Dinoflagellate cyst assemblages as tracers of sea-surface conditions in the northern North Atlantic, Arctic and sub-Arctic seas: the new ‘\( n = 677 \)’ data base and its application for quantitative palaeoceanographic reconstruction

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ABSTRACT: The distribution of dinoflagellate cyst (dinocyst) assemblages in surface sediment samples from 677 sites of the northern North Atlantic, Arctic and sub-Arctic seas is discussed with emphasis on the relationships with sea-surface parameters, including sea-ice cover, salinity and temperature of the coldest and warmest months. Difficulties in developing a circum-Arctic data base include the morphological variation within taxa (e.g. Operculodinium centrocarpum, Islandinium cezare and Polykrikos sp.), which probably relate to phenotypic adaptations to cold and/or low salinity environments. Sparse hydrographical data, together with large interannual variations of temperature and salinity in surface waters of Arctic seas constitute additional limitations. Nevertheless, the use of the best-analogue technique with this new dinocyst data base including 677 samples permits quantitative reconstruction of sea-surface conditions at the scale of the northern North Atlantic and the Arctic domain. The error of prediction calculated from modern assemblages is \( \pm 1.3^\circ \)C and \( \pm 1.8^\circ \)C for the temperature of February and August, respectively, \( \pm 1.8 \) for the salinity, and \( \pm 1.5 \) months yr\(^{-1}\) for the sea-ice cover. Application to late Quaternary sequences from the western and eastern subpolar North Atlantic (Labrador Sea and Barents Sea) provide reconstructions compatible with those obtained using the previous dinocyst data base (\( n = 371 \)), which mainly included modern data from the northern North Atlantic. Copyright © 2001 John Wiley & Sons, Ltd.

KEYWORDS: dinoflagellate cysts; northern North Atlantic and Arctic; temperature; salinity; sea-ice.

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Introduction

Organic-walled dinoflagellate cysts, or dinocysts, are useful proxies for the reconstruction of past sea-surface conditions, particularly in high-latitude marine environments. In contrast to siliceous or carbonate microfossils, dinocysts are generally well preserved in sediments affected by dissolution because they are composed of highly resistant refractory organic matter. Some dinocysts can be affected by oxidation of their organic wall under specific circumstances, in pelagic sediments with low accumulation rates (e.g. Zonneveld et al., 2001), but preservation in shelf and slope sediments is usually excellent (e.g. McCarthy et al., 2000). Moreover, dinoflagellate populations may thrive despite extremely cold conditions, and relatively abundant dinocysts can be found in sediments of most circumpolar environments of both hemispheres (e.g. Mudie, 1992; Harland and Pudsey, 1999). The encystment and dormancy period, which characterises the life cycle of many dinoflagellates in relation to their sexual reproduction, undoubtedly constitutes an adaptive strategy to disperse and survive in environments marked by seasonally adverse conditions (e.g. Dale, 1983, 1996). The encystment strategy together with heterotrophism of some taxa probably explains how dinoflagellates are able to occupy polar seas where extensive sea-ice cover prevails for a large part of the year and restricts vegetative activity based on autotrophy. Thus, dinoflagellates occupy a wide range of marine environments with respect to temperature, sea-ice cover and salinity, and diversified dinocyst assemblages accordingly can be recovered from high-latitude marine basins and epicontinental seas.

Previous studies of dinocysts in surface sediments from the northern North Atlantic and adjacent basins demonstrated close relationships between the distribution of assemblages and sea-surface conditions, notably temperature, salinity and seasonal duration of sea-ice cover (e.g. Harland, 1983; Turon, 1984; Mudie and Short 1985; Rochon and de Vernal, 1994; Matthiessen, 1995; Kunz-Pirrung, 1998). On these grounds, dinocyst data were used for quantitative reconstruction based on the modern analogue technique (de Vernal et al., 1993a, 1994, 1997; Rochon et al., 1999). They permitted quantitative estimates of late Quaternary sea-surface temperature, salinity and sea-ice cover along the continental margins of eastern Canada (de Vernal et al., 1993b, 1996; Levac and de Vernal, 1997; Levac et al., 2001) and western Europe (Rochon et al., 1998; Eynaud, 1999; Grøsfjeld et al., 1999). They also were used to reconstruct sea-surface conditions throughout the northern North Atlantic during the Last Glacial Maximum (de Vernal et al., 2000). The palaeoceanographic records available from dinocyst data are particularly interesting from an ocean dynamics viewpoint because they permit the reconstruction of sea-ice cover that regulates the albedo and energy exchange at the water–atmosphere interface (de Vernal and Hillaire-Marcel, 2000). These records also enable evaluation of the potential density of surface waters, calculated from temperature and salinity estimates, which may help to constrain variation in the vertical structure of water masses when combined with data from isotopic measurements in planktonic and benthic foraminifers (e.g. Hillaire-Marcel et al., 2001a,b).

In order to enlarge the domain of the dinocyst-based reconstructions for the study of the ocean dynamics in circum-Arctic regions, we have collectively undertaken the enlargement of the northern North Atlantic dinocyst data base to a multibasin scale with the addition of modern samples from the Arctic and sub-Arctic seas, and subpolar North Pacific. Workshops held in 1999 and 2000 helped the development of a standardised taxonomy, which was indispensable prior to combining data sets established on regional scales in different laboratories and to build the circumpolar data base. Here, we present the updated dinocyst data base that includes the previously published 371 assemblage counts from the northern North Atlantic (de Vernal et al., 1997; Rochon et al., 1999), to which are now added data from the Laptev Sea (Kunz-Pirrung, 1998, this issue), the Bering and Chukchi seas (Radi et al., this issue), the Irminger Sea (Boessenkool et al., this issue), the Barents Sea (Voronina et al., this issue), the Canadian Arctic (Hamel, 2001; Mudie and Rochon, this issue), the Norwegian coasts (Grøsfjeld and Harland, this issue), and many sites from the northern North Atlantic and Kara Sea (Plate 1 and Fig. 1). The new data base comprises a total of 677 reference sites. In the present paper, we report on the particularities of this data base with respect to taxonomy and hydrographic conditions. We report on the procedure developed using the best-analogue method for the reconstruction of past sea-surface salinity, temperature and sea-ice cover and, finally, we discuss the uses and limitations of such an approach with reference to examples of late Quaternary reconstructions. One example is from the Labrador Sea in the northwest North Atlantic, and the other from the Barents Sea in an area close to the boundary between Arctic waters and the northeastern end-member of the North Atlantic drift.

The new circum-Arctic data base

The dinocyst data

The standardisation of laboratory procedures and taxonomy is a prerequisite to the development of joined data bases. The protocol for preparation used for all samples of the data base can be found in de Vernal et al. (1999) or Rochon et al. (1999), for example. It consists simply of HCl and HF treatments of the greater than 10 µm or 7 µm fraction, and avoids oxidising treatment that may affect the preservation of organic-walled cysts (e.g. Marret, 1993). The dinocyst nomenclature conforms to Head (1996a), Rochon et al. (1999) and Head et al. (this issue). Three taxa that were not included in the northern North Atlantic data base (de Vernal et al., 1997; Rochon et al., 1999) have been added to the n = 677 data base (Table 1). They include cysts of Polykrikos kofoidii, which occurs in the Bering Sea (Radi et al., this issue), and cysts belonging to the genus Polykrikos referred to as cyst of Polykrikos sp. Arctic morphotype. This morphotype shows a wide range of variation, but is distinguished by its smaller size and reduced ornamentation in comparison to the cysts of Polykrikos schwartzi. It has been described informally by Kunz-Pirrung (1998) and Radi et al. (this issue), and seems to be a characteristic taxon of Arctic environments (Fig. 2). Other new taxa used for statistical treatment in the n = 677 data base include Quinquecuspis concreta, which has been treated separately from other proterodinioidos, as it constitutes a characteristic taxon of the North Pacific and Bering Sea.

Various morphotypes of Opeplaculodinium centrocarpum (de Vernal et al., 1989; Radi et al., this issue) also have been distinguished in the data base because of significant variations in the ornamentation of the cyst wall, and in the density, length and shape of the processes. These morphotypes include the form with short processes (e.g. Rochon et al., 1999), and the morphotype cezare first described by de Vernal et al. (1989) from post-glacial Champlain Sea sediments of Quebec. The latter constitutes the end member of a gradational lineage
Plate 1  Location map of surface sediment samples used to establish the reference dinocyst data base. The circles correspond to references sites of the 'n = 371' data base as published by de Verral et al. (1997) and Rochon et al. (1999). The squares correspond to the additional reference sites included in the 'n = 677' data base. The modern sea-ice cover (in months yr\(^{-1}\) with >50% of sea-ice concentration) is illustrated after data sets provided by the National Climate Data Center (NCDC) in Boulder, Colorado, which span the years 1953 to 1990. Note that the NCDC data set is incomplete for some epicontinental areas such as the Okhotsk Sea (no data reported) and the Gulf of St Lawrence (data extrapolated after Markham, 1980). Note also that interpolation for mapping was done using a window of 3°, which results in smoothing of the very sharp sea-ice gradients along the polar front.
with the almost complete disappearance of processes. Other specimens of *O. centrocarpum* have been assigned to an Arctic morphotype (Fig. 3). This morphotype is relatively frequent and shows a morphology intermediate between *O. centrocarpum* sensu Wall & Dale 1966 and *O. centrocarpum* morphotype cezare. It is distinguished by processes that are imperfectly developed and has a distribution that is of low density. It corresponds to *O. centrocarpum* type B described from the Champlain Sea sediment (de Vernal et al., 1989). The Arctic and cezare morphotypes probably represent morphological gradation of the same taxon. They seem to characterise Arctic and cold environments, whereas *O. centrocarpum* sensu Wall & Dale 1966 appears more ubiquitous (Fig. 3).

Although these morphotypes were distinguished in the raw data base, they remain grouped for statistical treatment for two main reasons. First, the *n* = 371 data base (Rochon et al., 1999) may include specimens belonging to the Arctic and cezare morphotypes of *Operculodinium centrocarpum* that were overlooked when initial counts were made. Second, because the morphological variations of *Operculodinium centrocarpum* are gradational, the identification of various morphotypes is a rather subtle and subjective matter, and it would be impossible to ensure consistency in relative counts from one analyst to another. Thus, although the morphological variations in *O. centrocarpum* very probably have ecological significance, we have grouped all morphotypes together for data treatments (cf. Table 1). It must be noted finally that we use the name *O. centrocarpum* not in the strict sense but according to Quaternary palynological custom. *Operculodinium centrocarpum* was first described from the Miocene of Australia (Deflandre and Cookson, 1955) and is larger and more robust than Quaternary forms (Head, 1996b; Rochon et al., 1999).

Spiny round brown cysts occur frequently in our high-latitude assemblages and represent another taxonomically problematic group. These cysts are referred to as *Algidasphaeridium? minutum* var. *minutum* and *Algidasphaeridium? minutum* var. *cezare* in the *n* = 371 data base (Rochon et al., 1999), and respectively as *Islandinium minutum* and *Islandinium? cezare* in the present work, following Head et al. (this issue). A third species, *Echinidinium karaense*, also occurs in our high-latitude assemblages (Head et al., this issue), and is
Table 1  List of dinocyst taxa systematically counted and reported in the raw n = 677 data base under four-letter codes. A total of 30 taxa (codes in bold) are used for statistical treatment. Some of these taxa result from grouping as indicated by notes in the table. The arrows point to taxa occurring currently in Arctic and sub-Arctic seas for which the distribution is illustrated in Figs 2–5 and Plate 2

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Code</th>
<th>Notes</th>
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<tr>
<td>cf. Alexandrium tamarense type cyst</td>
<td>Alex</td>
<td></td>
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<tr>
<td>Ataxiodinium choane</td>
<td>Atax</td>
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<tr>
<td>Bitectatodinium tepikiense</td>
<td>Btep</td>
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<tr>
<td>Impagidinium aculeatum</td>
<td>Iacu</td>
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<tr>
<td>Impagidinium pallidum</td>
<td>Ipal</td>
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<tr>
<td>Impagidinium paradoxum</td>
<td>Ipar</td>
<td></td>
</tr>
<tr>
<td>Impagidinium patulum</td>
<td>Ipat</td>
<td></td>
</tr>
<tr>
<td>Impagidinium sphaericum</td>
<td>Isph</td>
<td></td>
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<tr>
<td>Impagidinium striatulum</td>
<td>Istr</td>
<td></td>
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<tr>
<td>Impagidinium spp.</td>
<td>Ispp</td>
<td></td>
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<tr>
<td>Lingulodinium machaerophorum</td>
<td>Lmac</td>
<td></td>
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<tr>
<td>Nematosphaeropsis labyrinthus</td>
<td>Nlal</td>
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<tr>
<td>Operculodinium centrocarpum sensu Wall &amp; Dale 1966</td>
<td>Ocen</td>
<td>Grouped with O. centrocarpum sensu Wall &amp; Dale 1966 processes</td>
</tr>
<tr>
<td>O. centrocarpum sensu Wall &amp; Dale 1966 - short</td>
<td>Ocss</td>
<td>Grouped with O. centrocarpum sensu Wall &amp; Dale 1966 processes</td>
</tr>
<tr>
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<td>Oarc</td>
<td>Grouped with O. centrocarpum sensu Wall &amp; Dale 1966 processes</td>
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<tr>
<td>Operculodinium israelianum</td>
<td>Oisr</td>
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<tr>
<td>Operculodinium cf. janduchenei</td>
<td>Ojan</td>
<td></td>
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<tr>
<td>Operculodinium centrocarpum - morphotype cezare</td>
<td>Ocez</td>
<td>Grouped with O. centrocarpum sensu Wall &amp; Dale 1966 processes</td>
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<td>Pyxidinopsis reticulata</td>
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<td>Spiniferites membranaceus</td>
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<td>Spiniferites delicatus</td>
<td>Sdel</td>
<td>Grouped with S. membranaceus</td>
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<tr>
<td>Spiniferites elongatus</td>
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<td>Spiniferites ramosus</td>
<td>Sram</td>
<td></td>
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<tr>
<td>Spiniferites belerius</td>
<td>Sbel</td>
<td>Grouped with S. membranaceus</td>
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<td>Spiniferites bulloideus</td>
<td>Sbul</td>
<td>Grouped with S. ramosus</td>
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<td>Spiniferites frigidas</td>
<td>Sfri</td>
<td>Grouped with S. elongatus</td>
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<tr>
<td>Spiniferites lasz</td>
<td>Slaz</td>
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<tr>
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<td>Smir</td>
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<tr>
<td>Spiniferites spp.</td>
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<tr>
<td>Cyst of Pentapharsodinium dalei</td>
<td>Pdal</td>
<td></td>
</tr>
<tr>
<td>Islandinium minutum</td>
<td>Amin</td>
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<tr>
<td>Islandinium cezare</td>
<td>Amic</td>
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<td>Echinidinium karaense</td>
<td>Aspp</td>
<td>Grouped with Islandinium? cezare</td>
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<tr>
<td>Brigantedinium spp.</td>
<td>Bssp</td>
<td></td>
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<td>Brigantedinium cariacoense</td>
<td>Bcar</td>
<td>Grouped with Brigantedinium spp.</td>
</tr>
<tr>
<td>Brigantedinium simplex</td>
<td>Bsim</td>
<td>Grouped with Brigantedinium spp.</td>
</tr>
<tr>
<td>Protoperiidioids</td>
<td>Peri</td>
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<tr>
<td>Lejeuneycysta sabrina</td>
<td>Lsab</td>
<td>Grouped with Protoperiidioids</td>
</tr>
<tr>
<td>Lejeuneycysta oliva</td>
<td>Loli</td>
<td>Grouped with Protoperiidioids</td>
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<td>Selenopemphix nephroides</td>
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<td>Xandarodinium xanthum</td>
<td>Xand</td>
<td>Grouped with Protoperiidioids</td>
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<tr>
<td>Selenopemphix quanta</td>
<td>Squa</td>
<td></td>
</tr>
<tr>
<td>Cyst of Protoperiidioidium nudum</td>
<td>Pnud</td>
<td>Grouped with S. quanta</td>
</tr>
<tr>
<td>Trinovantedinium applanatum</td>
<td>Tapp</td>
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<tr>
<td>Trinovatedinium variabile</td>
<td>Tvar</td>
<td></td>
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<tr>
<td>Votadinium calvum</td>
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<tr>
<td>Votadinium spinosum</td>
<td>Vspl</td>
<td></td>
</tr>
<tr>
<td>Cyst of Protoperiidioidium americanum</td>
<td>Vame</td>
<td></td>
</tr>
<tr>
<td>Quinquecuspis concretaa</td>
<td>Qcon</td>
<td></td>
</tr>
<tr>
<td>Cyst of Polykrikos schwartzii</td>
<td>Psch</td>
<td></td>
</tr>
<tr>
<td>Cyst of Polykrikos sp.-Arctic morphotype^</td>
<td>Parc</td>
<td></td>
</tr>
<tr>
<td>Cyst of Polykrikos kofoidii^</td>
<td>Pkon</td>
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^ Not recorded in the n = 371 data base.

Figure 2  Distribution maps of the percentages of cysts of Polykrikos schwartzii (upper left panel) and Polykrikos sp. Arctic morphotype (upper right), and illustration of representative cyst specimens (lower panel). (1) Cyst of Polykrikos schwartzii as figured in Harland, 1981,1983, Firth of Forth (Scotland), specimen MPK2600. (2) Cyst of Polykrikos sp. Arctic morphotype: Core 9722-05B (0–1 cm), UQP 1246-3, M31/1. (3) Cyst of Polykrikos sp. Arctic morphotype: Core 9722-01E (0–1 cm), UQP 1246-6, E29/1. (4) Cyst of Polykrikos sp. Arctic morphotype: Core 9722-01E (0–1 cm), UQP 1246-6, C39/3-4. Scale bars on the photographs are 10 µm.
Figure 3  Distribution maps of the percentages of Operculodinium centrocarpum sensu Wall & Dale 1966 (upper left panel) and Operculodinium centrocarpum Arctic morphotype (upper right panel), and illustration of the respective morphology of the different morphotypes (lower panel). (1) Operculodinium centrocarpum sensu Wall and Dale 1966: slide HU-90-013-006, UQP 482-3, E26/4. (2) Operculodinium centrocarpum—short processes form: slide HU-90-013-017 (0–1 cm), UQP 482-6, N25/4. (3) Operculodinium centrocarpum Arctic morphotype (type B of de Vernal et al., 1989), from Saint-Césaire, Champlain Sea, Quebec, UQP 200-6B, M47/2. (4) Operculodinium centrocarpum morphotype cezare, from Saint-Césaire, Champlain Sea, Quebec, UQP 200-6B, O44/0. Scale bars on the photographs are 10 µm.

Most surface sediment samples included in the data base were collected by box or gravity coring and correspond to the top first centimetre of sediment. Samples from piston core were not used because the surface sediment is often missing. In case of doubt concerning the ‘recent’ age of the surface sediment, samples were discarded from the data base. More information concerning the sampling and sediment characteristics can be found in Rochon et al. (1999) and manuscripts reporting on regional data sets (Kunz-Pirrung, 1998; this issue; Radi et al., this issue; Voronina et al., this issue; Hamel, 2001; Mudie...
The hydrographic data

Sea-ice cover was compiled from data provided by the National Climate Data Center (NCDC) in Boulder, Colorado, comprising measurements for a 1° by 1° grid and spanning 1953 to 1990. Mean sea-ice cover is expressed here as the number of months per year with sea-ice concentration greater than 50% (see also de Vernal and Hillaire-Marcel, 2000; Plate 1). It should be noted that the NCDC data cover most of the Northern Hemisphere except for a few marine basins such as the Okhotsk Sea and the Estuary and Gulf of St Lawrence. In the case of the Estuary and Gulf of St Lawrence, the sea-ice data are from Markham’s (1980) atlas and consist of a compilation after a couple of years of observation.

Sea-surface (0 m depth) temperature and salinity are compiled from data published as CD-roms by the National Ocean Data Center (NODC, 1994). For most sites, simple averages were calculated from all values included within a radius of 60 nautical miles around the sites. A radius of 60 nautical miles was used in areas where instrumental measurements are sparse (miles was used in areas where instrumental measurements are sparse) around the sites. Ideally, a scan was done until a sum of at least 400 specimens was reached. In samples containing sparse assemblages, the entire slide was scanned. On average, 400 specimens were identified and counted in each sample. However, lower counts were performed for many samples; among the 677 samples retained in the data base, 40 have counts ranging 25–100. The raw dinocyst counts include 53 taxa, among which 30 were used for statistical treatment after grouping (cf. Table 1). The raw dinocyst counts and percentages of the 30 taxa selected in the 677 surface sediment samples of the updated data base presented here can be found on the websites of GEOTOP (http://www.geotop.uqam.ca/) and the PANGAEA data bank of the Alfred Wegener Institute for Polar and Marine Research (http://www.pangaea.de).

Relationships between dinocyst assemblages and hydrographic data with special attention to the Arctic domain

The updated dinocyst data base includes data from mid- to high northern latitudes. The distribution of assemblages in the northern North Atlantic Ocean has been documented previously (de Vernal et al. 1997; Rochon et al., 1999) and here we focus mostly on assemblages specific to the polar domain. In general, the species diversity is much larger in assemblages from lower latitudes than from Arctic environments. Of the 30 taxa retained within the updated
Operculodinium centrocarpum sensu Wall & Dale 1966 is particularly ubiquitous, although morphological variations in Arctic environments (see Operculodinium centrocarpum Arctic morphotype; Fig. 3) might be associated with phenotypes adapted to low salinity and cold environments, or to reduced season of growth and light levels. Brigantedinium spp. is another taxon that seems to be particularly cosmopolitan, especially in epicontinental environments (Fig. 5 and Plate 2). Its distribution does not show any preference with regard to temperature or salinity, nor with nutrient availability or productivity (Devillers and de Vernal, 2000). It probably is an opportunistic genus. The cyst of Pentapharsodinium dalei is another ubiquitous taxon, but it seems to be more specific of sub-Arctic environments and has limited occurrence in the coldest polar regions (Fig. 6 and Plate 2).

Other cosmopolitan taxa have limited occurrence in the coldest Arctic seas. For example, Nematosphaeropsis labyrinthus and Spiniferites elongatus are ubiquitous in middle-high latitudes, but they show some preference for open oceanic environments in the temperate to subpolar domains. Selenopemphix quanta also shows preference for the temperate to subpolar domain, and occurs mainly in neritic environments where salinity can be relatively low (Fig. 5 and Plate 2).

There are, however, taxa that are apparently more specific to Arctic and sub-Arctic seas. This is the case of Islandinium minutum, and more especially Islandinium cezare s.l., which are abundant mainly in assemblages of the continental margins where seasonal sea-ice cover is a conspicuous feature (Head et al., this issue; Fig. 5 and Plate 2). The polar taxa also include Impagidinium pallidum, recorded as having maximum occurrence in the Greenland Sea, where surface waters are cold and characterised by relatively high salinity (Fig. 6 and Plate 2), and finally, the cyst of Polykrikos sp. Arctic morphotype, which occurs almost exclusively in shelf environments of the Canadian Arctic and Laptev and Kara seas (Fig. 2).

Principal component analysis was performed after logarithmic (ln) transformation of percentage data for the 30 taxa selected using the software of Guiot and Goeury (1996). A logarithmic transformation is useful in as much as the dominant taxa are often cosmopolitan, whereas accompanying taxa generally have more specific environmental requirements and more restricted distributions. The first principal component (PC1), which explains 48.9% of the total variance, shows an opposition between the polar taxa, including the cyst of Polykrikos sp. Arctic morphotype, Islandinium minutum, Islandinium cezare s.l., Brigantedinium spp. and Impagidinium pallidum on one side, and most other taxa on the other side (Fig. 7). Scores of the first component reveal a distribution closely related to latitudinal gradients and water mass boundaries (Plate 3a), positive values being related to open ocean temperate–subpolar waters, and negative values corresponding to Arctic seas and areas that are marked by polar currents and extensive sea-ice. Actually, PC1 correlates positively with the temperature of August ($R = 0.802$) and February ($R = 0.798$) and with salinity ($R = 0.559$), whereas it correlates negatively with the sea-ice cover ($R = 0.728$) according to linear regression. Better fits can be obtained with polynomial of order 2 or 3 relationships. The second component (PC2) explains 22.2% of the variance and corresponds to an opposition between both Arctic and temperate taxa on one side, and taxa cosmopolitan in the sub-Arctic domain, such as the cyst of Pentapharsodinium dalei, Spiniferites elongatus and Operculodinium centrocarpum, on the other side. The geographical distribution of PC2 scores shows no relationship with temperature or salinity (Plate 3b). It probably is related to the distribution of another parameter, which could be linked, for example, to productivity, nutrient distribution or the trophic structure of planktonic populations (see also Devillers and de Vernal, 2000).

Some of the taxa occurring in the Arctic seas are cosmopolitan and appear to tolerate a wide range of environmental conditions. Operculodinium centrocarpum sensu Wall & Dale 1966 is particularly ubiquitous, although morphological variations in Arctic environments (see Operculodinium centrocarpum Arctic morphotype; Fig. 3) might be associated with phenotypes adapted to low salinity and cold environments, or to reduced season of growth and light levels. Brigantedinium spp. is another taxon that seems to be particularly cosmopolitan, especially in epicontinental environments (Fig. 5 and Plate 2). Its distribution does not show any preference with regard to temperature or salinity, nor with nutrient availability or productivity (Devillers and de Vernal, 2000). It probably is an opportunistic genus. The cyst of Pentapharsodinium dalei is another ubiquitous taxon, but it seems to be more specific of sub-Arctic environments and has limited occurrence in the coldest polar regions (Fig. 6 and Plate 2).

Principal component analysis was performed after logarithmic (ln) transformation of percentage data for the 30 taxa selected using the software of Guiot and Goeury (1996). A logarithmic transformation is useful in as much as the dominant taxa are often cosmopolitan, whereas accompanying taxa generally have more specific environmental requirements and more restricted distributions. The first principal component (PC1), which explains 48.9% of the total variance, shows an opposition between the polar taxa, including the cyst of Polykrikos sp. Arctic morphotype, Islandinium minutum, Islandinium cezare s.l., Impagidinium pallidum on one side, and most other taxa on the other side (Fig. 7). Scores of the first component reveal a distribution closely related to latitudinal gradients and water mass boundaries (Plate 3a), positive values being related to open ocean temperate–subpolar waters, and negative values corresponding to Arctic seas and areas that are marked by polar currents and extensive sea-ice. Actually, PC1 correlates positively with the temperature of August ($R = 0.802$) and February ($R = 0.798$) and with salinity ($R = 0.559$), whereas it correlates negatively with the sea-ice cover ($R = 0.728$) according to linear regression. Better fits can be obtained with polynomial of order 2 or 3 relationships. The second component (PC2) explains 22.2% of the variance and corresponds to an opposition between both Arctic and temperate taxa on one side, and taxa cosmopolitan in the sub-Arctic domain, such as the cyst of Pentapharsodinium dalei, Spiniferites elongatus and Operculodinium centrocarpum, on the other side. The geographical distribution of PC2 scores shows no relationship with temperature or salinity (Plate 3b). It probably is related to the distribution of another parameter, which could be linked, for example, to productivity, nutrient distribution or the trophic structure of planktonic populations (see also Devillers and de

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Figure 4 Relationships between sea-surface temperature in August and sea-surface salinity in August (a), sea-surface salinity in August (b) and sea-ice cover (c). The circles correspond to references sites of the ‘n = 371’ data base as published by de Vernal et al. (1997) and Rochon et al. (1999), whereas the squares correspond to the additional reference sites included in the ‘n = 677’ data base (see Plate 1). Temperature is in degrees Celsius and sea-ice cover in months/year.
Plate 2  Relationships between the percentages of the main dinocyst taxa occurring in the Arctic seas and the August sea-surface temperature and salinity, and the sea-ice cover. The distribution of the percentages of the other North Atlantic taxa (cf. Table 1) as illustrated in de Vernal et al. (1997) and Rochon et al. (1999) from the n = 371 data base is basically unchanged. In the n = 677 data base, the distribution of the additional taxa such as the cyst of Polykrikos kofoidii and Quinquecuspis concreta is restricted to the Bering Sea (for information on their regional distribution, see Radi et al., this issue). The geographical location of the spectra is indicated as follows: blue indicates data from the Arctic seas (squares = Canadian Arctic, including Beaufort Sea, Hudson Bay, Baffin Bay, and the Canadian Archipelago Channels; circles = Barents Sea; crosses = Kara Sea and Laptev Sea; diamonds = western Arctic, including the Chukchi Sea and the Siberian Sea), and red indicates data from the North Atlantic Ocean and adjacent basins (squares = Estuary and Gulf of St Lawrence; circles = Norwegian–Greenland seas; crosses = southeastern Canadian and eastern American margins; diamonds = all other sites from northwest to northeast North Atlantic).
Plate 2 (Continued)
Plate 3  Geographical distribution of PC1 (a) and PC2 (b), which represent 48.9 and 22.2% of the total variance respectively. The principal component analysis was done on logarithmic values of the relative frequency of taxa expressed in per mil, using the software of Guiot and Goeury (1996).
Plate 3 (Continued)
Quantitative estimates of past sea-surface conditions based on the best-analogue method

Vernal, 2000). As a matter of fact, all taxa with negative loading of both PC1 and PC2 belong to the Polykrikaceae (cyst of Polykrikos sp.) or Protoperidiniaceae (Brigantedinium sp. and Islandinium minutum), which relate to a heterotrophic rather than autotrophic productivity (e.g. Taylor, 1987; Head et al., this issue).

Many techniques for quantitative reconstructions of past environmental conditions have been developed during the past decades. They are based on multiple regression techniques (e.g. Imbrie and Kipp, 1971), modern analogue approaches (e.g. Hutson, 1980; Prell, 1985; Guiot, 1990; Pflaumann et al., 1996; Waelbroeck et al., 1998), or neural network methods (e.g. Malmgren and Nordlund, 1997; Peyron et al., 1998, 2000). Tentative estimation of past sea-surface conditions based on dinocyst assemblages has been made using several approaches, including canonical regressions and variants of the modern analogue techniques (de Verna et al., 1994), and the artificial neural network technique (Peyron and de Vernal, this issue). The artificial neural network approach generally yields accurate reconstruction, but may give estimates outside the range of training data sets by extrapolation in the case of non-analogue situations, as is the case with regression techniques. In contrast, the analogue approach permits identification of non-analogue situations and avoids reconstruction.
when the degree of uncertainty appears too high. Bootstrap neural network approaches also permit non-analogue situations to be identified, but in a less straightforward way. The artificial neural network method and its application for reconstructing past sea-surface parameters based on dinocyst data are fully developed by Peyron and de Vernal (this issue). Here, we present the procedure using the best-analogue technique that we adapted from the software of Guiot and Goeury (1996).

When developing a technique for quantitative estimates of a given parameter, a means to identify the most reliable procedure consists of validations, i.e. tests to quantify how accurately a given technique yields a reconstruction; in this case one that matches present-day environmental conditions. Many validation exercises were performed using successive updates of the dinocyst data base (de Vernal et al., 1993, 1994, 1997; Rochon et al., 1999). From these exercises, it appears that logarithmic transformation of percentages is most powerful for the identification of the best analogues with respect to hydrographic conditions. This is because dominant species in the assemblages generally are the most ubiquitous, whereas the accompanying taxa often have more narrow ecological affinities. In other words, the presence and relative occurrence of accompanying taxa appear to be most diagnostic of environmental conditions.

The procedure we have adapted from the Guiot and Goeury (1996) software, developed initially for the analyses of pollen data, includes a few adjustments. In particular, relative abundance is expressed per thousand, instead of per cent in order to deal with whole numbers and to avoid decimals, which yield negative values when they are logarithmically transformed. One (1) is added to the frequency of each taxon in order to deal with values greater than zero, and the relative frequencies of taxa range from 1 to 1000. Another minor
transformation consists of adjusting the frequency data ranging between 2 and 5 (i.e. 0.2 and 0.5%) to the value of 5 in order to make a better discrimination between absence (1) and presence (>5). This transformation is further justified because of the count limit, which occasionally is as low as 100 or 200 specimens. The zero elements are thus replaced by a value lower than the precision under which data were produced (cf. Kucera and Malmgren, 1998). After these transformations, the distance \( d \) between the spectrum to be analysed \((i)\) and the spectra in the reference data base \((j)\) is calculated based on the difference in relative frequency \((f)\) for each taxon \((j = 1–30)\) as follows

\[
d = \sum_{j=1}^{m} W_j [\ln f_{ij} - \ln f_{ij}]^2
\]

In the above equation, \( W \) is a factor that may be used to weight the taxa. In the case of dinocyst assemblages, no weighting factor is used as we have not demonstrated from validation exercises that selectively weighting taxa on the basis of principal component analyses or on the basis of empirically defined ecological affinities can improve the accuracy of the reconstruction.

The distances calculated from the above equation permit us to select samples in the reference data base as best analogues. Here, we have searched for five analogues. The hydrographic data corresponding to these analogues are used to calculate an average that is weighted inversely to the distance of the analogues. This average constitutes the most probable estimates, and the results are reported within a confidence interval defined from hydrographic data corresponding to these five best analogues. It is of note that a threshold value is defined on probabilistic grounds (i.e. a Monte-Carlo approach) in order to identify a non-analogue or poor-analogue situation. If the distance of the closest analogue is higher than the threshold calculated, no reconstruction is made. In the case of the \( n = 677 \) data base, the distance between pairs randomly taken in the data base averages 95.51, with a standard deviation of 42.41. The average minus standard deviation gives a threshold distance below which we consider the similarity to be significant. In the case of the \( n = 677 \) data base, the threshold distance is thus 53.1. For comparison, the \( n = 371 \) data base led to the calculation of a mean random distance of 82.9 ± 36.4 for a threshold value of 46.5. The slightly lower threshold value for the \( n = 371 \) data base than for the \( n = 677 \) data base results from the smaller size of the matrix with respect to both number of taxa and number of spectra.

The validation exercise permits assessment of the degree of accuracy of sea-surface reconstruction (Plate 4). It is performed on each surface sample for which we seek the best five analogues excluding the sample itself. It enables one to test the coherency of the spectra versus hydrographic parameters. Such a technique, also called leaving-one-out may, however, result in an underestimation of the error compared with the split-sampling technique that involves random division of the data set (cf. Birks, 1995). The reconstruction of four parameters is illustrated in Plate 4: the sea-surface temperature of the coldest and warmest month (February and August), the salinity for August and the seasonal extent of sea-ice cover. These
parameters have been shown to be most determinant on the distribution of dinoflagellate populations and dinocyst assemblages. It is of note that other validation exercises were done using seasonal (i.e., winter and summer) or annual means of temperature and resulted in reconstructions not as accurate as the ones obtained for monthly temperature means for the warmest and coldest month. This points to the fact that the annual cycle of temperature undoubtedly exerts a determinant control on the dinoflagellates and their cyst distribution. Seasonality certainly plays a major role in the life cycle of dinoflagellates, i.e., on the duration of vegetative versus encysted stages. Seasonality can be viewed as the difference between the temperature of the warmest and coldest months, or as the length of the season during which metabolic activities are interrupted, notably because of limited light owing to sea-ice cover. This would explain why the seasonal duration of sea-ice cover is one of the parameters that can be best reconstructed using dinocyst assemblages.

From the validation exercises, the linearity of the relationship around a slope of one over one, and the coefficients of correlation between estimates and observations provide a first indication of the reliability of the approach (see Plate 4). The degree of accuracy of the reconstruction is further constrained by the standard deviation of the difference between estimates and observations, which also is referred to as the root mean square error of prediction (RMSEP), and would be the best way to assess the error rate and to compare methods (cf. ter Braak and van Dam, 1989; Malmgren et al., 2001). As shown in Plate 4, the degree of accuracy or prediction error establishes at ±1.3°C and ±1.8°C for the temperature of February and August respectively, ±1.8 for the salinity, and ±1.5 months yr⁻¹ for the sea-ice cover.

On the whole, the validation exercise for the n = 677 data base yields results that are similar to those of the validation made for the n = 371 data base (de Vernal et al., 1997; Rochon et al., 1999). However, in the case of the n = 677 data base, there is a larger error for salinity, particularly in the low salinity domain that corresponds primarily to data from the Canadian Arctic and the Russian Arctic. The apparently poor accuracy of salinity estimates in this domain can be explained by the high variability of this parameter and by the lack of accuracy of instrumental data (see above). Actually, about half the spread of estimated versus observed salinity values can be attributed to inaccurate hydrographic measurements. In summary, the validation exercises reveal high accuracy of the approach for the reconstructions of sea-surface conditions, although some reservation has to be exercised when reconstructing low salinity in Arctic environments.

Examples of application

Two examples, using the procedure described above with the n = 371 and n = 677 data bases, are treated here. The first example is based on a core collected from the northern Labrador Sea (HU-84-030-021; de Vernal and Hillaire-Marcel, 1987). The coring site is located in the northernmost part of the North Atlantic, a domain well represented by the n = 371 data base. The second example is from the Barents Sea (core PL96-112; Voronina et al., this issue), at the northeastern limit of the area represented by the n = 371 data base. These two examples are selected because they represent distinct circum-Arctic areas. They also are selected because the sediments in both cores are characterised by abundant dinocysts, allowing statistically representative dinocyst counts.

The two examples illustrate the coherency or discrepancies of palaeoceanographic estimates resulting from the use of the two data bases and identify the strengths and weaknesses of the method.

The northwest North Atlantic

The sedimentary sequence of core HU-84-030-021 (58°22.06′N, 57°30.42′W; water depth = 2853 m) spans the past 20 000 yr. The core was collected on the continental slope from the western Labrador Sea, where surface waters are under the influence of an eastern branch of the West Greenland Current (Fig. 8a). At the coring site, present-day mean sea-surface temperature is 3.5 ± 0.4°C and 6.8 ± 1.05°C in February and August respectively, and the

![Figure 8](image)

Figure 8 Core location and time series from the northwestern North Atlantic (core HU-84-030-021; 58°22.06′N-57°30.42′W; 2853 m) spanning the last 20 000 yr. (a) Location map for core HU-84-030-021 showing the surface water circulation pattern, with cold currents from the Arctic illustrated by black arrows (Baffin Land Current = BLC; Labrador Current = LC; East Greenland Current = EGC) and the warmer West Greenland Current (WGC) illustrated by white arrows. (b) Summary diagram of dinocyst assemblages for core HU-84-030-021. The chronological marks indicated in the left margins of the diagrams correspond to accelerator mass spectrometry (AMS) ¹⁴C ages on planktonic foraminifers (Neogloboquadrina pachyderma left coiling). The ages were normalised for a δ¹³C of 25‰ and corrected by −400 yr to account for the air–sea difference (for stratigraphical information see Hillaire-Marcel et al., 1994, or the GEOTOP website).

(c) Reconstruction of sea-surface parameters for core HU-84-030-021. Sea-surface temperature is in °C. The dashed line corresponds to the best estimates using the n = 371 data base, and the solid line to the best estimates using the n = 677 data base with the modern analogue technique protocol as described in the text. The confidence interval calculated from the hydrographic values corresponding to the five best analogues in the n = 677 data base is shown by the grey zone. The distance of the best analogues is given on the right of the diagram (dashed line for the n = 371 data base, and solid line for the n = 677 data base).
Plate 4  Results of the validation test for the reconstruction of sea-surface temperature, salinity and sea-ice cover after the procedure described in the text. The x-axis shows hydrographic averages resulting from instrumental observations, and the y-axis shows estimates from the dinocyst data. The coefficients of correlation (R) and the standard deviation $\sigma$ of the difference between reconstruction and observation or root mean square error of prediction (RMSEP) provide the degree of accuracy of estimates (see text). These accuracy indicators were calculated for all data points ($n = 677$) although the prediction error clearly depends upon the geographical domain considered.
The stratigraphy of core HU-84-030-021 has been documented by de Vernal and Hillaire-Marcel (1987), and notably by Hillaire-Marcel et al. (1994) (see also the GEOTOP website). The stratigraphy shows a clear change in both lithology and palynological assemblages at the glacial–interglacial transition, which is dated around 11 000 14C yr BP (Fig. 8b and c). This transition is marked by a change from glaciomarine sedimentation with abundant ice-rafter debris under cold conditions, to epipelagic sedimentation under oceanic and subpolar conditions. A major change in dinocyst assemblages also is recorded at this time. The glacial interval dated prior to ca. 11 000 14C yr BP generally is characterised by assemblages dominated by Brigantedinium spp. and accompanied by Islandinium minutum. Above the transition, the assemblages are characterised by higher species diversity and the replacement of Brigantedinium spp. by Opeculodinium centrocarpum, the cyst of Pentapharsodinium dalei and Nematosphaeropsis labyrinthus, which dominate the Holocene assemblages (Fig. 8b). The reconstruction of sea-surface conditions using both data sets reflects a major change at the glacial–interglacial transition, with a sharp decrease in sea-ice cover extent together with increasing temperature and salinity (cf. Fig. 8c).

In the post-glacial part of the record, the best analogues are found regionally and the distances are approximately identical whichever data base is used. The estimates are the same for all parameters considered and both curves of reconstruction are superimposed (Fig. 8c). In this case, it is clear that the n = 371 data base provided suitable analogues for reliable reconstructions. The use of the n = 677 data base also allows reliable reconstructions. In the lower part of the record, corresponding to the glacial episode, there are slight discrepancies between estimates depending upon the data base used. In general, the distance of analogues is slightly larger with the n = 371 data base. Closest analogues are found in the n = 677 data base, notably in the area of the North Water polynya, northernmost Baffin Bay, and in the Laptev Sea and northern Barents Sea, which were not represented in the n = 371 data base. Nevertheless, reconstructions of temperature and extent of sea-ice cover are almost identical, whether using the n = 677 or n = 371 data base. The main discrepancy occurs in the reconstruction of salinity, which yields slightly higher values and has more fluctuations with the n = 677 data base. The n = 677 data base thus seems to be more sensitive to salinity than the n = 371 data base. Nevertheless, the reconstructions are consistent in as much as they both indicate low salinity (<32) during the glacial interval. Another point of interest in the record of the glacial interval is the peak of gonyaulacalean cysts, including Bitectatodinium tenkiense, that is recorded between 430 and 446 cm. The assemblages in this interval have poor analogues in both data bases, but particularly in the n = 371 data base, as the distance for the closest analogue is above the threshold value for two samples.

The Barents Sea

Core PL-96-112P (71°44.18N-42°36.31E; 286 m), spanning the past 8500 yr (Voronina et al., this issue), was collected on the east Barents Shelf. This area is particularly interesting from a palaeoceanographical point of view because it presently constitutes the northernmost end-member of the North Atlantic Drift, at the boundary with Arctic waters flowing southward (see Fig. 9a; e.g. Loeng, 1991). At the coring site, sea-surface temperature is 7.8 ± 1.9 °C and 1.8 °C (σ unknown) in August and February respectively, with salinity in August of 34.8 ± 0.2. Sea-ice cover develops occasionally during the coldest years (mean sea-ice duration = 0.3 month yr−1).

The dinocyst assemblages from core PL-96-112 have a high species diversity and generally are dominated by Opeculodinium centrocarpum, the cyst of Pentapharsodinium dalei, and Spiniferites elongatus, these being accompanied notably by Nematosphaeropsis labyrinthus and Brigantedinium spp. (Fig. 9b). Throughout the sequence, the percentages of the main taxa record some tenuous variations. The most distinct trend, towards the top of the core, is the increased percentages of Pentapharsodinium dalei relative to a decrease in the occurrence of Opeculodinium centrocarpum. Other variations in the assemblages that may be significant include fluctuations in the percentages of Spiniferites elongatus, maximum occurrence of Nematosphaeropsis labyrinthus between ca. 1300 and 3000 14C yr BP, and sporadic occurrences of the cold water taxa Islandinium minutum and Impagidinium pallidum.
The reconstruction of sea-surface conditions in core PL-96-112 relies on different sets of analogues depending upon the data base considered (Fig. 9c). Both $n = 371$ and $n = 677$ data bases yield close analogues, with distances much lower than the threshold value, thus allowing estimations of hydrographic parameters. However, the distance is slightly larger when using the $n = 371$, the closest analogues being selected from the few available sites in the Barents Sea, in addition to sites from the Norwegian Sea and the Hudson Bay. When using the $n = 677$ data base, closer analogues are found in the Barents Sea and the eastern Arctic, in addition to sites from the Bering Sea, whereas spectra from the Norwegian Sea are selected only exceptionally. In spite of the different selection of analogue spectra depending upon the data base used, the estimates of sea-surface conditions appear consistent. The variations in sea-ice cover and sea-surface salinity are almost superimposed, and the trend of increasing salinity recorded during the early–middle Holocene appears significant. There are slight discrepancies concerning the estimated temperatures. However, these discrepancies are not very important because they fall within the range of variations presently recorded at the coring site (i.e. $\pm 1.9^\circ C$ in August). Nevertheless, both reconstructions suggest limited changes in temperature, with the exception of a few cooling pulses, possibly significant, around 2500 and 3500–4000 $^{14}$C yr BP, and prior to 8000 $^{14}$C yr BP.
Discussion and conclusions

Uncertainties and limitations

The development of any technique for the reconstruction of past climatic parameters implies a number of approximations and assumptions. The main one is that the recent assemblages recovered in surface sediment samples are contemporaneous with the reference hydrographic data, which are averaged over a few tens of years. Another assumption is that the microfossil assemblages result from vertical fluxes from surface waters to the sea floor, and thus are representative of local sea-surface conditions above the coring site, with limited impact of lateral transport through intermediate or deep currents. Although the mechanisms of biogenic particle fluxes through the water column could be better documented, marine snow and fecal pellets in the area of plankton production no doubt contribute to rapid settling of micro-organism remains, which thus form microfossil assemblages with distribution patterns closely related with sea-surface conditions on a regional scale. The technique we have developed using dinocyst assemblages of the northern North Atlantic Ocean and circum-Arctic seas bears a few additional particularities.

1 Several new morphotypes are apparently characteristic of Arctic seas. Although it is uncertain whether they are ecophenotypic variants or new taxa, their ecological and biological affinities still need documenting.
2 The rarity of hydrographic measurements in the Arctic domain, and the lack of consistent oceanographic data on a hemispheric scale constitute a real problem. We hope such data will be available in the near future, and will contribute to the improvement of the accuracy of the proposed technique of reconstruction.
3 In Arctic environments that are marked by large freshwater discharges such as the Laptev Sea (e.g. Kunz-Pirrung, this issue), the upper water masses may be characterised by a very shallow halocline or pycnocline (<20 m). Although we are using the surface layer (0 m) to establish relationships with dinocyst assemblages, we cannot demonstrate that original dinoflagellate populations are indeed living above the pycnocline in such nearshore environments. This could be a source of error, which could partly explain the limited accuracy of salinity reconstructions in the low-salinity domain. We have tried to raise a data base of hydrographic conditions within the water column in order to address this question. However, here again the scarcity of data prevents any reasonable statistical treatment.
4 It is unquestionable on empirical grounds that dinocyst assemblages are related to the distribution of temperature, salinity and sea-ice cover in surface waters. However, the dinocyst assemblages also are dependent upon other parameters as shown by principal component analyses. These parameters may be linked to nutrient distribution or to the trophic structure of planktonic populations (e.g. Devillers and Vernal, 2000). For example, in Arctic environments, the distribution of dinocyst assemblages, and particularly the proportion of Gyoneaulacales versus Peridiniales show close relationships with the distribution of polynyas (e.g. Hamel, 2001).

The choice of a conservative approach

Despite the above-mentioned uncertainties or limitations it has been possible to develop a reasonably accurate technique for the reconstruction of sea-surface conditions based on the artificial neural network technique (Peyron and de Vernal, this issue) and on the basis of the best-analogue method, as presented here. The approach described in the present paper is rather conservative. It relies on interpolation and so cannot yield reconstructions outside the range of modern hydrographic conditions. Moreover, by using threshold values to identify non-analogue situations, we avoid speculative reconstruction when assemblages reveal different situations to those represented by the modern environment. Of course, such an approach requires a large reference data base. As the $n = 371$ and $n = 677$ data bases yield consistent results for subarctic seas adjacent to the northwest and northeast North Atlantic, we may assume that they are both adequate for reconstructions in the subpolar domain. Moreover, the $n = 677$ covers a geographical and hydrographic domain wide enough to permit reconstruction of past sea-surface conditions in circum-Arctic regions.

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