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# Geographical and seasonal differences in morphology and dynamics of the coccolithophore *Calcidiscus leptoporus*

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## Abstract

*Calcidiscus leptoporus* is a cosmopolitan coccolithophore species, composed of three morphotypes characterised by differences in morphology and size. The seasonal dynamics of this species have been studied in four sediment trap and plankton time series covering different biogeographic settings. Investigated parameters were: variations in absolute and relative abundances of the three morphotypes, average size variations of the *C. leptoporus* assemblages, and intra-morphotype size variations. For each time series, and for the complete data set, the relationship between *C. leptoporus* dynamics and some environmental parameters was investigated. Seasonal variations can be recognised in the four time series, but the biogeographic pattern governing this seasonality is complex. The two best documented morphotypes show comparable seasonal fluctuations in absolute abundances, mainly co-varying with temperature and related factors such as water mixing. However, their relative abundances change with varying nutrient contents in the surface water masses, suggesting slight differences in their respective ecological preferences. Average size of the *C. leptoporus* assemblage provides information about the morphotype composition and allows a comparison of the seasonal variations observed in the present study and Holocene geographic patterns reported in the literature. Additionally, intra-morphotype size variations might be related to environmental changes.

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**Keywords:** nannoplankton; sediment trap; environmental parameters; ecology; morphotype

## 1. Introduction

Coccolithophores are a group of calcareous nannoplankton producing calcite platelets (cocco-

liths) surrounding the cell. At present they are one of the main open ocean primary producers and coccoliths are major contributors to deep-sea carbonate sediments. Their community variability can provide palaeoceanographic information about environmental variables such as temperature and productivity (McIntyre et al., 1970). However, a prerequisite for their use as palaeoenvironmental proxies is the understanding of their ecology. Although their large-scale geographic distribution is well known (e.g. McIntyre and Bé, 1967; Okada and Honjo, 1973; Kleijne,

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1993), the environmental parameters controlling their distribution and small-scale variations are still poorly understood.

The extant cosmopolitan species *Calcidiscus leptoporus* is well suited to a study attempting to relate intra-specific variations to environmental factors, because its ecological preferences can be traced along a wide environmental gradient. Although this species never reaches high abundances in surface waters, it can dominate coccolith assemblages in sediments due to its resistance to dissolution (McIntyre and McIntyre, 1970). Thus, its morphological characteristics can be determined in fossil samples even when it is present at low abundances.

*Calcidiscus leptoporus* has been shown to have a wide morphological variability both in a global set of sediment samples (Knappertsbusch et al., 1997) and along seasonal variations in plankton samples (Renaud and Klaas, 2001). However, these studies show inverse morphological trends with temperature. This discrepancy needs to be resolved before any morphological signal obtained in the fossil record can be used for palaeo-environmental reconstructions. The present study aims to identify fine-scale ecological preferences of *C. leptoporus* by comparing the seasonal variations at several geographic locations covering different hydrographic regimes with respect to both temperature and nutrient availability. The variations in abundances and morphology of *C. leptoporus* were therefore studied in four time series

(Fig. 1; Table 1): subtropical NABE-34 and temperate NABE-48 sediment traps in the NE Atlantic; oligotrophic subtropical Hydrostation-S in the NW Atlantic; and MST-9 sediment trap in the Arabian Sea exemplifying tropical, nutrient-rich conditions. In order to identify the ecological factors controlling the dynamics and distribution of *C. leptoporus*, the variations of this species are compared to environmental parameters for individual time series, and within the complete data set.

## 2. Seasonal dynamics and total coccolithophores flux

The four time series are characterised by average annual sea-surface temperature (SST) ranging from 14.9°C (NABE-48) to 26.5°C (MST-9) (Levitus and Boyer, 1994), and variable nutrient contents, as exemplified by sea-surface nitrate concentration ranging from the most oligotrophic H-S (0.60 µmol/l) to the most nutrient-rich MST-9 (3.04 µmol/l) (Levitus et al., 1994). Also, the dynamics of the water column vary. At NABE-48, the annual averaged mixed layer depth exceeds 150 m, whereas it does not exceed 30 m at MST-9 (Table 1). The seasonal dynamics at each station are briefly presented in the following sections.

### 2.1. NE Atlantic (NABE)

The seasonal hydrographic patterns at NABE-34 and NABE-48 are relatively similar. They are characterised by winter mixing of the water column, more important at NABE-48, followed by summer stratification. The nutrient availability is relatively stable all through the year. At NABE-48, but not at NABE-34, spring is characterised by an increase of the nutrient levels close to the sea-surface. However, the seasonal variations of productivity are similar at NABE-34 and NABE-48 and show a spring-bloom at the onset of the summer stratification. During the experiment period, four major periods of mass fluxes could be identified at both stations: bloom 1989 (spring), post-bloom (summer), pre-bloom

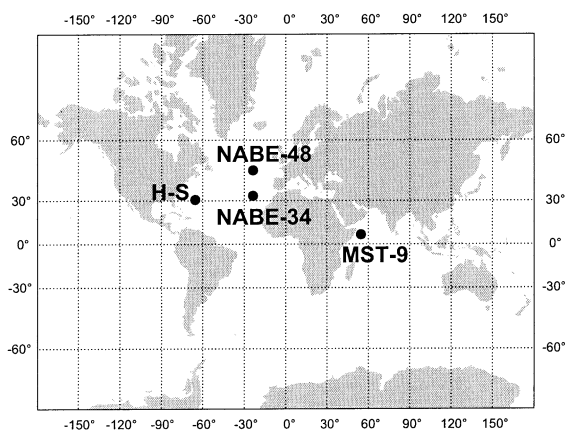


Fig. 1. Location of the sites considered in this study.

Table 1

Location of the stations, and environmental parameters: annual sea-surface temperature (SST), sea-surface nitrate concentration (NO<sub>3</sub>), and mixed layer depth (MLD)

Station	Latitude	Longitude	SST (°C)	NO <sub>3</sub> (μmol/l)	MLD (m)
NABE-48	48°N	21°W	14.9	1.61	154
NABE-34	34°N	21°W	20.0	1.82	69
H-S	32°N	64°W	23.2	0.60	58
MST-9	10°N	53°E	26.5	3.04	28

Data derived from the World Ocean Atlas 1994 (Levitus and Boyer, 1994; Levitus et al., 1994).

(autumn–beginning of winter), and spring-bloom 1990 (Honjo and Mangani, 1992).

At NABE-34 the coccolithophore flux pattern showed a pronounced seasonal variation with an increase during late winter and beginning of the spring-bloom period. This increase in the coccolithophore flux is correlated with the lowest levels of diversity (Broerse et al., 2000b). At NABE-48, coccolithophores showed an enhanced flux during spring, followed by low fluxes in summer and winter. The diversity of the coccolithophore community was relatively constant, except for a decrease in spring 1990, reflecting the increasing dominance of *Emiliana huxleyi* (Broerse et al., 2000b). *Calcidiscus leptoporus* abundance within the coccolithophore community was limited at NABE-34 (~2%), but more important at NABE-48, where it reaches 7% of the coccolith flux.

## 2.2. NW Atlantic (H-S)

The temperature variations off Bermuda are similar to those at the stations of the NE Atlantic, with overall slightly warmer conditions and more oligotrophic conditions. Nutrient availability is low throughout the year, but seasonal variations are nevertheless important. The winter period is characterised by convective mixing followed by a summer thermal stratification building up from April to August and subsequently eroding during autumn (Michaels and Knap, 1996). Nutrient supply to the euphotic zone is strongly dependent on the depth of mixing with highest values during winter and lowest values during the summer stratified period. Therefore, if the level of chloro-

phyll content is low throughout the year, an increase can be recognised in winter associated with the increase of nutrient availability, leading to a situation of winter-bloom.

This pattern can be recognised in the variations of the coccolithophore assemblages off Bermuda, which have been studied in detail for the 1991–1994 period (Haidar and Thierstein, 2001). Highest coccolithophore abundances were found during the winter-spring period, associated with a low diversity of the coccolithophore community dominated by *Emiliana huxleyi*. Summer and fall periods were characterised by somewhat lower abundances and a more diverse coccolithophore assemblage. Average contribution of *Calcidiscus leptoporus* to the coccolithophore assemblage was very low (<1%).

## 2.3. Arabian Sea (MST-9)

The Arabian Sea is strongly influenced by wind-driven seasonal reversals of surface currents. The SW monsoon starts in spring (April or beginning of May), when southerly winds develop along the Somali coast, and intensifies until mid-summer (Fisher et al., 1996). It induces the Somali Current to flow northward and generates upwelling along the coast of NE Africa and Arabia. During winter (December to February) the NE monsoon develops because of moderate northeasterly winds causing the Somali Current to flow to the southeast. No active upwelling occurs, but the SSTs decrease due to winter cooling. The inter-monsoon periods occur generally during autumn and early spring (Schott et al., 1990). During these periods of low winds the water column is

stratified and nutrient concentrations are low, only sustaining a low primary productivity (Smith and Codispoti, 1980). However, these nutrient concentrations are still higher than the ones encountered at the other sites.

Based on SST, wind velocity, nutrient concentration, and  $\delta^{15}\text{N}$  of biogenic fluxes in the sediment trap samples, six phases have been identified at the MST-9 mooring site (Broerse et al., 2000a). These phases represent the first inter-monsoon, the onset, peak and decline of the SW monsoon, the second inter-monsoon, and the NE monsoon.

Considering the dynamics of the coccolithophore community, high coccolith and coccosphere fluxes were detected during both monsoons (Broerse et al., 2000a). Maximum upwelling coincided with low diversity, while stable oceanographic conditions during the inter-monsoon period were reflected by a high diversity, indicating that none of the coccolithophore species was dominant. *Calcidiscus leptoporus* relative abundances are low (< 1%).

### 3. Materials and method

#### 3.1. Samples

##### 3.1.1. NABE-34 and NABE-48 (NE Atlantic)

Sediment trap moorings were deployed at two sites in the NE Atlantic (Fig. 1, Table 1) as part of the JGOFS North Atlantic Bloom Experiment (NABE) (Ducklow, 1989). Depth of sea floor at NABE-34 and NABE-48 is approximately 5100 and 4400 m, respectively. The mooring designs used were automated PARFLUX Mark 7G-13 time series sediment traps (Honjo and Doherty, 1988), deployed at approximately 1 km water depth. Deployment was from 3 April 1989 to 16 April 1990, with a hiatus from 26 September to 16 October 1989 (Appendix B-I and B-II). Generally the sampling interval for all deployments was 14 days. Due to clogging by an Argentine fish, one NABE-34 sample (#3) could not be used for absolute quantification but only for relative abundances. A detailed description of the mooring design and results from all individual samples are given in Honjo and Manganini (1992).

For the coccolith analyses, aliquots of each sample were wet-splitting using a rotary precision wet-splitter. The rinsing solution used for splitting and sieving was prepared from a 2% solution of formaldehyde in prefiltered sea water, which was buffered by adding sodium tetraborate until pH 8.6 was obtained. The aliquots were then wet-sieved over a 32- $\mu\text{m}$  mesh. Faecal pellets and aggregates > 32  $\mu\text{m}$  which remained on the sieve were disintegrated using a small soft brush and sieved again. The < 32- $\mu\text{m}$  fraction was filtered over a 0.45- $\mu\text{m}$  HA Millipore filter (cellulose acetate; 47 mm diameter) and rinsed with buffered distilled water to prevent crystallisation of salt. The filters were dried at 40°C and stored in petri dishes.

##### 3.1.2. MST-9 (Arabian Sea)

Sediment traps were deployed as part of the NIOP-JGOFS effort in the NW Indian Ocean off Somalia to intercept particle fluxes throughout both the SW and NE monsoons and the inter-monsoon period for a period of 9 months (7 June 1992 to 21 February 1993). No samples were collected during the spring inter-monsoon which is expected to be the most oligotrophic period (Rixen et al., 1996). The array MST-9 was moored in the deep Somali Basin at 10°43'N 53°34'E with a bottom depth of 4047 m. From the traps at 1052 m depth *Calcidiscus leptoporus* absolute abundances were determined and from the trap at 3050 m depth *C. leptoporus* morphometrical parameters were measured. The traps used were Technicap PPS-5 with a baffled collecting area of 1.0 m<sup>2</sup> and 24 collecting cups. A detailed description of the mooring design, deployment and analytical methods, as well as the major mass fluxes are given in Brummer (1995). Sample cups were poisoned with HgCl<sub>2</sub> and buffered to pH 8.8 with Na<sub>2</sub>B<sub>4</sub>O<sub>7</sub> prior to deployment. Sampling intervals were 7 or 14 days (Appendix B-III).

Samples were wet-splitting using a Folsom and a PARFLUX Wet Sample Divider (WSD-10) until an appropriate aliquot for coccolithophore analysis was obtained. Each aliquot was then sieved, prepared, and samples from the 3050-m depth were used for morphometric analysis.

### 3.1.3. Hydrostation-S (NW Atlantic)

A comparison of the results derived from the sediment traps NABE-34, NABE-48 and MST-9 was performed with a plankton time series off Bermuda, where seasonal variations of *Calcidiscus leptoporus* have previously been studied (Renaud and Klaas, 2001). Water samples were collected by the BATS group of the Bermuda Biological Station for Research Inc. at the time series Hydrostation-S in the Sargasso Sea, near Bermuda (Fig. 1, Table 1). The samples considered were taken through the year 1991 at roughly monthly intervals. Four-litre water samples were filtered onto 0.45- $\mu\text{m}$  MF-Millipore<sup>®</sup> membrane filters. Samples were analysed at 1 and 10 m and whenever available at 25, 50, 75, 100, 150 and 200 m water depth (Appendix B-IV). Below 200 m, average coccolithophore standing stock has been reported to be very low (Haidar and Thierstein, 2001) and therefore, no deeper samples were considered.

### 3.2. Definition of the morphotypes

*Calcidiscus leptoporus* is characterised by large morphological variability. This can be accounted for by splitting the species into morphotypes. Several such attempts have been made, basing the morphotypes definition on various criteria but usually agreeing in defining three extant morphotypes. One approach was qualitative, defining the morphotypes on shape of the suture and central area (Kleijne, 1993); the other was quantitative and based on definition of size boundaries between the coccolith diameter of the morphotypes (Knappertsbusch et al., 1997). Although such a quantitative approach may appear more robust, further analysis of size distribution in plankton samples showed that this definition based on size boundaries unsatisfactorily fits the data (Renaud and Klaas, 2001), because coccolith diameter was characterised by a polymodal frequency distribution, indicating the mixing of subpopulations with size overlap. We adopted here a definition of morphotypes based both on morphological criteria and on size, following the scheme of Baumann and Sprengel (2000). Morphotypes are defined here as follows

(Fig. 2): (Ti) coccoliths with smoothed, angular suture lines which can be traced to a conical central pore, in general of intermediate size ( $\sim 5 \mu\text{m} < \text{coccolith diameter} < \sim 8.5 \mu\text{m}$ ). (Tl) Coccoliths with curved suture lines, which become obscured towards a diffused central pore, of large size. (Ts) Coccoliths with angular and serrated suture lines that can be traced into the deep conical central pore, of small size (coccolith diameter  $< \sim 5 \mu\text{m}$ ).

### 3.3. Morphometric measurements

For each sample from NABE-34, NABE-48 and MST-9, a radial piece of filter was cut and mounted on a scanning electron microscope (SEM) stub, and was scanned manually using a SEM until approximately 50 loose coccoliths of *Calcidiscus leptoporus* were found (NABE-34:  $52 \pm 2$ ; NABE-48:  $53 \pm 2$ ; MST-9:  $52 \pm 3$ ). Images of *C. leptoporus* coccoliths were digitally recorded at a magnification of  $6000\times$ . For each coccolith, the diameter of the distal shield and the number of radial elements in the distal shield were measured.

At H-S, samples were available from different water depths. For each sample, a radial piece of filter was cut and mounted on a SEM stub, and was entirely scanned manually, looking for all *Calcidiscus leptoporus* coccospheres (Renaud and Klaas, 2001). Images were recorded at a magnification of  $6000\times$  or  $3000\times$ . On each coccosphere, the coccolith diameter and the number of elements of three coccoliths were measured. The diameter and number of elements were also measured on some additional loose coccoliths to increase sample size in case of samples with few or no *C. leptoporus* coccospheres. For each date of sampling, measurements of the samples from different water depths were pooled together, providing measurements on  $110 \pm 74$  coccoliths per date.

In all cases, measurements were achieved using a Phillips XL30 SEM. The SEM calibration was successfully checked using calibrated microbeads of  $4 \mu\text{m}$  (Bollmann et al., 1999), since measurement of 78 microbeads led to a mean diameter value of  $4.0 \pm 0.03 \mu\text{m}$ .

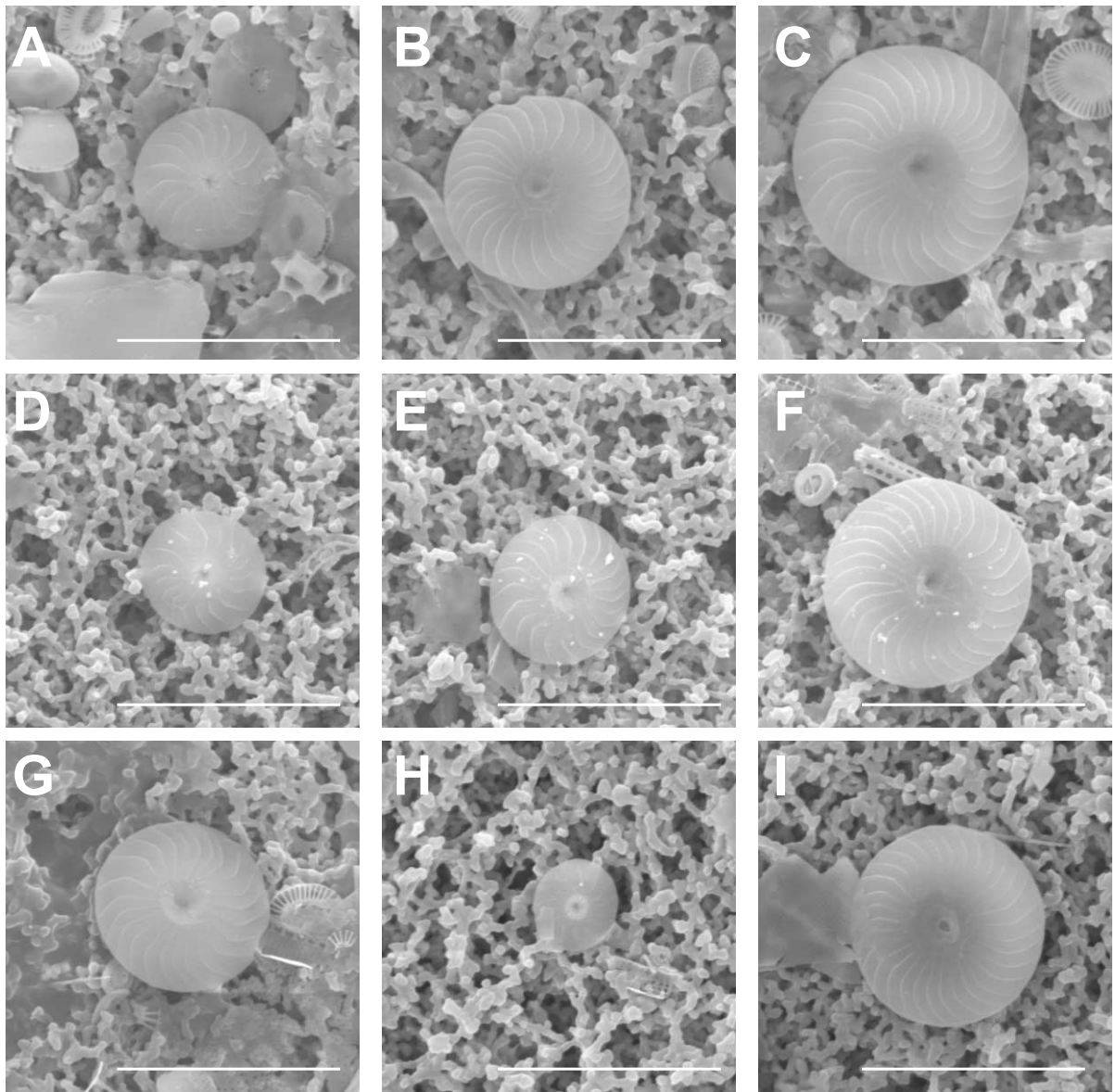


Fig. 2. Coccoliths exemplifying the morphological variability of *Calcidiscus leptoporus*. (A–C) NABE-48, 26 March 1990. (D–F) NABE-34, 27 June 1989. (G) NABE-34, 15 January 1990. (H, I) MST-9, 19 July 1992. Morphotypes: ‘intermediate’ A, D, E, G; ‘large’ B, C, F, I; ‘small’ H. Scale bar 10  $\mu\text{m}$ .

### 3.4. Abundance estimates

Absolute abundances at NABE-34, NABE-48 and MST-9 have been derived from Broerse (2000). For counting, a segment of the circular filter was cut and prepared on a microslide. Using

an Olympus polarising microscope, coccoliths were counted along several parallel scans from the border to the centre, considering over 1000 coccoliths in most of the samples. Coccolith counts were converted into fluxes (in coccoliths/ $\text{m}^2/\text{day}$ ), by extrapolating the number of counted

specimens to the entire effective filtration area and total sample, considering duration days and trap aperture area (Broerse, 2000).

In order to compare the abundances at H-S time series with the other observations in sediment traps, coccosphere abundances at H-S (expressed as coccospheres/l; cf. Renaud and Klaas, 2001) were integrated over depth through the whole photic zone (0–250 m) to provide a value expressed as coccospheres/m<sup>2</sup>. The number of coccoliths per coccosphere had been estimated to be 31 for *Calcidiscus leptoporus* (Knappertsbusch, 1993) and the abundances were converted into coccoliths/m<sup>2</sup>. The growth rate of *C. leptoporus* in culture has been estimated as ~0.5 divisions/day (Renaud et al., 2000). The number of coccoliths present at a given time in the water column (coccoliths/m<sup>2</sup>) was multiplied by this division rate to provide an estimate of coccolith flux (coccoliths/m<sup>2</sup>/day) comparable to fluxes in our sediment traps.

Relative abundances of the morphotypes were obtained as percentages within the *Calcidiscus leptoporus* coccoliths measured for morphometric analysis. From these relative abundances, absolute abundances of the morphotypes were calculated, based on the total absolute abundance of *C. leptoporus* in the different time series. Absolute abundances provide a direct estimate of the dynamics of each morphotype, whereas relative abundances result from combined variations of all the morphotypes. However, both absolute and relative abundances have been discussed, because absolute abundances may be biased by changes in sedimentation processes in addition to changes in the primary production (Beaufort and Heussner, 2001).

### 3.5. Environmental parameters

For quantitative comparisons with *Calcidiscus leptoporus* dynamics, environmental parameters were retrieved from global data sets, using the stations closest to our time series locations. Monthly SST data corresponding to the year and month of sampling were retrieved from the Integrated Global Ocean Services System (IGOSS) data set (<http://ingrid.ldeo.columbia.edu/SOURCES/IGOSS/>;

Reynolds and Smith, 1994). Seasonal values of nitrate concentration and chlorophyll amount at sea-surface were retrieved from the World Ocean Atlas 98 (<http://ingrid.ldeo.columbia.edu/SOURCES/NOAA/.NODC/WOA98>; Conkright et al., 1998). Monthly values of the mixed layer depth were retrieved from the World Ocean Atlas 1994 (<http://ingrid.ldeo.columbia.edu/SOURCES/LEVITUS94>; Levitus et al., 1994).

These data were interpolated to get values corresponding to the mid-date of each sampling interval. For comparison with morphological parameters of *Calcidiscus leptoporus* at MST-9, derived from the sediment trap at 3050 m depth, a time-lag of 20 days was taken into account between the sea-surface signal and the signal obtained at 3050 m (Ziveri et al., 2000).

The advantage of using these data sets is to provide homogeneous environmental data for all the locations. A drawback is that the comparison between *Calcidiscus leptoporus* variations and environmental conditions is therefore limited since we have to rely on global average data sets instead of in situ values. This may be especially important at MST-9, where hydrography changes locally and very rapidly, due to the passage of gyres. These hydrographical changes are reflected in the abundances of species, but hardly in the average monthly SST used here for comparison. However, *C. leptoporus* is not a species that seems to respond rapidly to the passage of the gyres, unlike *Emiliania huxleyi* (Broerse et al., 2000a), and the comparisons performed should still provide insight into the relationship of *C. leptoporus* dynamics with environmental variations. Additionally, the use at MST-9 of the 3050-m-depth series should provide samples where local signals have been buffered by lateral transport of material from surrounding environments.

### 3.6. Statistics

Different variables were considered in order to characterise the seasonal dynamics of *Calcidiscus leptoporus*: absolute and relative abundances of the morphotypes, and morphological parameters,

Table 2

Linear regression between coccolith diameter and number of elements, for all the specimens of a station (Tot) and the three morphotypes separately (i, l, s) ( $r$ : coefficient of correlation;  $P$ : probability;  $a$ : slope of the regression)

	Tot				i				l				s			
	$r$	$P$	$a$	$\pm$	$r$	$P$	$a$	$\pm$	$r$	$P$	$a$	$\pm$	$r$	$P$	$a$	$\pm$
NABE-48	0.672	0.000	2.985	0.059	0.500	0.000	2.083	0.071	0.654	0.000	2.185	0.082	0.677	0.002	4.432	1.206
NABE-34	0.838	0.000	2.814	0.054	0.679	0.000	2.115	0.077	0.704	0.000	1.858	0.128	0.672	0.000	3.665	0.808
H-S 91	0.864	0.000	2.691	0.048	0.591	0.000	1.989	0.093	0.735	0.000	2.054	0.128				
MST-9	0.955	0.000	2.931	0.035	0.290	0.216		0.642	0.000	1.818	0.101	0.681	0.000	3.856	0.308	

based on measurements of the coccoliths diameter and number of elements.

In order to provide morphological indicators independent of the morphotype definition, and characteristic of the entire *Calcidiscus leptoporus* assemblage, for each sample the average coccolith diameter and average number of elements, as well as the 75-percentile (value corresponding to 75% of the distribution) and 25-percentile (25% of the distribution) were estimated. Intra-morphotype morphological variations were estimated by calculating the average coccolith diameter and number of elements per morphotype and per sample. The relationship between coccolith diameter and number of elements within the total *C. leptoporus* assemblage, and within each morphotype, was studied using simple linear regression. The amount of morphological differences within each time series was tested using univariate analysis of variance (ANOVA).

The relationship of the different characteristics of *Calcidiscus leptoporus* with environmental factors (temperature, nitrate, mixed layer depth and chlorophyll content) was investigated using linear regression, as a first approximation to detect any co-variation among parameters.

## 4. Results

### 4.1. Distribution of the morphological parameters

All the morphotypes are characterised by a lin-

ear relationship between coccolith diameter and number of elements, which as a consequence also holds true for the total assemblage (Table 2). However, in Ts, the number of elements increases faster with coccolith diameter than in the other morphotypes. The bivariate plots between coccolith diameter and number of elements (Fig. 3A) shows the expected different size ranges of the three morphotypes, although overlap exists between the morphotypes distribution.

The relative abundance of the morphotypes varies at the different sites (Fig. 3B). The subtropical sites (NABE-34 and H-S) are characterised by a large dominance of Ti. The temperate site (NABE-48) seems to have a more even distribution between Ti and Tl, although Ti is still dominant. Finally, the tropical site (MST-9) exhibits a completely different distribution, being mainly composed of Tl and Ts, with only a minor contribution of Ti.

### 4.2. Seasonal variations in abundances and morphology

For all the four time series, significant seasonal changes were found in absolute and relative abundances, as well as in morphology (Table 3).

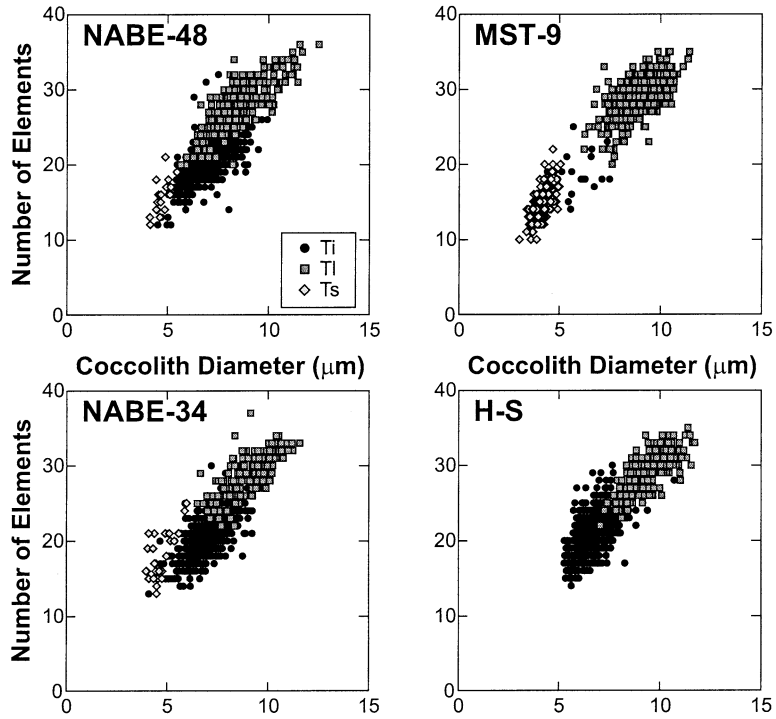
#### 4.2.1. NABE-48, NE Atlantic (Fig. 4)

Absolute abundances of *Calcidiscus leptoporus* show a spring peak, associated with an increase of both morphotypes, Ti and Tl, with a dominance of Tl during the onset of the spring-bloom.

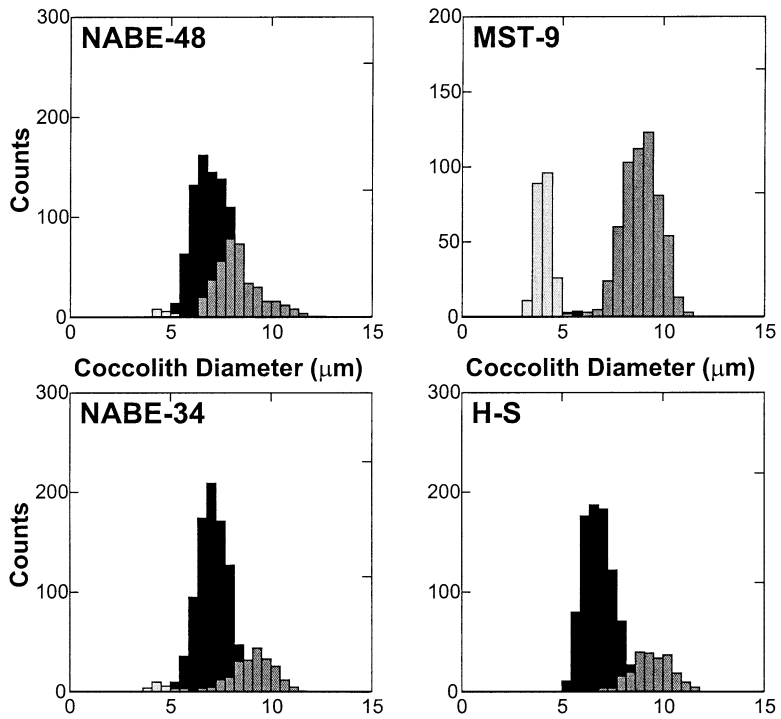
Fig. 3. Distribution of the morphological parameters characteristic of *Calcidiscus leptoporus* in the four sites. (A) Bivariate plot of coccolith diameter ( $\mu\text{m}$ ) vs. number of elements. (B) Frequency histogram of coccolith diameter.



**A**



**B**



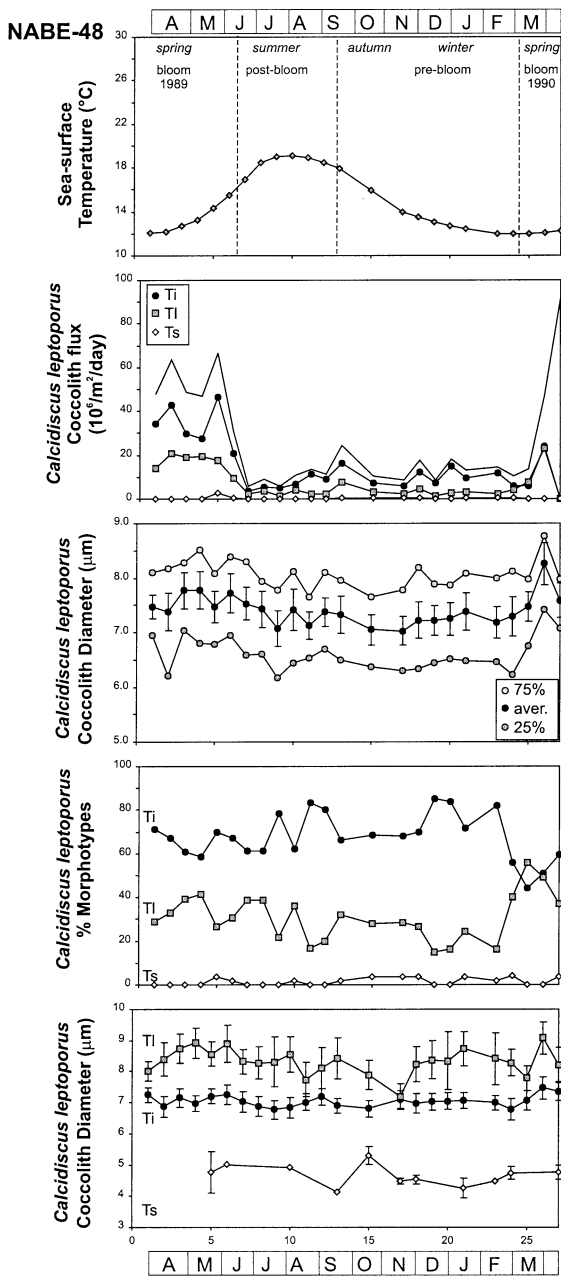


Fig. 4. Environmental and morphological variations of *Calcidiscus leptoporus* at NABE-48. SST (IGOSS data base, Reynolds and Smith, 1994). Absolute abundances, total and three morphotypes (total *C. leptoporus* abundances derived from Broerse, 2000). Seasonal variations in average coccolith diameter of *C. leptoporus* assemblage, relative abundance of the three morphotypes, and variations in average coccolith diameter of the three morphotypes. Error bars: 95% standard error.

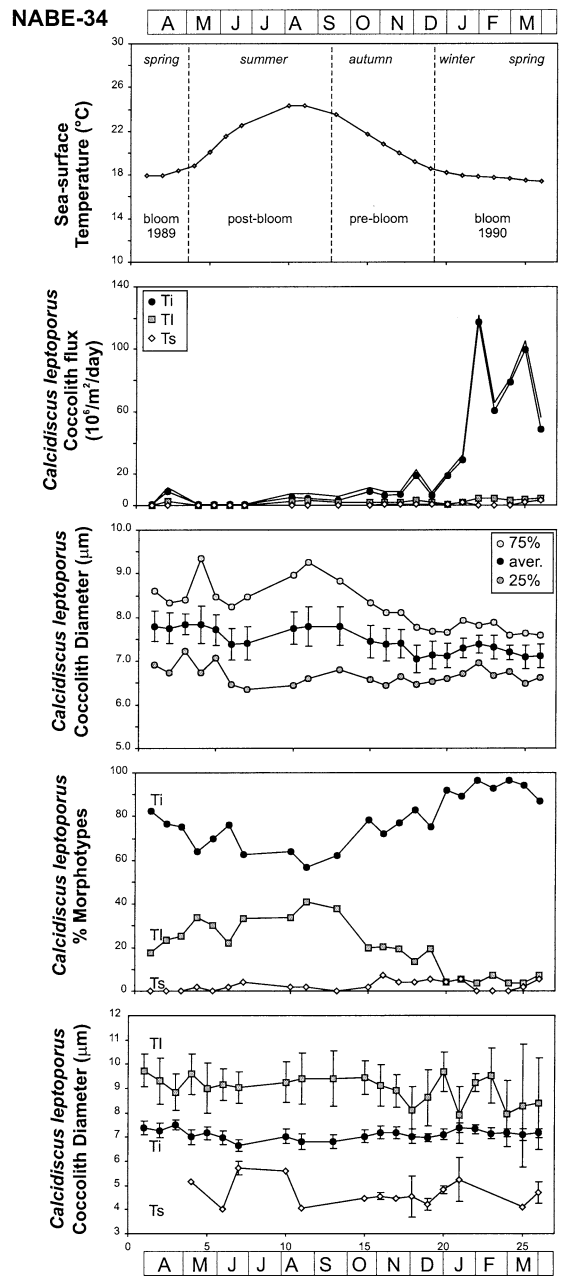


Fig. 5. Environmental and morphological variations of *Calcidiscus leptoporus* at NABE-34. Data: idem Fig. 4.

Changes in relative abundances lead to variation of the average size of the *Calcidiscus leptoporus* assemblage. The spring increase of TI leads to an increasing size of the assemblage, with the larg-

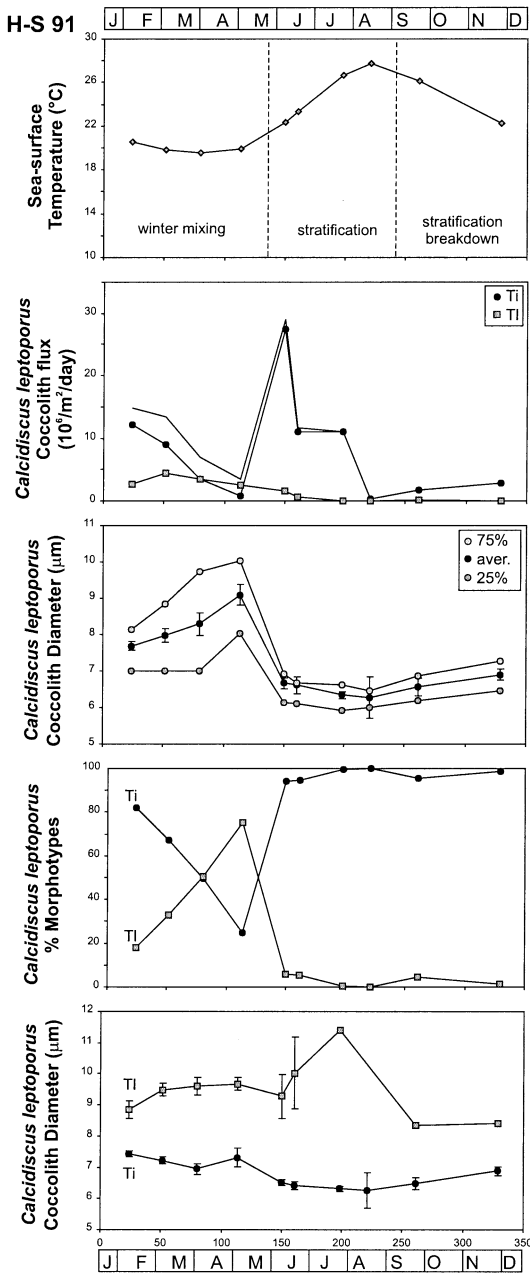


Fig. 6. Environmental and morphological variations of *Calcidiscus leptoporus* at H-S 91 (total *C. leptoporus* abundances derived from Renaud and Klaas, 2001).

est size corresponding to the dominance of Tl in spring 1990. Associated with these variations in the size of the assemblage, intra-morphotype size variations seem to exist. Although of limited im-

portance, they could correspond to an increasing size of Ti during the spring 1990, and to a decreasing size of Tl during the inter-bloom period. Ts occurrence is low and no clear pattern emerges for this morphotype.

4.2.2. NABE-34, NE Atlantic (Fig. 5)

Variations in abundances are important and correspond to a winter-spring increase of absolute abundances of both, Ti and Tl, with a major input of Ti. The increasing proportion of Tl during summer is therefore related to a relative decrease in abundance of Ti, rather than an increasing absolute abundance of Tl. The third morphotype Ts is always very rare. These changes in relative abundance cause significant seasonal variations in average size of *Calcidiscus leptoporus*, with a decrease in size of the assemblage during the spring-bloom, related to the increasing relative abundances of Ti. Additionally, significant intra-morphotype size changes exist for the three morphotypes (Table 3). Ti tends to become larger during the spring-bloom. Tl and Ts variations are more erratic and difficult to interpret, due to small sample size especially for Ts.

4.2.3. H-S 91, NW Atlantic (Fig. 6)

Two peaks of *Calcidiscus leptoporus* abundance can be recognised: one major peak in late spring–beginning of summer, almost exclusively composed of Ti, and a second, less important winter peak, with an increase in both, Ti and Tl. At this plankton station, no specimen of Ts was found.

The average size changes resulting from these dynamics are significant and result in a sharp decrease in average size of the *Calcidiscus leptoporus* assemblage at the onset of the summer water stratification, when Ti becomes the major component of the assemblage. Intra-morphotype variation also exists, with a minor increasing size of Ti in winter and an increasing size of Tl in early summer.

4.2.4. MST-9, Arabian Sea (Fig. 7)

Both monsoon periods are characterised by an increase in *Calcidiscus leptoporus* abundance, although more limited than at the other stations. Unlike NABE-34 and NABE-48, Ti is not the

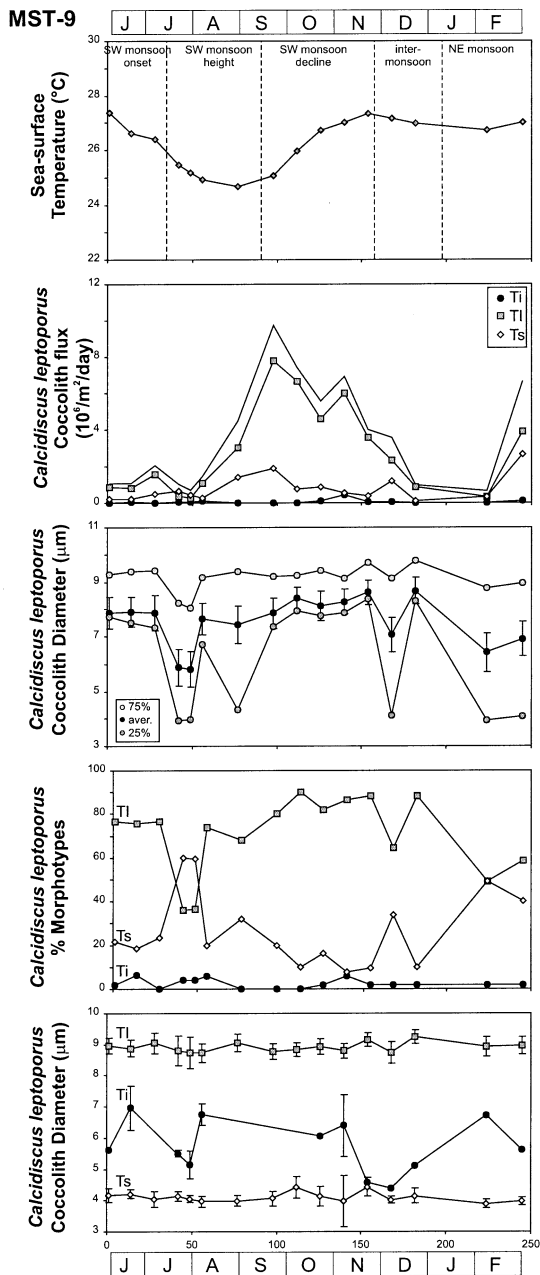


Fig. 7. Environmental and morphological variations of *Calcidiscus leptoporus* at MST-9. Data: idem Fig. 4.

major component of the *C. leptoporus* flux. Tl is dominant in almost all the samples, except at the onset of the SW and NE monsoons, when Ts becomes temporarily more abundant. However,

the absolute abundances reached by Ts in this site are not much higher than those observed in the other sites.

The average size changes resulting from pooling the different morphotypes together are quite different from what is observed at the other sites, with an overall large size of the assemblage and a dramatic decrease in size when Ts becomes dominant. No clear pattern of intra-morphotype size variations emerges in this time series.

#### 4.3. Relationship with environmental parameters

In order to identify the factors underlying the seasonal dynamics of *Calcidiscus leptoporus*, the variables related to abundances and morphology, for the total assemblage and each morphotype separately, have been compared to environmental variables. Regarding the abiotic factors possibly influencing coccolithophore dynamics, SST has been considered, together with nitrate concentration, as a proxy for nutrient content. Additionally, depth of the mixed layer provided an estimate for intensity of water mixing. Among the biotic parameters, chlorophyll content has been considered as indicating the dynamics of the total phytoplankton community. Significant relation with *C. leptoporus* dynamics might be due to direct interaction, e.g. competition for uptake of limiting nutrients, or similar response to environmental variations. Choosing a few parameters is necessarily a simplification of the environmental setting, however, it can be used as a first approach to decipher complex interactions.

##### 4.3.1. Absolute abundances (Fig. 8)

Over the whole range of environmental conditions covered by the four time series, the most obvious relationship is an increase in absolute abundances of the intermediate and large morphotypes with decreasing temperature. A significant positive relationship is also found with the mixed layer depth (Ti:  $P < 0.05$ ; Tl:  $P < 0.001$ ), an expected result since temperature and water mixing are inversely co-varying in most of the settings. Additionally, abundances of Tl increase with increasing nitrate concentrations ( $P < 0.01$ ) and chlorophyll content ( $P < 0.001$ ).

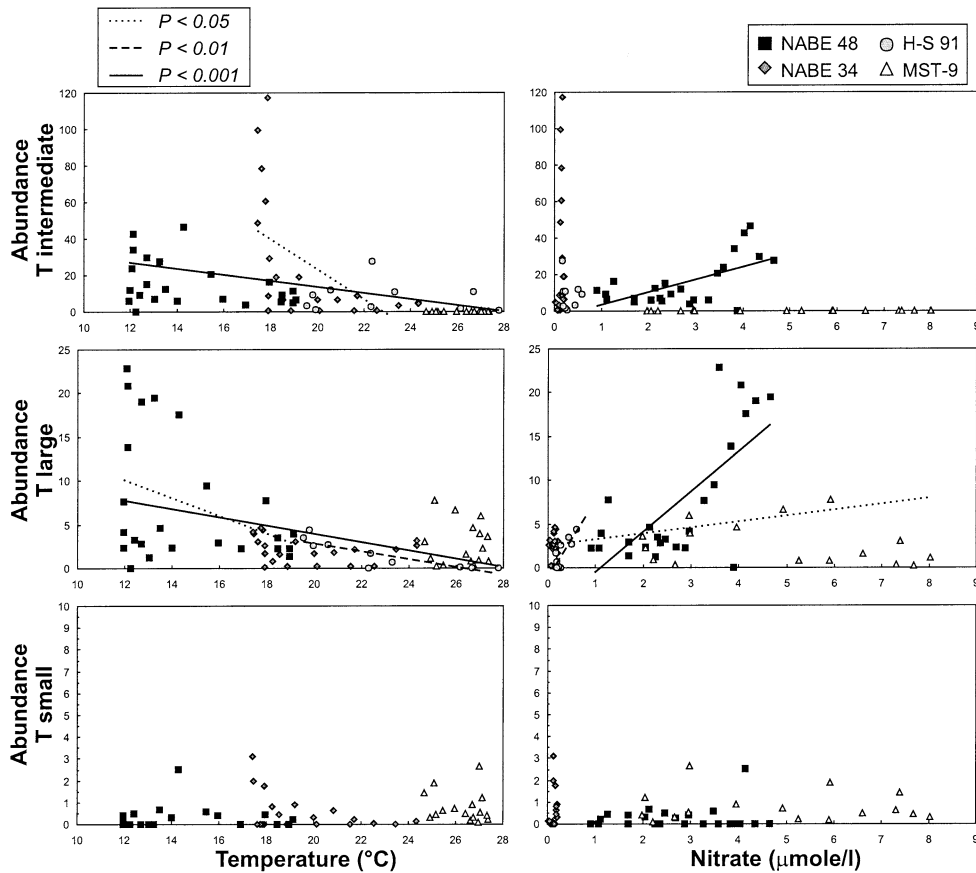


Fig. 8. Variations in absolute abundance of the morphotypes in the four time series as a function of temperature (left) and nitrate content (right), with significant trends.

In many cases, these general relationships cannot be found locally, within the seasonal variation at one time series. However, whenever a significant relationship exists, it is in agreement with the general trend. Abundances of the intermediate morphotype are co-varying with nitrate and chlorophyll at NABE-48 and with temperature and mixed layer depth at NABE-34; no significant relationship can be recognised at the warmer stations (H-S 91 and MST-9). Abundances of the large morphotype display significant relationships ( $P < 0.05$ ) with environmental parameters at all the stations (NABE-48: SST, nitrate, chlorophyll, mixed layer depth; NABE-34: SST, nitrate, and chlorophyll; H-S 91: SST, nitrate, chlorophyll, mixed layer depth; MST-9: mixed layer depth).

No clear pattern emerges for  $T_s$ , neither locally or globally. Its absolute abundances appear to be constantly low throughout the environmental gradients.

#### 4.3.2. Relative abundances (Fig. 9)

Patterns of relative abundances are more complex, because they are the result of the differential success of the morphotypes through the environmental gradients. The relative contribution of the intermediate morphotype decreases with increasing temperature, nitrate concentration, and water stratification ( $P < 0.05$ ). As a counterpart, the large morphotype increases in relative abundance with increasing temperature and nitrate content. Relative abundances of the

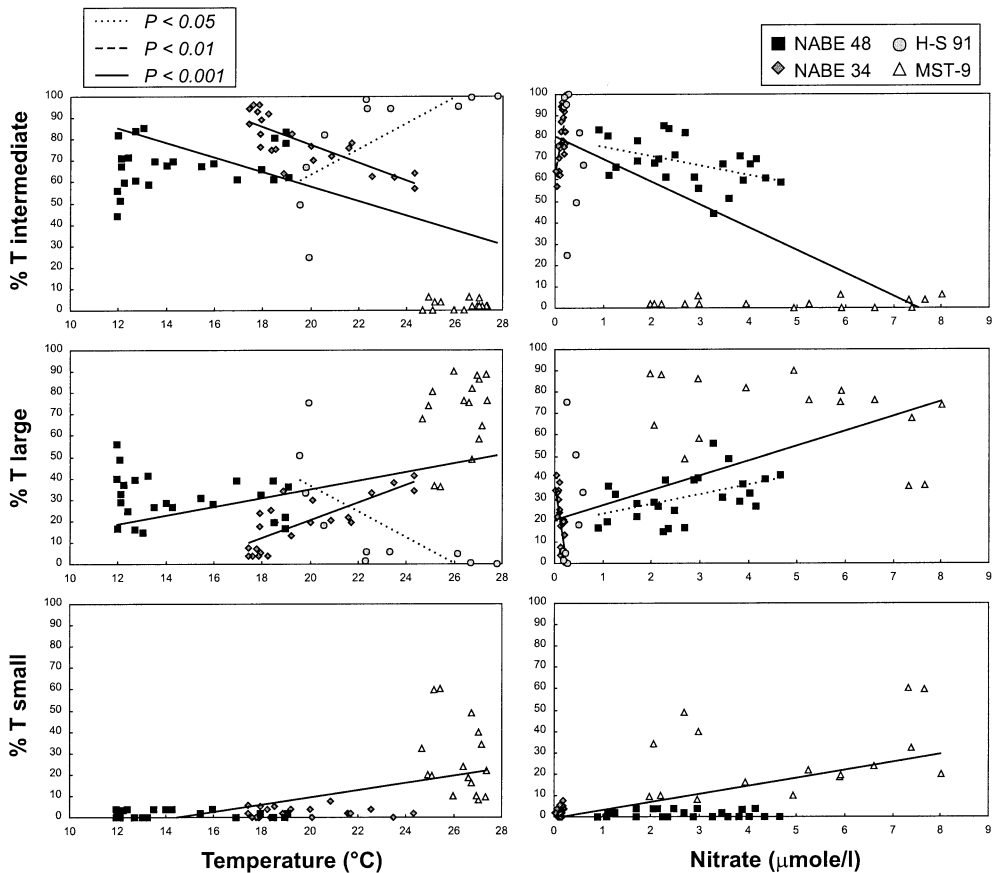


Fig. 9. Variations in relative abundance of the morphotypes in the four time series as a function of temperature (left) and nitrate content (right), with significant trends.

small morphotype increase when temperature, nitrate content and stratification increase. The relationships are reverse compared to those found with the intermediate morphotype; it underlines that variations in relative abundances of Ts are rather the result of varying contribution of the other morphotypes, than of varying production of Ts itself.

Differently of what is observed with absolute abundances, patterns observed locally can be reversed compared with the general trend.

#### 4.3.3. Morphological variations (Fig. 10)

The morphological parameters of the total *Calcidiscus leptoporus* assemblage reflect the variations in relative abundances of the morphotypes,

and therefore provide a complex pattern. Over the whole environmental gradient, no relationship of the average diameter or number of elements can be found with any environmental parameters, although locally some relationship may emerge. The diameter 75-percentile co-varies with temperature and nitrate ( $P < 0.05$ ), because an increase of the upper size range of the distribution corresponds to an increase in proportion of the large morphotype.

The three morphotypes display significant size variability (Table 3). The clearest pattern emerges for Ti. A general trend of increasing size is found with decreasing temperature and increasing water mixing ( $P < 0.01$ ), relationships that also hold true locally at NABE-34 and H-S 91. The pattern

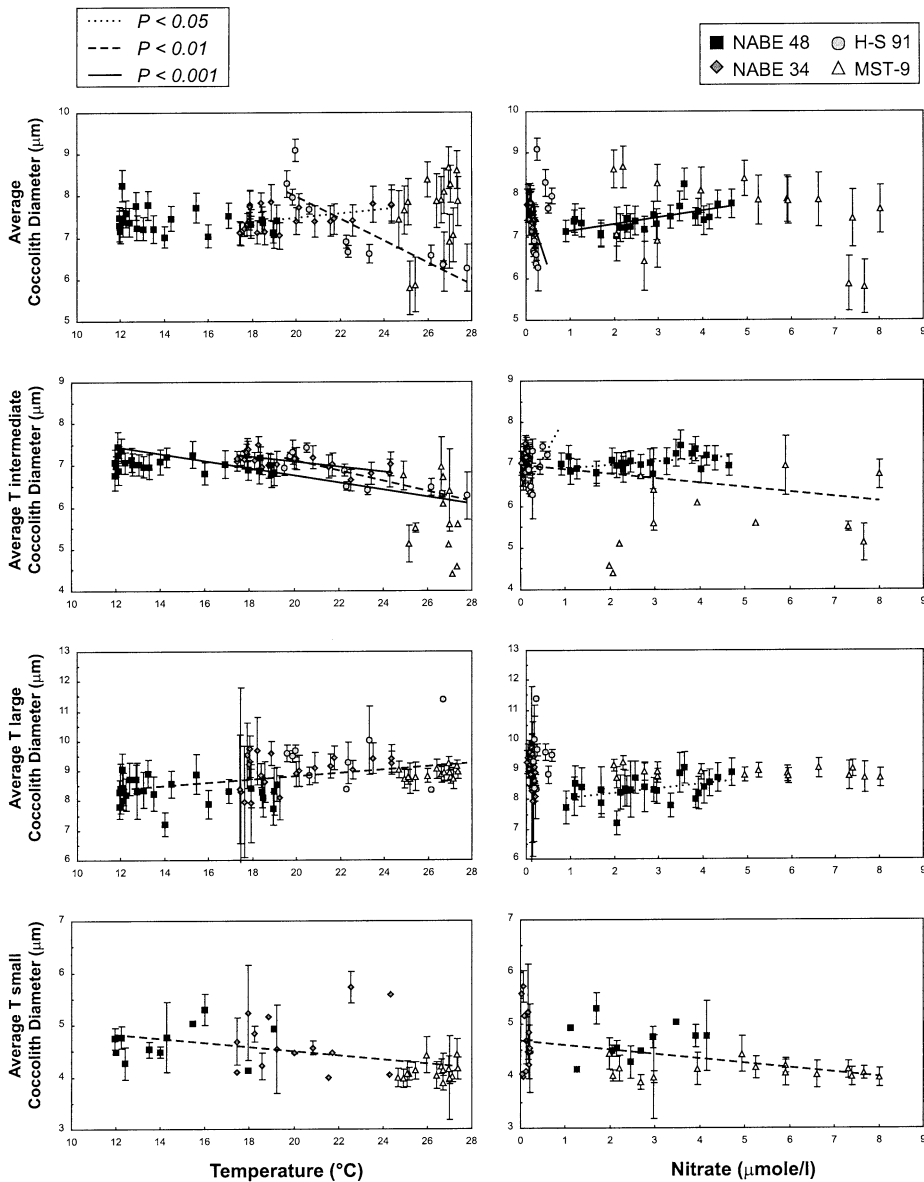


Fig. 10. Variations in average coccolith diameter of the total *Calcidiscus leptoporus* assemblage, and of the different morphotypes, as a function of temperature (left) and nitrate content (right), with significant trends.

is less clear with nutrients, since a size increase with increasing nitrate concentration is found at NABE-48 and H-S 91, although the general trend is reversed. The large morphotype does not show any clear local pattern; however, globally, it seems to increase in size with increasing temperature ( $P < 0.001$ ) and stratification ( $P < 0.05$ ),

and decreasing chlorophyll content ( $P < 0.01$ ). Although the results about the small morphotype should be considered cautiously because of the low number of specimens available at most of the stations, it seems that this morphotype decreases in size with increasing temperature and nutrient content.

Table 3

Probabilities of ANOVA on the coccolith diameter (D) and the number of elements (EL), for each time series; all specimens considered (Tot) or each morphotype separately (i, l, s).

	D				EL			
	Tot	i	l	s	Tot	i	l	s
NABE-48	<b>0.000</b>	0.087	<b>0.000</b>	0.067	<b>0.000</b>	0.083	<b>0.013</b>	0.110
NABE-34	<b>0.000</b>	<b>0.000</b>	<b>0.013</b>	<b>0.034</b>	<b>0.000</b>	0.181	0.065	0.209
H-S 91	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		<b>0.000</b>	<b>0.000</b>	<b>0.008</b>	
MST-9	<b>0.000</b>	<b>0.037</b>	0.257	0.129	<b>0.000</b>	0.354	0.479	0.832

Factors are sampling date. In bold, significant ( $P < 0.05$ ) probabilities.

## 5. Discussion

### 5.1. Temperature-related trend in absolute abundances

*Calcidiscus leptoporus* has a wide distribution area, but it is a typical component of the cold water flora (McIntyre and Bé, 1967), suggesting that its relative success compared to other coccolithophore taxa increases with increasing latitude. This ecological preference explains its increasing contribution to the coccolithophore community from the warm time series MST-9 (0.6%) to the coldest station NABE-48, where it reaches 7% of the assemblage, being the second most important contributor to the total coccoliths fluxes (Broerse, 2000). This trend seems to be attributable to an increase in absolute abundances of both, the intermediate and large morphotypes, with decreasing temperature (Fig. 8), and/or factors co-varying with temperature, such as water mixing. Thus, at a large scale, intermediate and large morphotypes seem to have similar ecological characteristics. However, considering their relationship with other environmental parameters, some discrepancies emerge, since the large morphotype displays additional relationships with nitrate and chlorophyll content. It suggests that both morphotypes have similar variations in abundance according to the temperature-related gradient, but that they could differ along a gradient of productivity, the large morphotype being more opportunistic and associated with productive waters.

No clear pattern emerges regarding the small morphotype, that shows similar, low abundances throughout the environmental gradients. This

suggests that this morphotype could be relatively invariant according to abiotic parameters, but this result is weakened by the scarce data about this morphotype, seldom found in all stations except MST-9.

### 5.2. Relative abundances expressing the differences in ecological preferences

The main feature emerging from the variations in absolute abundances of Ti and Tl is a temperature-related trend. However, other abiotic factors, such as nutrient availability, seem to interfere with this general trend and modulate the success of the different morphotypes along the environmental gradients. Relative abundances are the combined results of the variations in absolute abundance of each morphotypes, and hence are prone to display the differences in ecological preferences, independently of the main temperature-related trend. Ti appears to be relatively better adapted in cold, nutrient-poor waters with important vertical mixing, whereas Tl's relative success increases with increasing temperature and nutrient availability (Fig. 9). The pattern of relative abundance of Ts seems mostly due to the decreasing fitness of the two other morphotypes in warm, nutrient-rich, stratified waters.

These results are corroborated by observations at another time series, in an environmental setting comparable to H-S, where environmental dynamics, linked to seasonal succession, trigger a shift in relative abundance of *Calcidiscus leptoporus* morphotypes (Beaufort and Heussner, 2001), although a different measurement technique limits the possible comparison.



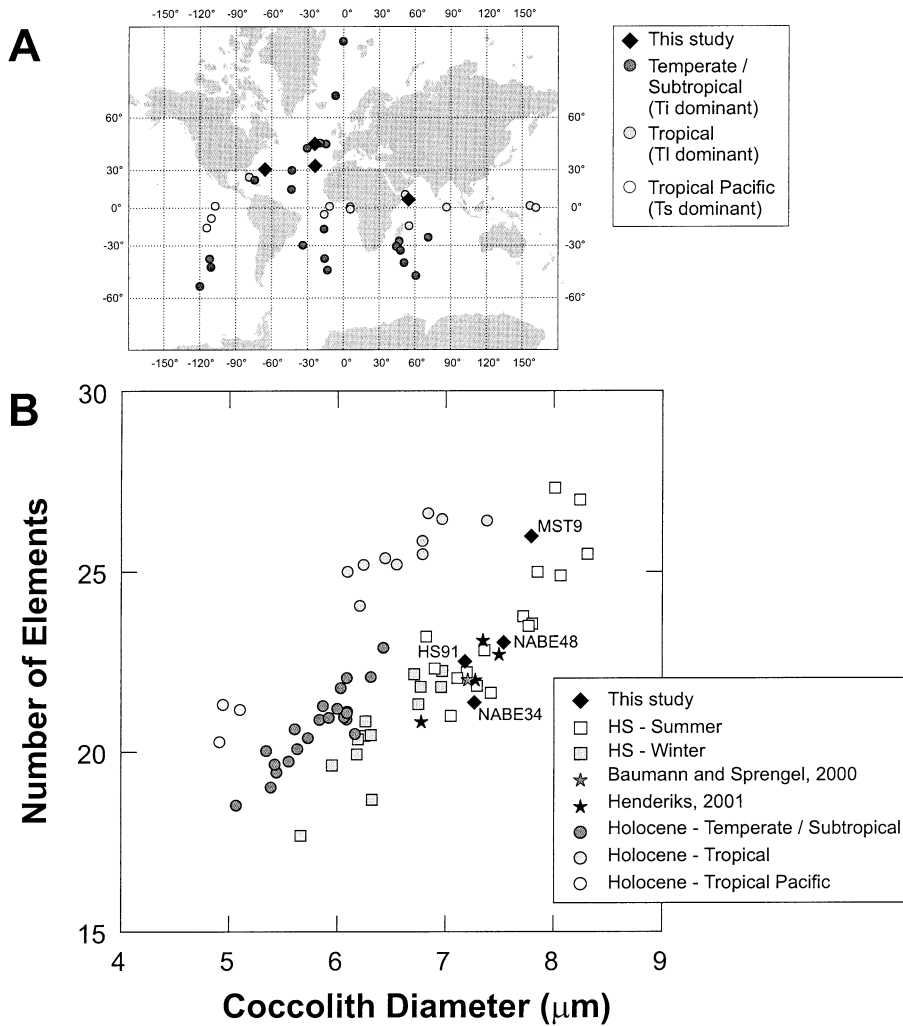


Fig. 11. Comparison of morphological variations of *Calcidiscus leptoporus* in the sediment traps with seasonal variations at H-S (after Renaud and Klaas, 2001), biogeographic variations observed in Holocene sediment samples (after Knappertsbusch et al., 1997), Holocene NE Atlantic samples (Hendericks, 2001) and NE Atlantic sediment traps sample (Baumann and Sprengel, 2000).

### 5.3. Comparison with biogeographic patterns

The results derived from seasonal dynamics have to be confronted to comparable data available on *Calcidiscus leptoporus* distribution. There are few data sets directly comparable to our results, since usually abundances are given for *C. leptoporus* as a whole. However, the most comprehensive data set on *C. leptoporus* biogeography, based on a global study of Holocene sediment samples, considered the average mor-

phological values of each assemblage (Knappertsbusch et al., 1997). A similar comparison is possible with the detailed dynamics at H-S (Renaud and Klaas, 2001). Additionally, a few mean values are available in the literature, from a sediment trap series off Canary Islands (Baumann and Sprengel, 2000), and Holocene sediments from NE Atlantic (Hendericks, 2001). For comparison with these data sets, the measurements at each of our time series were summed to obtain an approximation of the annual average diameter and num-

ber of elements at this location. This comparison (Fig. 11) shows a shift of the linear relationship of coccolith diameter vs. number of elements between samples from Knappertsbusch et al. (1997) and the other samples, suggesting a problem of SEM calibration of around 10%. A qualitative comparison of the different data sets is nevertheless possible.

Comparing the values obtained for the different data sets shows a close correspondence between average morphological parameters of the *Calcidiscus leptoporus* assemblage and the composition in the different morphotypes. MST-9 plots with the winter H-S assemblages, and this corresponds in both cases to a dominance of T1. NABE-48 also rather corresponds to the winter H-S samples, because of the important relative contribution of T1 all the year round. Finally, NABE-34 and H-S 91 annual averages, corresponding to the integration of the seasonal production on a year, appear as intermediate between summer and winter H-S assemblages.

Based on this correspondence between the average morphological characteristics of the assemblage and its morphotype composition, the biogeographic pattern observed within the Holocene data set can be further considered. Three distinct types of assemblages can be recognised: temperate-subtropical, tropical and tropical Pacific (Knappertsbusch et al., 1997; Fig. 9). Temperate-subtropical assemblages are characterised by intermediate morphological values similar to NABE-48, NABE-34, H-S 91, and NE Atlantic samples from the literature, due to a dominance of T1 in these assemblages (Baumann and Sprenkel, 2000; Hendericks, 2001). The tropical assemblages, like MST-9, have large mean values corresponding to T1's dominance. Finally, the very small coccolith diameter of the tropical Pacific group suggests a high contribution of T3. A good agreement therefore exists between our interpretation about the relative ecological preferences among *Calcidiscus leptoporus* assemblage and the global Holocene data set of Knappertsbusch et al. (1997). T1 dominates *C. leptoporus* assemblage at low/intermediate temperatures whereas T3 dominates over T1 in a range of intermediate/high temperatures. The atypical morphological features

of the tropical Pacific Holocene group could be due to peculiar environmental conditions in this area, characterised both by high temperatures and high nutrient contents (cf. World Ocean Atlas 98 (Conkright et al., 1998)), conditions that could be unfavourable to both T1 and T3, leading to a relative dominance of T3.

#### 5.4. Three morphotypes with different ecological preferences and seasonal dynamics

Our results suggest that at a large scale, both well documented T1 and T3 morphotypes show preferences for cold waters. However, considering their relative abundances within the *Calcidiscus leptoporus* assemblage reveals a difference in their ecological preferences, T3 being a more opportunistic species whose dynamics follow the dynamics of the total flora.

These results argue for considering the three morphotypes as genetically different entities within *Calcidiscus leptoporus*, that might correspond to a complex of species. This view is supported by new observations on associations between heterococcoliths of *C. leptoporus* and holococcoliths. Such associations have been interpreted to represent transition from the haploid (holococcolithophore) to diploid (heterococcolithophore) life-cycle phase (Billard, 1994). The association between heterococcoliths of *C. leptoporus* and holococcoliths of *Crystallolithus rigidus* has been reported several times (Kleijne, 1991; Cortés, 2000; Renaud and Klaas, 2001); in all cases, this association involved the intermediate morphotype. However, a new association has been described between *Syracolithus quadriperforatus* and the large morphotype of *C. leptoporus* (Geisen et al., 2000). This difference in the holococcolithophore associated with the T1 and T3 morphotypes supports the hypothesis of discrete genetic entities with independent life-cycles and different ecological preferences.

#### 5.5. Intra-morphotype size variations

Average morphological parameters of *Calcidiscus leptoporus* assemblage can provide insight into the relative contribution of each morphotype.

Hence, based on the observations about their respective ecological preferences, some information about the palaeoenvironmental context of growth of the assemblage might be deduced.

Further information might be gathered, based on intra-morphotypic size variations. Especially, the intermediate morphotype displays a consistent trend of decreasing size with increasing temperature (Fig. 10), valid even at a local scale (NABE-34 and H-S 91). The large specimen may also display an intra-morphotypic trend of size increase with increasing temperature. Gathering more data about these patterns of intra-morphotypic size variations is necessary before any further interpretation; they might provide useful palaeoenvironmental information to be cross-checked with results based on abundances and average size of the total *Calcidiscus leptoporus* assemblage.

## 6. Conclusions

(1) Seasonal variations in abundances and average morphological parameters of *Calcidiscus leptoporus* have been recognised in the four time series considered. However, the geographical pattern governing this seasonality is complex.

(2) *Calcidiscus leptoporus* assemblages have been decomposed into three morphotypes characterised by different morphologies and size distributions: intermediate Ti, large Tl, and small Ts. Ti and Tl display comparable seasonal patterns in absolute abundances; however, the variations in their relative abundances within *C. leptoporus* assemblage suggest that they could have slightly different ecological preferences.

(3) Based on relative abundances, it can be suggested that among *Calcidiscus leptoporus* morphotypes, Ti prefers low temperature and nitrate content, whereas Tl seems to have more opportunistic dynamics, increasing its relative dominance over the other morphotypes with increasing temperature and nutrients availability, in more productive environments. Data about Ts are scarce, but suggest that variations in its relative

abundance are rather the result of varying contributions of Ti and Tl than of variations in Ts fluxes.

(4) Average morphological parameters of the *Calcidiscus leptoporus* assemblage can provide insight into the morphotype composition. A comparison with an existing Holocene biogeographic data set is therefore possible. The temperate–subtropical samples are dominated by Ti, favoured at low–intermediate temperatures, tropical assemblages by Tl, in a range of intermediate–high temperatures, and tropical Pacific samples by Ts, possibly because of a particular environmental situation characterised by high temperature and high nutrients content, that might be unfavourable to the other morphotypes.

(5) Intra-morphotype morphological variations exist for all three morphotypes. They can be related to environmental changes, especially in the case of Ti showing a trend of decreasing size with increasing temperature.

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## Appendix A. Species list

- Order Coccolithophorales Schiller, 1926
- Calcidiscus leptoporus* (Murray and Blackman, 1898) Loebich and Tappan, 1978
- Crystallolithus rigidus* (Gaardner, in Heimdal and Gaardner, 1980) Norris, 1985
- Emiliana huxleyi* (Lohmann, 1902) Hay and Mohler, 1967
- Syracolithus quadriperforatus* (Kamptner, 1937) Gaardner, 1962

**Appendix B-I. NABE-48**

Sample	Code (day)	Cum (day)	Nb			D				EL				
			Tot	i	l	s	aver	i	l	s	aver	i	l	s
06-Apr-89	1	1	52	37	15	0	7.47	7.25	8.01	–	22.37	20.49	27.00	–
15-Apr-89	2	10	55	37	18	0	7.38	6.87	8.40	–	22.30	19.44	28.19	–
29-Apr-89	3	24	51	31	20	0	7.77	7.15	8.74	–	23.74	20.94	28.32	–
13-May-89	4	38	58	34	24	0	7.78	6.97	8.91	–	23.77	20.50	28.82	–
29-May-89	5	53	53	37	14	2	7.47	7.20	8.56	4.77	22.86	21.26	27.71	17.00
13-Jun-89	6	69	52	35	16	1	7.72	7.26	8.90	5.03	23.63	21.34	29.00	18.00
27-Jun-89	7	83	54	33	21	0	7.53	7.03	8.32	–	23.81	21.00	28.24	–
11-Jul-89	8	97	54	33	21	0	7.42	6.88	8.28	–	23.38	20.97	27.05	–
25-Jul-89	9	111	51	40	11	0	7.07	6.78	8.31	–	21.67	19.90	28.60	–
08-Aug-89	10	125	50	31	18	1	7.41	6.83	8.55	4.92	22.51	20.03	28.00	17.00
22-Aug-89	11	139	54	45	9	0	7.13	7.01	7.74	–	21.46	20.42	26.67	–
05-Sept-89	12	153	51	41	10	0	7.37	7.19	8.11	–	22.29	20.95	27.80	–
19-Sept-89	13	167	53	35	17	1	7.33	6.89	8.42	4.13	22.38	20.29	27.63	12.00
23-Oct-89	15	201	54	37	15	2	7.05	6.80	7.88	5.30	21.87	20.05	26.87	18.00
20-Nov-89	17	229	53	36	15	2	7.02	7.09	7.21	4.48	21.92	21.22	24.53	15.00
04-Dec-89	18	243	53	37	14	2	7.22	6.97	8.24	4.53	22.13	20.89	27.00	13.50
18-Dec-89	19	257	54	46	8	0	7.22	7.02	8.37	–	21.63	20.61	27.25	–
01-Jan-90	20	271	50	42	8	0	7.24	7.04	8.34	–	22.24	21.12	28.13	–
15-Jan-90	21	285	53	38	13	2	7.37	7.07	8.73	4.27	22.48	20.86	28.46	13.50
12-Feb-90	23	313	55	45	9	1	7.18	6.99	8.41	4.48	21.75	20.69	27.78	15.00
26-Feb-90	24	327	50	28	20	2	7.29	6.77	8.28	4.75	23.20	20.61	27.70	14.50
12-Mar-90	25	341	50	22	28	0	7.47	7.06	7.79	–	23.63	20.36	26.30	–
26-Mar-90	26	355	51	26	25	0	8.25	7.46	9.08	–	24.86	21.15	28.88	–
09-Apr-90	27	369	57	34	21	2	7.58	7.36	8.21	4.77	23.52	21.70	26.86	18.50

Nb: number of specimens per sample. D: diameter. EL: number of elements. aver: average of the total *C. leptopus* assemblage. Morphotypes: i, l, s.

**Appendix B-II. NABE-34**

Sample	Code (day)	Cum (day)	Nb			D				EL				
			Tot	i	l	s	aver	i	l	s	aver	i	l	s
06-Apr-89	1	1	51	42	9	0	7.80	7.38	9.75	–	23.52	22.02	30.33	–
15-Apr-89	2	10	50	39	12	0	7.75	7.27	9.32	–	23.24	21.71	28.08	–
29-Apr-89	3	24	52	39	13	0	7.84	7.50	8.86	–	23.46	21.43	29.23	–
13-May-89	4	38	50	32	17	1	7.84	7.00	9.59	5.16	24.57	21.58	30.29	20.00
29-May-89	5	53	50	35	15	0	7.71	7.16	9.01	–	23.72	21.60	28.67	–
13-Jun-89	6	69	50	38	11	1	7.39	6.97	9.16	4.00	22.32	20.61	28.82	16.00
27-Jun-89	7	83	51	32	17	2	7.41	6.65	9.04	5.72	23.54	20.27	29.81	22.50
08-Aug-89	10	125	53	34	18	1	7.76	7.03	9.26	5.59	23.68	20.97	28.94	21.00
22-Aug-89	11	139	51	29	21	1	7.80	6.81	9.41	4.04	24.48	20.61	29.95	19.00
19-Sept-89	13	167	50	31	19	0	7.80	6.82	9.41	–	24.41	21.30	29.32	–
23-Oct-89	15	201	51	40	10	1	7.45	7.02	9.45	4.47	22.34	20.92	28.50	16.00
06-Nov-89	16	215	54	39	11	4	7.39	7.19	9.11	4.56	21.89	20.79	28.90	15.00
20-Nov-89	17	229	52	40	10	2	7.40	7.17	8.90	4.47	22.42	21.15	29.00	15.00
04-Dec-89	18	243	52	43	7	2	7.05	7.03	8.10	4.54	21.40	21.00	26.00	16.50
18-Dec-89	19	257	57	43	11	3	7.15	6.97	8.62	4.21	22.39	20.98	28.91	18.67
01-Jan-90	20	271	50	46	2	2	7.13	7.11	9.68	4.84	21.00	20.73	29.50	18.50
15-Jan-90	21	285	56	50	3	3	7.29	7.38	7.91	5.23	21.93	21.55	29.33	20.67

**Appendix B-II (Continued).**

Sample	Code (day)	Cum (day)	Nb				D				EL			
			Tot	i	l	s	aver	i	l	s	aver	i	l	s
29-Jan-90	22	299	55	53	2	0	7.39	7.32	9.23	–	21.27	20.92	30.50	–
12-Feb-90	23	313	56	52	4	0	7.32	7.15	9.53	–	21.36	20.62	31.00	–
26-Feb-90	24	327	54	52	2	0	7.21	7.18	7.96	–	20.94	20.73	26.50	–
12-Mar-90	25	341	53	50	2	1	7.09	7.11	8.28	4.09	20.79	20.50	28.00	21.00
26-Mar-90	26	355	54	47	4	0	7.11	7.16	8.38	4.69	20.96	20.72	26.50	17.33

**Appendix B-III. Hydrostation-S**

Sample	Code (day)	Cum (day)	Nb				D				EL			
			Tot	i	l	s	aver	i	l	s	aver	i	l	s
24-Jan-91	1	55	217	178	39	0	7.69	7.43	8.84	–	22.98	21.88	28.34	–
20-Feb-91	2	82	182	122	60	0	7.97	7.22	9.49	–	24.36	21.98	29.31	–
21-Mar-91	3	111	99	49	50	0	8.29	6.94	9.60	–	25.48	21.57	29.32	–
23-Apr-91	4	144	85	21	64	0	9.09	7.32	9.68	–	28.29	22.67	30.19	–
30-May-91	5	181	141	133	8	0	6.67	6.51	9.28	–	21.37	20.86	29.88	–
10-Jun-91	6	192	73	69	4	0	6.62	6.42	10.03	–	21.63	21.12	30.50	–
17-Jul-91	7	229	205	204	1	0	6.35	6.32	11.40	–	20.57	20.50	35.00	–
09-Aug	8	205	4	4	0	0	6.27	6.27	–	–	19.00	19.00	–	–
18-Sept-91	9	292	22	21	1	0	6.57	6.48	8.35	–	21.38	20.95	30.00	–
25-Nov-91	11	329	68	67	1	0	6.90	6.88	8.39	–	21.63	21.58	25.00	–

**Appendix B-IV. MST-9**

Sample	Code (day)	Cum (day)	Nb				D				EL			
			Tot	i	l	s	aver	i	l	s	aver	i	l	s
07-Jun-92	2	1	51	1	39	11	7.87	5.60	8.97	4.17	26.56	16.00	29.17	15.67
21-Jun-92	3	14	49	3	37	9	7.90	6.97	8.87	4.20	24.89	19.33	28.88	14.00
05-Jul-92	4	28	51	0	39	12	7.87	–	9.05	4.03	26.44	–	29.88	14.22
19-Jul-92	5	42	50	2	18	30	5.87	5.50	8.80	4.13	19.33	14.50	28.69	14.32
26-Jul-92	6	49	52	2	19	31	5.81	5.13	8.73	4.06	19.72	19.50	28.11	14.24
02-Aug-92	7	56	50	3	37	10	7.66	6.76	8.73	3.98	25.03	20.33	29.12	14.00
30-Aug-92	11	77	50	0	34	16	7.43	–	9.05	3.99	25.17	–	29.26	14.46
13-Sept-92	13	98	51	0	41	10	7.86	–	8.78	4.06	26.54	–	28.79	15.88
27-Sept-92	14	112	50	0	45	5	8.39	–	8.83	4.42	27.75	–	28.88	15.33
11-Oct-92	15	126	50	1	41	8	8.10	6.07	8.93	4.14	26.55	18.00	29.17	14.29
25-Oct-92	16	140	51	3	44	4	8.28	6.39	8.80	3.98	28.14	22.00	29.97	15.33
08-Nov-92	17	154	52	1	46	5	8.61	4.58	9.15	4.43	27.55	17.00	29.71	15.00
22-Nov-92	18	168	56	1	36	19	7.06	4.39	8.74	4.01	24.02	19.00	29.28	14.32
06-Dec-92	19	182	51	1	45	5	8.66	5.11	9.24	4.15	27.83	19.00	29.49	15.50
17-Jan-93	22	224	51	1	25	25	6.42	6.72	8.93	3.89	21.84	17.00	30.22	14.00
14-Feb-93	24	245	60	1	35	24	6.91	5.60	8.95	3.98	23.25	19.00	29.49	14.33

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