klaas, 2001 for details).

3. Results
3.1 Morphology in Holocene assemblages

The frequency distribution of diameter and number of elements of all *Calcidiscus leptoporus* coccoliths in Holocene sediments is bimodal (Figure 2). The frequency of coccoliths with a diameter of between 6 and 7μm, and with 20 to 22 radial elements, is the highest (Figures 2a, c). Morphometric data of individual samples are given in Appendix A (Holocene), in which the bimodal distribution with an inflexion point at around 8μm, as observed by Knappertsbusch *et al*. (1997), is clearly expressed.

Sample means are given in Table 2. The smallest sizes and numbers of elements were encountered in sample T88-9P (mean diameter (D) = 6.24μm; mean number of elements (E) = 19.6), which underlies surface-waters with modern MSSTs below 14°C. Samples taken in the vicinity of coastal upwelling regions off Cape Ghir (Morocco: GeoB 5559 and 4216) and Cape Blanc (Mauritania: V23-98) display similar, small mean-sizes (of about 7.3μm)
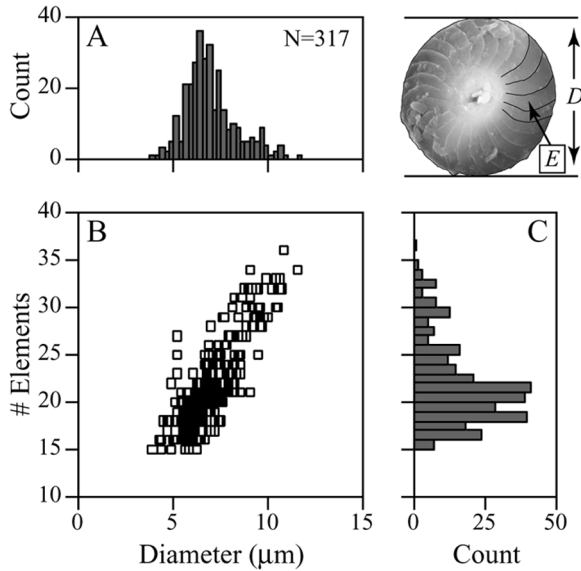
and mean numbers of elements (22-23).

Figure 2: Distribution of diameter and number of elements of all *C. leptoporus* coccoliths measured in the Holocene samples. **A)** Histogram of coccolith diameter (μm). **B)** Number of radial elements *vs*. coccolith diameter. **C)** Histogram of number of radial elements. Note bimodal distribution of the histograms. **Top right**: SEM image of a single *C. leptoporus* coccolith illustrating morphometric measurements of diameter (D) and number of elements (E); this specimen contains 25 elements

3.2 Morphology during the LGM

Scatter plots of morphometric data of all LGM samples can be found in Appendix B (LGM). The frequency distributions of *Calcidiscus leptoporus* diameter and number of elements measured in LGM samples are also bimodal (Figure 3), but show a distinct shift towards increased frequencies of larger coccoliths compared to the Holocene (Figure 2). This is also expressed in the sample means (Table 2, Figure 4a), which are larger during the LGM. The largest glacial-interglacial size-difference occurred at Sites GeoB 5559 and 4216, with mean-size increases during the LGM of 1.58μm and 0.92μm, respectively.

A significant increase in size of the largest specimens within a sample is clear when the 75 percentile is considered, the measured size-value separating the largest 25% of the *C. leptoporus* coccolith assemblage from the smaller 75% (Figure 4b). An increase in size is also found in the smallest 25% of coccoliths, although less pronounced (25 percentile: Figure 4c).

3.3 Seasonal morphological variability

The seasonal variability in morphology of living *Calcidiscus leptoporus* at the Bermuda time-series station (BATS) is described in detail by Renaud & Klaas (2001). Two main periods could be recognised: 1) from January to April, a mixture of both 'intermediate' (5-8μm) and 'large' (≥8μm) morphotypes were present throughout the photic zone, down to 200m; and 2) from May and thereafter, the 'large' morphotypes disappear, but the 'intermediate' ones are present mostly in the upper 25m (Renaud

& Klaas, 2001). The mean size and number of elements of two typical 'summer' and 'winter' samples are plotted on Figure 4a, as well as the means for three separate years. The annual and summer means all plot within the range of Holocene samples from the NE Atlantic, whereas the winter mean shows a large deviation from the same. The latter plots within the range of observations in sediment samples from the LGM (Figure 4a).

This seasonal deviation in size is even more strongly expressed if the 75 percentile is compared (Figure 4b). For the 25 percentile, a less pronounced deviation in size is observed (Figure 4c), but here also the winter value is

	NE Atlantic		Canary Basin							Cape Blanc	
			Oceanic					Nearshore			
			GeoB	GeoB	GeoB	GeoB	GeoB	GeoB	GeoB		GeoB
	N3KF21	T88-9P	4242_01	4242_93	4241_43	5559_03	5559_48	4216_02	4216_73	V23-98	1048_78
N=	51	55	56	54	51	48	58	49	31	58	51
Aver. Size	6.92	6.24	6.78	7.43	7.50	7.28	8.86	7.35	8.27	7.25	7.22
STDEV	1.36	1.02	1.05	1.79	1.52	1.48	1.77	1.31	1.51	1.55	1.65
stdev mean (95%)	0.37	0.27	0.28	0.48	0.42	0.42	0.46	0.37	0.53	0.40	0.45
Variance	1.84	1.05	1.11	3.21	2.30	2.19	3.14	1.70	2.27	2.40	2.71
Aver. Elements	21.22	19.62	20.84	22.43	23.08	22.00	26.28	23.10	25.45	22.66	22.33
STDEV	4.14	3.06	3.80	5.82	5.65	5.41	5.79	4.76	4.87	4.79	4.97
stdev mean (95%)	1.14	0.81	1.00	1.55	1.55	1.53	1.49	1.33	1.71	1.23	1.37
Variance	17.17	9.39	14.46	33.87	31.95	29.32	33.50	22.68	23.72	22.90	24.75
Time-slice	HOL	HOL	HOL	LGM	LGM	HOL	LGM	HOL	LGM	HOL	LGM

Table 2: Morphometric measurements of *C. leptoporus*: sample means of size and number of radial elements. Grey columns denote samples corresponding to the LGM time-slice

larger than the one in summer. A comparable pattern was found in sediment trap NABE-48, between the spring bloom and summer seasons (Figure 4).

Figure 5 shows the relationship between mean coccolith size and number of elements with sea-surface temperature (SST) for Holocene sediment samples from this study, and sediment trap (Renaud *et al*., 2002) and plankton assemblages from the Atlantic (Knappertsbusch *et al*., 1997; Renaud & Klaas, 2001).
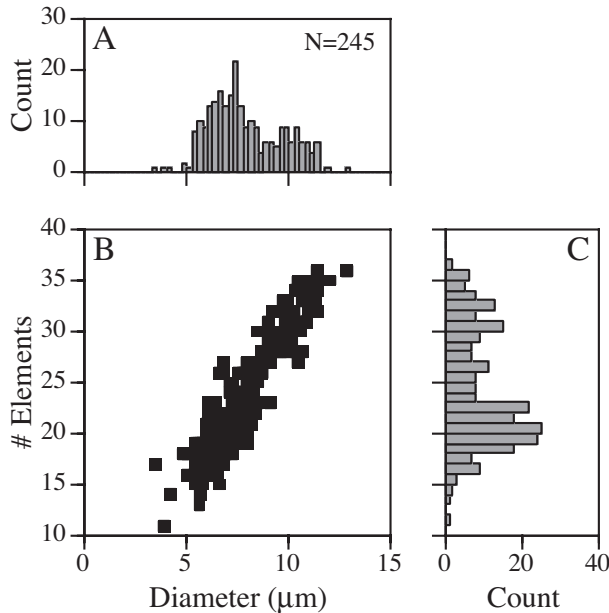
(A), for the measured size-value separating the largest 25% of the *C. leptoporus* coccolith assemblage from the smaller 75% (75 percentile). **C**) As (A), for the measured size-value separating the smallest 25% of the *C. leptoporus* coccolith assemblage from the larger 75% (25 percentile).

Figure 5: Relationship between SST and **A**) mean coccolith diameter, and **B**) mean number of radial elements for all Holocene sediment, seasonal sediment trap (NABE-48) and plankton (BATS) samples, as well as additional plankton samples from the Atlantic (data from Knappertsbusch *et al*., 1997; see legend). Although a positive correlation exists between the Holocene mean morphological features and temperature (solid lines), the opposite appears for the seasonal samples (dashed lines)

Figure 3: Distribution of diameter and number of elements of all *C. leptoporus* coccoliths in samples corresponding to the LGM. **A**) Histogram of coccolith diameter (μm). **B**) Number of radial elements *vs*. coccolith diameter. **C**) Histogram of number of radial elements. Note bimodal distribution of both histograms, and significant increase in larger coccoliths compared to Holocene (Figure 2)
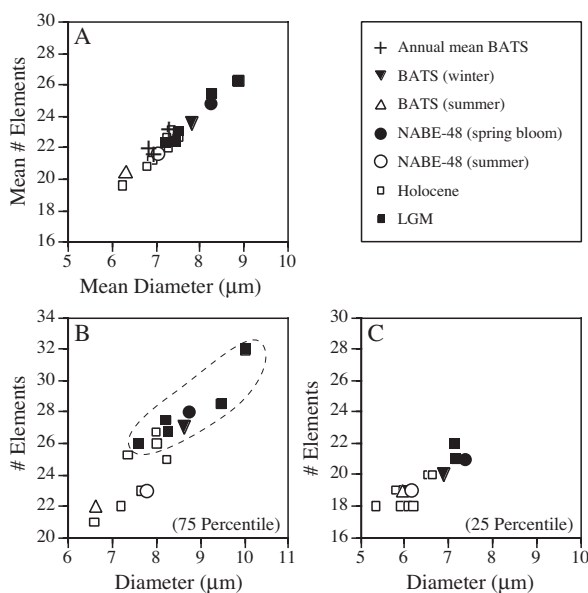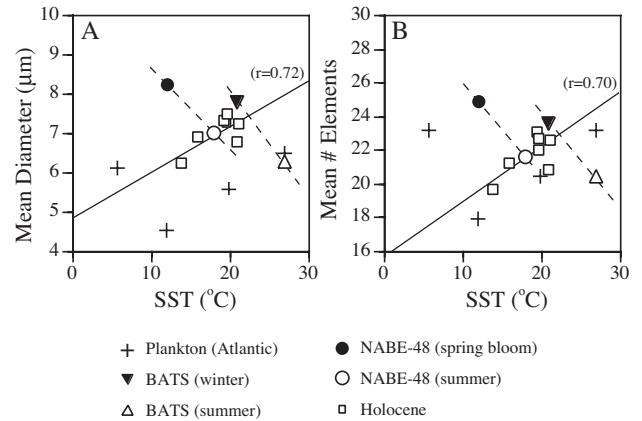
4. Discussion

Knappertsbusch *et al*. (1997) found that the relative frequency of larger coccoliths (≥8μm) within Holocene surface sediments increased in tropical samples. Average coccolith diameter showed a distinct step towards larger size at about 24°C, resulting in an overall positive correlation between mean size and annual MSST (r = +0.530; Knappertsbusch *et al*., 1997, tab.7). Mean coccolith size also appears to increase with increasing MSST, within the temperature range we studied in the NE Atlantic (14°-21°C; Figure 5).

If these observations from Holocene sediments were to be used to predict morphological characteristics of *Calcidiscus leptoporus* coccoliths during the LGM in the Canary Basin, when surface-waters were up to 6∞C colder in the investigated area (CLIMAP, 1981; Henderiks & Bollmann, in review), a decrease in the contribution of large coccoliths would be expected. Consequently, also a decrease in the mean size would be predicted. However, the opposite was found in this pilot study. Mean coccolith size, as well as the size of the largest specimens within LGM samples, was significantly larger than within their Holocene counterparts, especially in Cores GeoB 4216 and 5559. Figure 6 illustrates the reversed relationship between MSST and mean coccolith size, with estimated MSSTs for the LGM in each sample based on the *Gephyrocapsa* palaeotemperature proxy (Henderiks & Bollmann, in review).

The main question is, therefore, to assess whether the observed glacial-interglacial variability in coccolith size could be explained by environmental processes, or

Figure 4: **A**) Mean number of elements *vs*. mean diameter of all samples considered in this study, including plankton (BATS), sediment trap (NABE-48), Holocene and LGM sediment samples (see legend). **B**) As

whether they occurred due to other processes, such as sediment reworking and/or coccolithophore evolution. Reworking of coccoliths from the Pliocene/Early Pleistocene may have induced larger coccoliths of the species *Calcidiscus macintyrei* (Bukry & Bramlette, 1969) Loeblich & Tappan 1978, with a last occurrence at 1.54Ma (see Hine & Weaver, 1998 for overview). In general, coccoliths of this species are larger (>10μm) than those of *C. leptoporus* (Knappertsbusch *et al.*, 1997). However, no specimens of *Discoaster* spp. were found in the same samples and, therefore, extensive sediment reworking from the Early Pleistocene can be excluded.

In this pilot study, and in the following discussion, the focus lies on the first objective, ecological response, by comparing data from the plankton and sediment traps with our findings in the sediment.
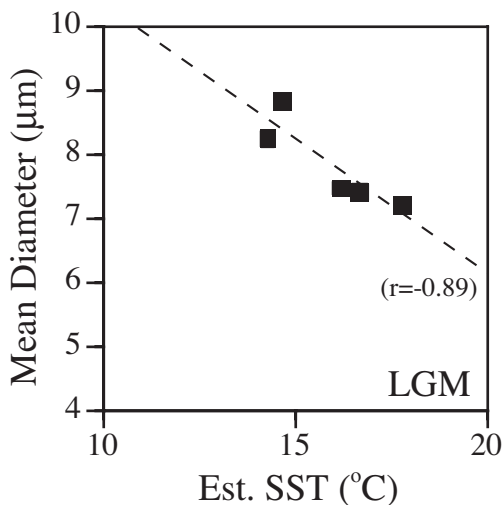

Figure 6: Mean diameter of *C. leptoporus* in samples corresponding to the LGM in relation to the estimated SSTs for the same samples based on *Gephyrocapsa* morphometry (Henderiks & Bollmann, in review). Note, again, a reversed correlation (dashed line) in comparison to the Holocene (Figure 5)

4.1 Seasonal variability in *Calcidiscus leptoporus* morphology

Winter temperatures in the Sargasso Sea range between 19°C and 21°C, whereas temperatures reach 27°C in summer. The annual range in SST in the Canary Islands region today is 17-23°C, *i.e.* within the winter range at BATS. Therefore, we are not able to make absolute temperature estimates based on the BATS-CANIGO comparison of *Calcidiscus leptoporus* morphology (see Figure 5), especially not for the significantly colder LGM. The relationship of *C. leptoporus* morphology and SST remains obscure, which is illustrated in Figure 7, where size distributions in the plankton, as well as our Holocene and LGM sediment data, are plotted against temperature. However, we can possibly deduce changes in seasonality of other important oceanographic parameters, *i.e.* nutrients, from the pattern observed. That is, assess the amount of 'winter-type' *versus* 'summer-type' *C. leptoporus* being added

to the sediment assemblages.

The glacial-interglacial pattern in the Canary Islands region is compared to the seasonal pattern at BATS in Figure 8. The similarity of the size distribution between a typical winter plankton sample at BATS and the LGM sediment samples suggests that a change in seasonality between the LGM and Holocene in the Canary Islands region may be responsible for the observed shift in the mean size of *C. leptoporus*. The larger coccoliths occur only in winter and are distributed within the entire photic zone at BATS (Renaud & Klaas, 2001). The winter condition in the Sargasso Sea is characterised by convective mixing, associated with storm-fronts moving from North America (Michaels & Knap, 1996), and by highest nutrient concentrations in the surface-waters. Enhanced input of larger 'winter' coccoliths during the LGM, when winter conditions similar to those off Bermuda prevailed in our area of investigation, would lead to a mixture of *C. leptoporus* in the sediments with larger means.

In the Canary Islands region, deep mixing of the surface-waters in winter leads to coccolithophore blooms in a similar way (*e.g.* Sprengel *et al.*, 2000 and references therein). Additional nutrient input occurs in summer during coastal upwelling events, especially nearshore. Highest fluxes of *C. leptoporus* were recorded in February and March in sediment traps north of the Canary Islands, related to the winter phytoplankton blooms, after breakdown of seasonal (summer) stratification within the upper photic zone (Sprengel et al., 2000, 2002). Largest coccoliths of *C. leptoporus* (>10μm) were encountered in the same sediment traps in February to April, although the average diameter showed no distinct seasonal variation (Baumann & Sprengel, 2000). Very recently, Renaud *et al*. (2002) reported on the seasonal variability of *C. leptoporus* morphotypes and their relationship with environmental parameters in two additional sediment traps from the NE Atlantic (NABE-48 and NABE-34). In the northernmost deployment, NABE-48, highest absolute abundances of the large morphotype were found in cool (12°-16°C) water-temperatures, when high nitrate (*i.e.* nutrient) contents prevailed (Figures 7, 8). This supports our hypothesis that a change in seasonality, and hence changed input of *C. leptoporus* coccoliths to the sediments, could explain the observed glacial-interglacial variability in morphology. Using an empirical calibration of *C. leptoporus* morphology in Holocene sediments with MSST alone proved to be inadequate, since reversed trends were found not only in seasonal plankton and sediment trap studies (Figure 5), but also in this LGM time-slice study (Figure 6).

The average size of *C. leptoporus* assemblages depends on the success of the individual morphotypes. Depending on what part of the temperature gradient is considered, a different mixture of successful morphotypes is found. For instance, the stepwise increase to large *C. leptoporus* in tropical samples (above 24°C: Knappertsbusch *et al.*, 1997) may be a reflection of
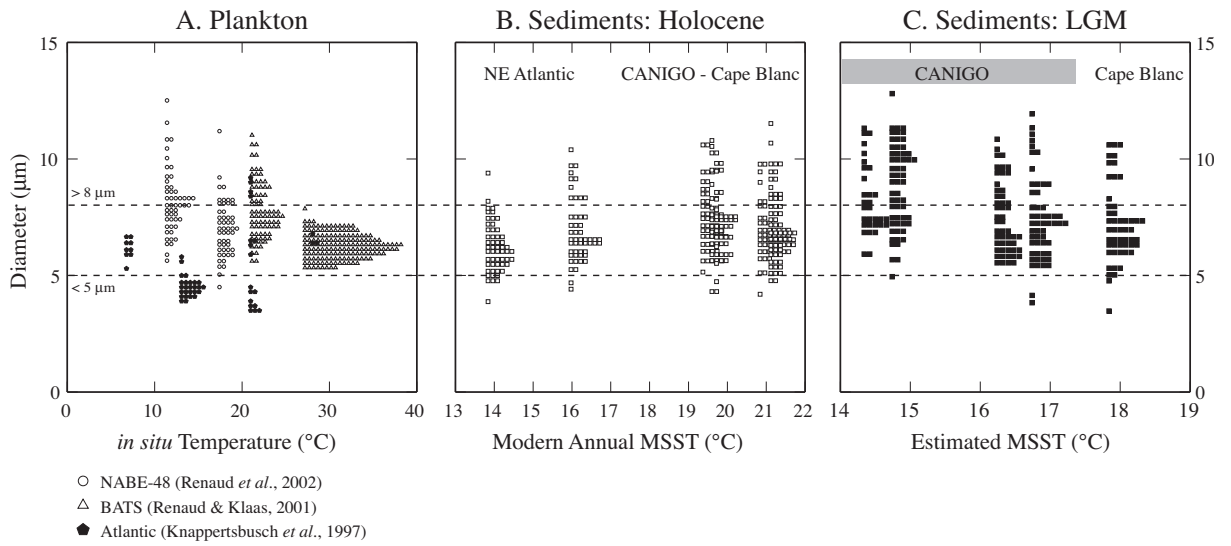
Figure 7: Histograms of *C. leptoporus* coccolith size *vs.* SST, comparing **A**) plankton data (against *in situ* SST) with **B**) Holocene sediment data (against modern annual MSST; Levitus *et al.*, 1998) and **C**) sediment data from the LGM (plotted against estimated MSST; Henderiks & Bollmann, in review). Morphotype boundaries at <5μm and >8μm, as defined by Knappertsbusch *et al.* (1997), are indicated in graphs. Note increased amounts of large coccoliths during LGM
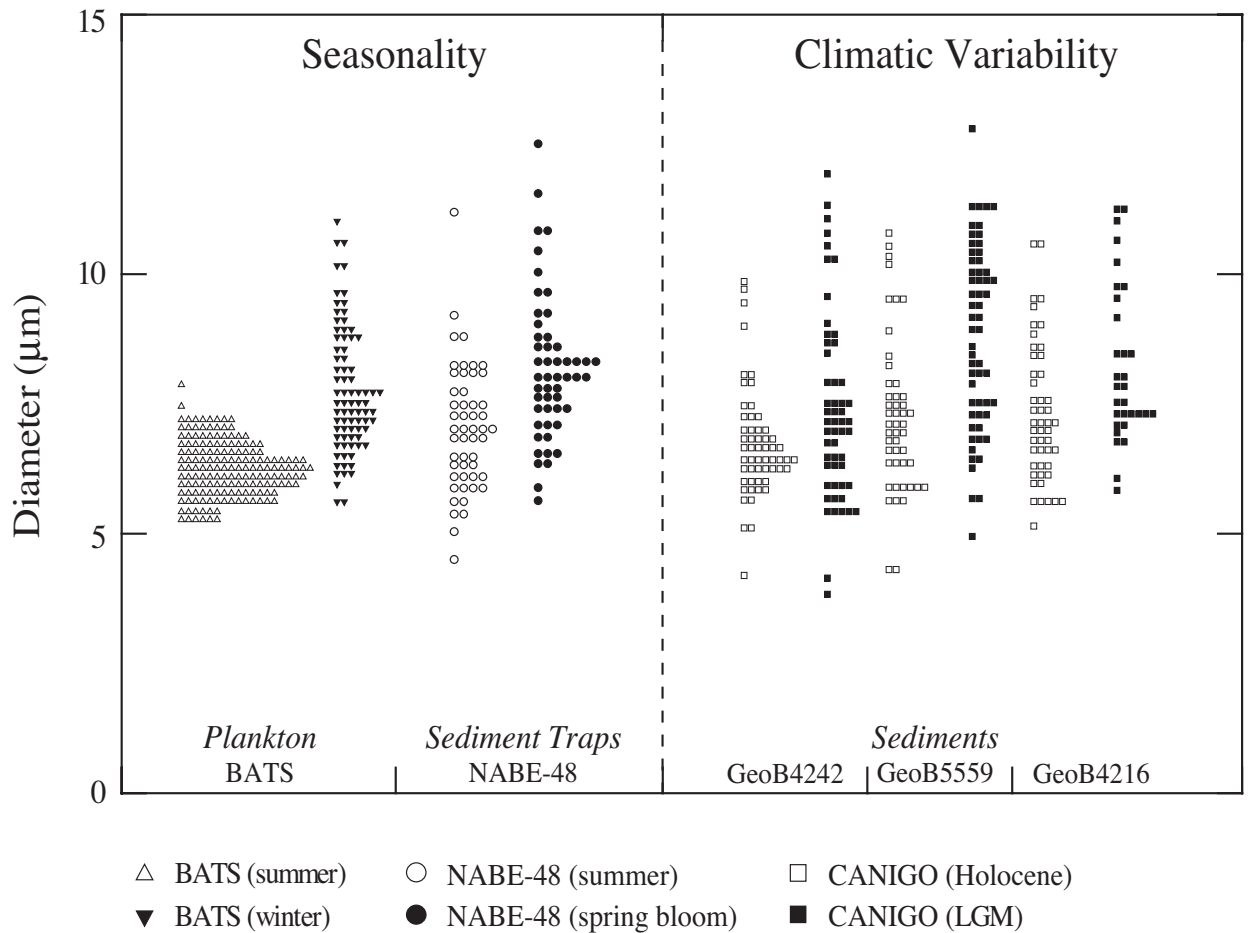

Figure 8: Summary of main variability in morphology discussed in this study. Histograms of *C. leptoporus* coccolith size comparing the seasonal variability (summer *vs.* winter/spring bloom) at BATS and NABE-48, and climatic variability (interglacial *vs.* glacial) in the Canary Basin at three locations (GeoB 4242, 5559 and 4216). Note that the LGM sediment samples and winter/spring bloom samples display highly similar size-distributions

decreasing success of the intermediate morphotype alone, rather than increased production of the larger morphotype. Below this threshold of 24°C, both the intermediate and large morphotypes have a potential to dominate, and the average size of the assemblage will depend on the relative success of both. In the NE Atlantic, this relative success appears to depend on the seasonal variations in nutrients, with significant increases of the large morphotype during bloom conditions.

4.2 *Calcidiscus leptoporus* morphology in the context of LGM palaeoceanography

The reconstruction of glacial-interglacial variability of coastal upwelling, and related changes in palaeoproductivity off NW Africa, is currently being reassessed. Various studies in this region have shown enhanced intensity of the trade-winds during the LGM (Sarnthein *et al*., 1981; Hooghiemstra *et al*., 1987), resulting in higher coastal upwelling and productivity than during the Holocene (*e.g*. Sarnthein *et al*., 1982, 1988; Abrantes, 2000; Sicre *et al*., 2000; Freudenthal *et al*., 2002; Henderiks *et al*., 2002). However, high glacial productivity appears geographically limited to the northernmost latitudes of the NW African upwelling system (north of 25∞N). Evidence for lowered glacial productivity was found off Cape Blanc, in today's centre of the perennial upwelling system (Bertrand *et al*., 1996; Martinez *et al*., 1999; Ternois *et al*., 2000; Zhao *et al*., 2000). Reportedly, productivity records are highly influenced by local oceanographic processes, and could be controlled by advection from the shelf and/or offshore shifts of the upwelling cells related to sea-level changes (Bertrand *et al*., 1996; Zhao *et al*., 2000). A glacial sea-level drop of about 120m must have had major implications for the process of coastal upwelling. The cross-shelf morphology of the NW African margin during the LGM would imply an upwelling system more confined to the shelf edge (*e.g*. Fütterer, 1983; See Figure 1a, in which the grey area represents exposed shelf area during the LGM).

In the Canary Basin, the greatest glacial-interglacial difference in mean coccolith size, of 1.58μm, was found at Site GeoB 5559, and to a lesser extent (0.92μm) at Site GeoB 4216 (Table 2). Today, these sites are in the vicinity of areas with seasonally-increased pigment concentrations that are presumably related to the coastal upwelling process (*e.g*. Davenport *et al*., 1999). Freudenthal *et al*. (2002) gave evidence for increased activity of these filaments during glacial times, influencing the surface-waters and export production to Site GeoB 4216 more directly. Site GeoB 4242 is well outside the influence of coastal upwelling, in the outer oceanic domain, and showed the least glacial-interglacial variability in *Coccolithus leptoporus* morphology (0.65μm).

Considering all available data on *C. leptoporus* morphology, we therefore propose that an increase of nutrient input during enhanced glacial coastal upwelling off Morocco led to the production of more 'winter/bloom'-type coccoliths than during the Holocene. In contrast, offshore Cape Blanc, no significant variability in coccolith size was observed between the Holocene and LGM samples (Figure 7, Table 2), supporting previous observations of lowered glacial productivity in this area. In addition, the glacial drop in temperature of maximal 4°C (to about 18°C: Henderiks & Bollmann, in review) in this area is not reflected in a change in morphology of *C. leptoporus* coccoliths.

5. Conclusions

A plausible explanation for the overall size increase of *Calcidiscus leptoporus* coccoliths in the Canary Islands region during the LGM could be a change in coccolithophore productivity, which promoted the production of larger 'winter/bloom'-type *C. leptoporus*s. The winter conditions found off Bermuda in the Sargasso Sea today agree well with the proposed environmental conditions during the LGM in the Canary Islands region. Atmospherically-driven mixing of the surface-waters makes nutrients available in the surface-waters of the Sargasso Sea during the winter, which is the period in which the larger coccoliths were observed.

In the Canary Islands region, deep mixing of the surface-waters in winter leads to coccolithophore blooms in a similar way and, during these times, highest fluxes of *C. leptoporus*, as well as largest coccoliths, were found in sediment traps (Sprengel *et al*., 2000; Baumann & Sprengel, 2000). Additional nutrient input occurs in summer during coastal upwelling events, especially nearshore.

Enhanced coastal upwelling off Morocco during the LGM, due to the intensification of the trade-winds, led to even higher input of nutrients to the photic zone and would have lowered the seasonal variability in environmental parameters that determine the morphological characteristics of *C. leptoporus* coccoliths. Nevertheless, additional morphometric research on plankton samples from the Canary Islands region is necessary to further constrain present day seasonal variability of *C. leptoporus* size in the Azores and Canary currents.

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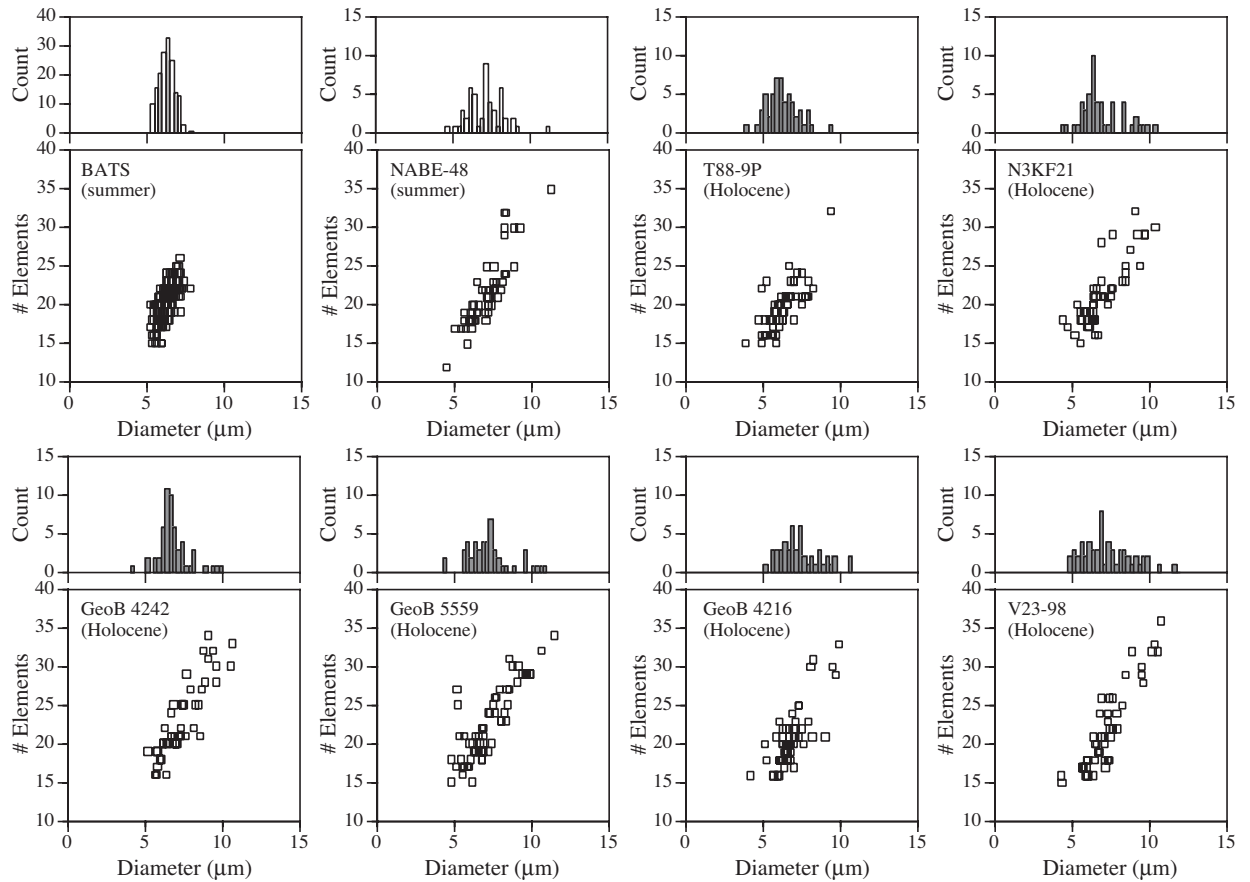
Appendix A: Distribution of coccolith diameter and number of elements of all *C. leptoporus* in Holocene sediment samples, as described in this study. For comparison, the seasonal summer samples from BATS and NABE-48 are included (Renaud & Klaas, 2001; Renaud *et al*., 2002)
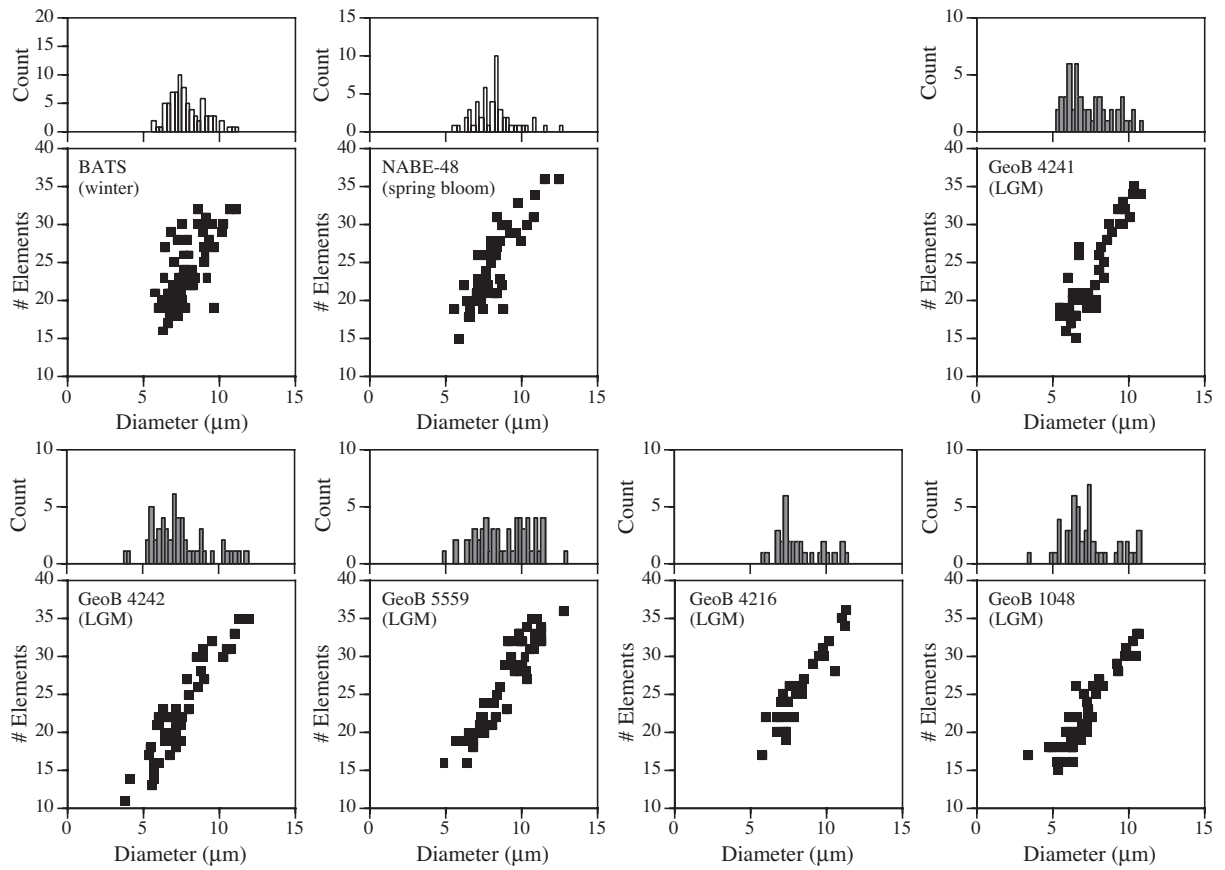
Appendix B: Distribution of coccolith diameter and number of elements of all *C. leptoporus* in sediment samples corresponding to the LGM, as described in this study. For comparison, the seasonal winter sample from BATS and spring-bloom sample at NABE-48 are included (Renaud & Klaas, 2001; Renaud *et al*., 2002)