CHAPTER NINE

ORGANIC-WALLED DINOFLAGELLATE CYSTS: TRACERS OF SEA-SURFACE CONDITIONS

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Contents

1. INTRODUCTION

Dinoflagellates are microscopic unicellular organisms belonging to the division of Dinoflagellata (Fensome et al., 1993). They inhabit most types of aquatic

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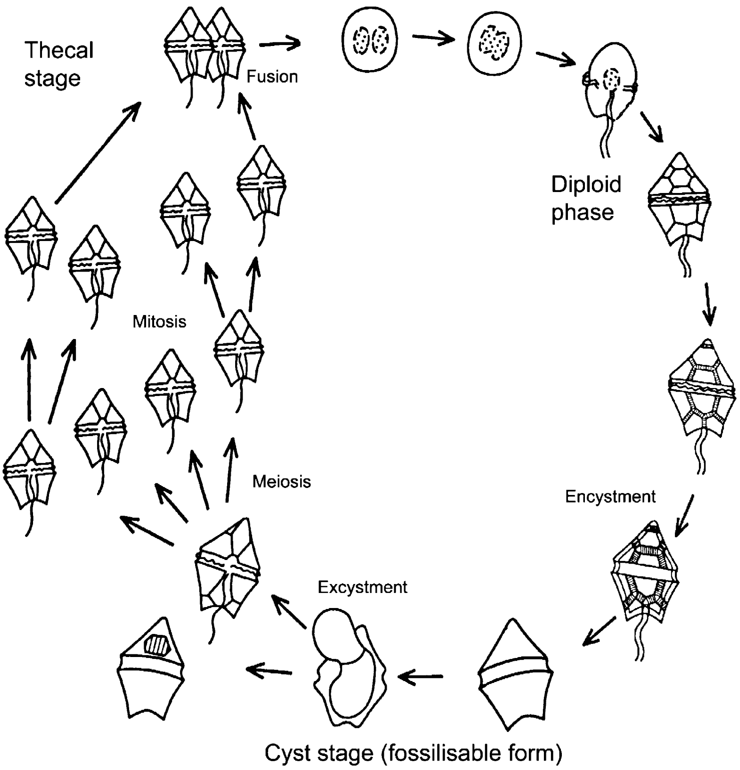

Figure 1 Diagram of the life cycle of a dinoflagellate showing the alternation of the motile stage (cannot be fossilized) and the cyst stage (yielding fossil remains).

environments, from lakes to open ocean, and occur at all latitudes from the Equator to Polar seas. During their motile or vegetative phase, dinoflagellates bear two flagella used for swimming with a spiral-like motion that is at the origin of their name (from the Greek word *dinos* meaning whirling). Together with diatoms and coccolithophorids, dinoflagellates constitute important primary producers. Approximately half of the extant dinoflagellate taxa are autotrophic; others are heterotrophic, mixotrophic, parasitic or symbiotic. Some dinoflagellates, such as those belonging to the genus *Symbiodinium*, and commonly referred to as zooxanthellae, are symbionts of various organisms including corals, radiolarians and foraminifera (Pawlowski, Holzmann, Fahrni, Pochon, & Lee, 2001; Pochon, LaJeunesse, & Pawlowski, 2004).

The motile cell of dinoflagellates does not yield remains that can be fossilized. However, many dinoflagellates have a complex life cycle involving several stages, asexual and sexual, motile and non-motile (Figure 1). During the course of sexual reproduction, some species form a diploid cell protected within a cyst, which permits survival of the organism during a dormancy period of variable length (*cf.* Wall & Dale, 1968; Fensome et al., 1993). A few dinoflagellate taxa produce calcareous cysts (Zonneveld et al., 1999), and approximately 10–20% of the species produce cysts composed of highly resistant organic matter (e.g., Dale, 1976; Head, 1996). The organic cyst material is called dinosporin: it has been compared to the sporopollenin of pollen grains, but shows distinct chemical macromolecular composition, which varies depending upon the taxon (Fensome et al., 1993; Kokinos et al., 1998; Versteegh & Blokker, 2004). The organic-walled cysts, also known as "dinocysts," are typically 15 to 100 μm in diameter. They are routinely observed at magnifications ranging from 250 × to 1,000 × in palynological slides, prepared following laboratory procedures used for pollen analyses, which involve treatments with hydrofluoric and hydrochloric acids. The study of dinocysts is often considered to be a sub-discipline of palynology.

Fossil dinocysts are mainly known from marine sediments, and appear to be particularly abundant along continental margins (estuaries, continental shelves and slopes, epicontinental seas). Dinocysts are widely used in biostratigraphy and paleoecology of the Mesozoic and Tertiary (e.g., Powell, 1992; Fensome & Williams, 2004). In the field of Late Cenozoic paleoceanography and paleoecology, the study of dinocysts is of growing interest. Because they are composed of resistant organic matter, dinocysts are generally well preserved in most sediment, unlike calcareous or siliceous biological remains that can be affected by dissolution. Moreover, unlike many biological tracers that are stenohaline and thus restricted to open ocean, dinoflagellates dwell in a wide range of salinities and permit investigations in nearshore environments, epicontinental seas or estuaries, in addition to full oceanic environments. However, the concentration of dinocysts in sediment decreases significantly offshore, in low productivity ocean gyre areas (e.g., de Vernal, Turon, & Guiot, 1994; Marret, 1994a; Vink et al., 2000). Thus, dinocyst assemblages seem to be more useful along continental margins and are often viewed as complementary to other tracers more adapted to open ocean conditions, such as calcareous dinoflagellates (e.g., Vink, Brune, Holl, Zonneveld, & Willems, 2002; Vink, 2004), coccoliths (e.g., Winter, Jordan, & Roth, 1994) and planktonic foraminifera (e.g., Bé & Tolderlund, 1971).

Since the early work of Wall, Dale, Lohmann, and Smith (1977), many studies have documented the geographical distribution of modern dinocysts on the sea floor. There are now regional data sets for the North Atlantic and the Arctic Oceans, the circum-Antarctic Ocean, the low latitudes of the Atlantic Ocean, the eastern and western Pacific Ocean margins (see for example, synthesis by Rochon, de Vernal, Turon, Matthiessen, & Head, 1999; de Vernal et al., 2001, 2005a; Marret & Zonneveld, 2003; see also Figure 2; Table 1). These data sets were used to define relationships between the distribution of dinocyst assemblages and hydrographic parameters, notably the temperature, salinity, sea-ice cover and productivity or eutrophication (*cf.* Section 4). In parallel to studies dealing with modern distribution of assemblages, the number of paleoceanographical studies using dinocysts has increased significantly during the last two decades. Many of these studies present empirical interpretations of the assemblages in terms of productivity, salinity or temperature changes. Quantitative reconstructions of oceanographical parameters from dinocyst assemblages were tentatively made using various approaches, including the modern analogue technique (de Vernal et al., 1994). It has been used in particular to estimate late Quaternary temperature and salinity in the North

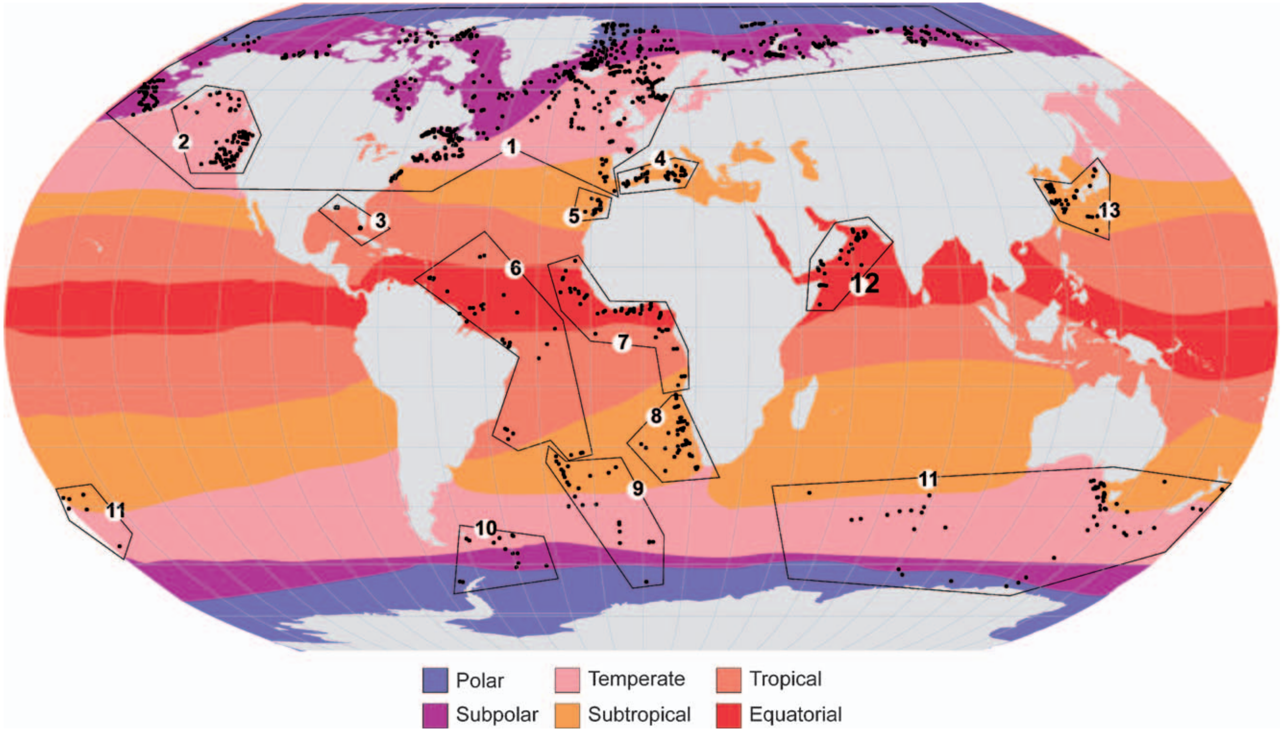

Figure 2 Map of the World Ocean showing the areas where the distributions of organic-walled dinoflagellate cysts in sediment have been documented from the study of assemblages in surface sediments. Climatic provinces after Gross and Gross (1994). For references, see Table 1.

Table 1 List of Publications Documenting the Distribution of Organic-Walled Dinocysts in Surface Sediments.

Data set no.	Location	References
1	Northern Hemisphere	de Vernal et al. (1994); de Vernal, Rochon, Turon, and Matthiessen, (1997); de Vernal et al. (2001, 2005a); Rochon and de Vernal (1994); Rochon et al. (1999); Radi et al. (2001); Voronina, Polyak, de Vernal, and Peyron (2001); Kunz-Pirrung (2001); Grosfjeld and Harland (2001); Mudie and Rochon (2001); Hamel, de Vernal, Gosselin, and Hillaire-Marcel (2002)
2	NE Pacific Ocean	Radi and de Vernal (2004)
3	Gulf of Mexico, Mississippi Sound, Florida Bay	Edwards in Marret and Zonneveld (2003)
4	Mediterranean Sea	Mangin (2002)
5	Canary Islands	Targarona, Warnaar, Boessenkool, Brinkhuis, and Canals (1999)
6	Western tropical and equatorial Atlantic Ocean	Vink, Zonneveld, and Willems (2000)
7	Eastern equatorial Atlantic Ocean	Marret (1994a), Marret and Dupont in Marret and Zonneveld (2003)
8	Namibian margin and SW tropical Atlantic Ocean	Zonneveld, Hoek, Brinkhuis, and Willems (2001a)
9	Southern Atlantic Ocean	Esper, Zonneveld, and Willems (2002)
10	Antarctic and Scotia Sea	Harland, Pudsey, Howe, and Fitzpatrick (1998)
11	Southern Ocean	Marret and de Vernal (1997); Marret, de Vernal, Benderra, and Harland (2001a)
12	Arabian Sea	Zonneveld (1997)
13	W Pacific (Japan)	Matsuoka (1981, 1985); Matsuoka et al. (1999); Kobayashi, Matsuoka, and Lizuka (1986); Cho and Matsuoka (1999)

Source: Updated from Marret and Zonneveld (2003).

Atlantic (e.g., Hillaire-Marcel, de Vernal, Bilodeau, & Weaver, 2001; Solignac, de Vernal, & Hillaire-Marcel, 2004) and in the Southern Ocean (Marret et al., 2001a), as well as to estimate sea-ice cover extent in the North Atlantic during the Last Glacial Maximum (LGM) (de Vernal et al., 2005a; de Vernal, Hillaire-Marcel, Turon, & Matthiessen, 2000). The use of dinocysts in paleoceanography therefore seems useful and unique with respect to some hydrographic parameters (e.g., sea-ice cover). In the present paper, we discuss the state of the art knowledge that allows for the use of dinocysts in paleoceanography, with an emphasis on the strengths and weaknesses of the methods, and we present a few examples of applications selected from the literature.

2. ECOLOGY OF DINOFLAGELLATES

Dinoflagellates live in various types of aquatic environments, including lakes, estuaries, epicontinental seas and oceans, from equatorial to polar settings (e.g., Taylor & Pollingher, 1987; Matthiessen et al., 2005). However, most dinoflagellates are marine: about 2,000 species are known to live in the modern marine waters, whereas only a few hundred species are known to live in freshwater. In marine environments, and within the planktonic communities, dinoflagellates show particularly high species diversity, together with high variability in morphology, and adaptation to a wide range of environments (e.g., Sournia, 1995; Smayda & Reynolds, 2003).

Dinoflagellates are usually abundant in neritic environments, including the estuaries, epicontinental seas and continental shelves. This is due to the high tolerance of many species toward low salinity, in addition to nutrient availability and stratification of water masses (e.g., Pemberton, Rees, Miller, Raine, & Joint, 2004; Gowen & Stewart, 2005). Dinoflagellates can also be abundant offshore in the open ocean (e.g., Pitcher, Walker, Mitchell-Innes, & Moloney, 1991; Veldhuis, de Baar, Kraay, Van Bleijswijk, & Baars, 1997; Smayda & Reynolds, 2003). Particularly high species diversity can be observed near the shelf edge where both low-salinity tolerant taxa and oceanic species can occur together or successively throughout the year.

In addition to salinity gradients, the nearshore to offshore distribution of dinoflagellates can be related to many parameters that include nutrients and water mass stratification. Smayda and Reynolds (2001, 2003) examined the ecology of dinoflagellates and the relationships between their living populations and abiotic parameters. They distinguished nine pelagic habitats characterized by specific life forms and assemblages, which correspond to a nearshore–offshore gradient of decreasing nutrients, reduced mixing and increasingly deeper euphotic zone. Turbulence, in particular, is an important parameter in dinoflagellate distribution because it has an inhibitory effect on dinoflagellate cyst growth and reproduction, which may vary depending on the species (e.g., Gibson & Thomas, 1995; Gibson, 2000).

Dinoflagellates are adapted to a wide range of temperatures. Although particularly high species diversity is observed in intertropical areas, assemblages show a relatively high number of species in polar environments, where some taxa appear tolerant toward extensive sea-ice cover (e.g., Matthiessen et al., 2005). The ability of dinoflagellates to encyst in relation to sexual reproduction, or to make temporary cysts in case of adverse conditions possibly explains their occurrence even in extremely harsh environments (e.g., Graham & Wilcox, 2000).

The feeding strategies of dinoflagellates are diverse. Many are phototrophic, with peridinin as the dominant pigment, and account for an important part of the primary production together with coccolithophorids and diatoms (e.g., Parsons, Takahashi, & Hargrave, 1984; Taylor & Pollingher, 1987). In general, dinoflagellates produce their blooms after diatoms, which have the ability to reproduce much more rapidly than dinoflagellates. Many dinoflagellate species are heterotrophic or mixotrophic, feeding on other organisms or on dissolved organic substances (e.g., Taylor & Pollingher, 1987; Gaines & Elbrachter 1987). Most families actually include both autotrophic and heterotrophic taxa (Schnepf & Elbrächter, 1999; Smayda & Reynolds, 2003). Dinoflagellates as a group belong to either to phytoplankton or to microzooplankton. They are usually recovered together in plankton samples collected in the upper 50 m (e.g., Dodge & Harland, 1991) or 100 m (e.g., Raine, White, & Dodge, 2002) of the water column. Their living depth is relatively shallow (down to the bottom of the euphotic zone) because the autotrophic taxa are dependant upon light penetration, and because the habitat of the heterotrophic species appears to be closely coupled to diatoms, on which they particularly feed, and/or to the maximum chlorophyll zone (e.g., Gaines & Elbrachter, 1987).

Dinoflagellates are mobile in the water column. They have two flagella, one around the cingulum and the other longitudinal (Figure 3), which allow swimming with a "whirling" motion at a speed ranging from a few centimeters to a few meters per hour. They use their flagella together with physiological adjustments of buoyancy to migrate vertically on a diurnal basis in the upper waters, in order to optimize their metabolic and feeding activities. Despite their ability to move vertically, dinoflagellates generally inhabit a relatively thin and shallow surface layer, especially in stratified marine environments, because most of the taxa cannot migrate across the pycnocline, which represents an important physical barrier (*cf.* Levandowsky & Kaneta, 1987).

The reproduction of dinoflagellates is most commonly asexual by mitosis. In bloom periods, vegetative cell division occurs at a rate of about one per day. Sexual reproduction has been observed for many species. During blooms, dinoflagellates can be responsible for "red tides," so-called because the very large number of cells in the surface water induces a color change. Some dinoflagellates are bioluminescent and cause sparkling of the sea at night. A few dinoflagellate species produce neurotoxins that may be bioconcentrated by filtering organisms, notably shellfish, which then become poisonous and dangerous for human consumption, as well as to the animals feeding on them.

3. DINOFLAGELLATES VS. DINOCYSTS AND TAPHONOMICAL PROCESSES (FROM THE BIOCENOSES TO THANATHOCENOSES)

3.1. Living vs. Fossil Dinoflagellates

The relationships between living populations and the cyst assemblages in sediment are difficult to establish for several reasons. (1) Dinocysts represent only a fragmentary

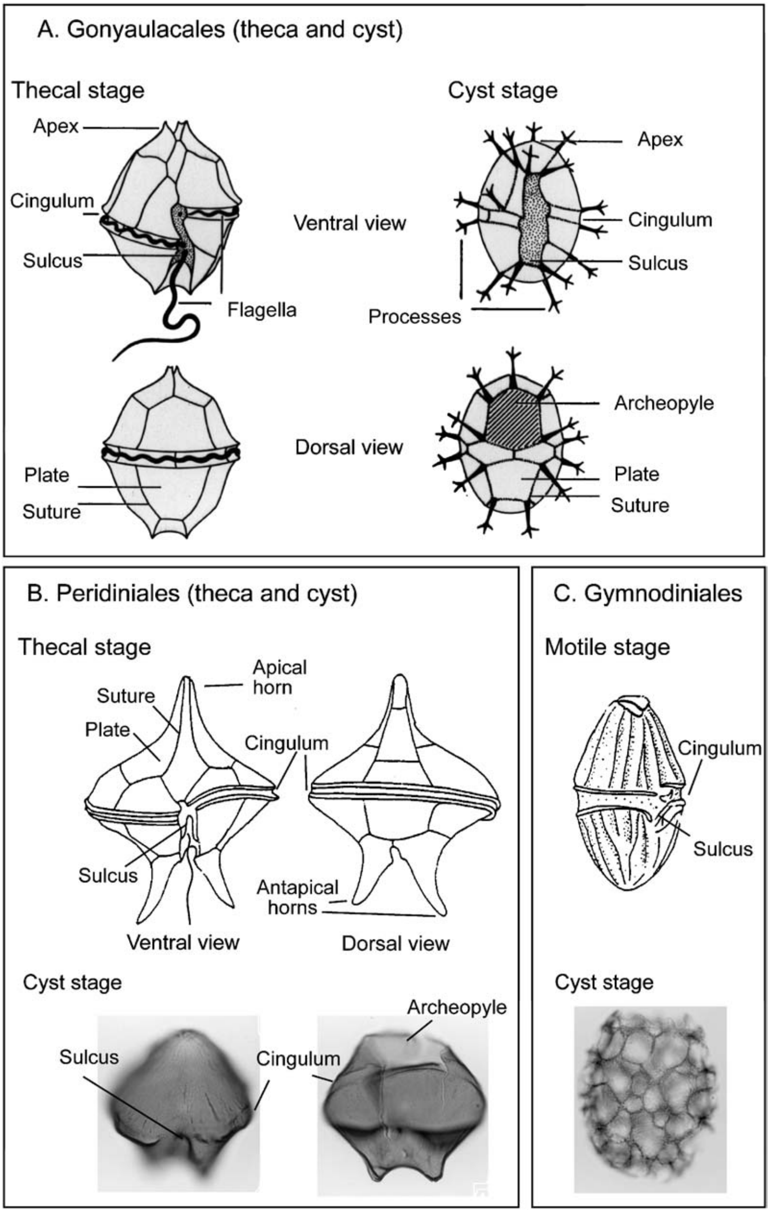

Figure 3 Schematic illustration of the main types of dinoflagellate cysts routinely recovered in marine sediments. A: Illustration of the morphology of Gonyaulacales (theca of *Gonyaulax* sp. and corresponding cyst belonging to the genus *Spiniferites*). B: Illustration of the morphology of Peridiniales (theca of *Protoperidinium* sp. and photograph of the cyst of *Quinquecuspis concreta*). C: Illustration of Gymnodiniales, which are athecate by definition (motile stage and cyst of *Polykrikos schwartzii*).

picture of the original dinoflagellate populations, as only 10–20% of the species produce cysts that can be fossilized (Dale, 1976; Head, 1996; Matthiessen et al., 2005; *cf.* Table 2). Amongst dinoflagellates, there are three main groups producing organic-walled microfossils: the Gymnodiniales and the Peridiniales that mostly include heterotrophic taxa, and the Gonyaulacales that are autotrophic (Figure 3, Table 2). Many of the dinoflagellate taxa producing organic-walled cysts belong to life-form types that are characteristic of nearshore and continental margin habitats (*cf.* Smayda & Reynolds, 2001). (2) The morphology of dinoflagellate cells and that of their cysts often differ significantly, which led to the development of different nomenclatures by biologists and paleontologists. (3) Finally, because the biological affinities of many Quaternary and most pre-Quaternary dinocysts are still uncertain (*cf.* Head, 1996; *cf.* Figure 3, Table 2 and Plates), the ecological affinities of most taxa cannot be documented easily from that of their living counterparts.

Laboratory cultures have permitted the life cycle of many dinoflagellate species to be reproduced to the motile cells starting from cysts recovered in sediment, and from living populations to the cyst stage. These studies have shown that cysts are viable many years after burial and sampling of the sediments (Lewis, Harris, Jones, & Edmonds, 1999; McQuoid, Godhe, & Nordberg, 2002), and have helped to confirm the taxonomical affinities of many taxa (e.g., Wall & Dale, 1968; Head, 1996; Ellegaard, Daugbjerg, Rochon, Lewis, & Harding, 2003). They also showed that cysts of the same motile species may differ morphologically depending on salinity and temperature (e.g., Ellegaard, Lewis, & Harding, 2002; Zonneveld & Susek, 2006).

3.2. Biogeography of Motile Cells vs. Distribution of the Cysts in Sediments

There are limited studies coupling information on planktonic dinoflagellates and fluxes of dinocysts to the sea floor. Nevertheless, it seems that the biogeographical distributions of cyst-forming dinoflagellates in surface waters and that of dinocysts in sediments are generally consistent with each other (e.g., Dodge, 1994). There is a general consistency with respect to nearshore–offshore patterns and latitudinal gradients, which closely relate to salinity and temperature controlled by current patterns (e.g., Dodge & Harland, 1991; Dodge, 1994; Raine et al., 2002). However, the detailed comparison of observations based on motile populations in the water column, sediment-trap contents, and cyst assemblages on the sea floor does not yield a perfect correspondence. This can be due in part to the fact that motile dinoflagellates sampled from the plankton correspond to an instantaneous time interval, whereas the cysts in the upper first centimeter of the sediments may represent several years, decades or even centuries of sedimentary fluxes. The analyses of traps collected throughout annual cycles illustrate seasonal patterns of cyst production, with the maximum recorded during summer, and species-specific duration of cyst production periods; they also show variations from one year to another in the overall fluxes (Montresor, Zingone, & Sarno, 1998).

Table 2 List of Main Dinocyst Taxa Recovered in Recent Marine Sediments and General Affinities.

Dinocyst species name	Motile affinity	Order
Ataxiodinium choane	*Gonyaulax* sp.	Gonyaulacales
Bitectatodinium spongium	Unknown	Gonyaulacales
Bitectatodinium tepikiense	*Gonyaulax* sp.	Gonyaulacales
Brigantedinium cariacoense	*Protoperidinium avellanum*	Peridiniales
Brigantedinium simplex	*Protoperidinium conicoides*	Peridiniales
Dalella chathamensis	*Gonyaulax* sp.	Gonyaulacales
Dubridinium caperatum	*Preperidinium meunieri*	Perdiniales
Echinidinium aculeatum	Unknown	Peridiniales
Echinidinium bispiniformum	Unknown	Peridiniales
Echinidinium delicatum	Unknown	Peridiniales
Echinidinium granulatum	Unknown	Peridiniales
Echinidinium karaense	Unknown	Peridiniales
Echinidinium transparantum	Unknown	Peridiniales
Cysts of *Gymnodinium catenatum*	*Gymnodinium catenatum*	Gymnodiniales
Impagidinium aculeatum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium pacificum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium pallidum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium paradoxum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium patulum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium plicatum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium sphaericum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium strialatum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium variaseptum	*Gonyaulax* sp.	Gonyaulacales
Impagidinium velorum	*Gonyaulax* sp.	Gonyaulacales
Islandinium brevispinosum	*Protoperidinium* sp.	Peridiniales
Islandinium? cezare	*Protoperidinium* sp.	Peridiniales
Islandinium minutum	*Protoperidinium* sp.	Peridiniales
Leipokatium invisitatum	Unknown	Peridiniales
Lejeunecysta oliva	Unknown	Peridiniales
Lejeunecysta Sabrina	*Protoperidinium leone*	Peridiniales
Lingulodinium machaerophorum	*Lingulodinium polyedrum*	Gonyaulacales
Nematosphaeropsis labyrinthus	*Gonyaulax spinifera*	Gonyaulacales
Nematosphaeropsis rigida	*Gonyaulax* sp.	Gonyaulacales
Operculodinium centrocarpum-short processes form	*Protoceratium reticulatum*	Gonyaulacales
Operculodinium short processes	*Protoceratium reticulatum*	Gonyaulacales
Operculodinium israelianum	*Protoceratium* sp.	Gonyaulacales
Operculodinium janduchenei	Unknown	Gonyaulacales
Operculodinium longispinigerum	Unknown	Gonyaulacales
Cysts of *Pentapharsodinium dalei*	*Pentapharsodinium dalei*	Peridiniales
Cysts of *Pheopolykrikos hartmannii*	*Pheopolykrikos hartmannii*	Gymnodiniales
Cyst of *Polykrikos* sp.-Arctic morphotype	*Polykrikos* sp.	Gymnodiniales
Cysts of *Polykrikos kofoidii*	*Polykrikos kofoidii*	Gymnodiniales
Cysts of *Polykrikos schwartzii*	*Polykrikos schwartzii*	Gymnodiniales
Polysphaeridium zoharyi	*Pyrodinium bahamense*	Gonyaulacales

Table 2 (*Continued*)

Dinocyst species name	Motile affinity	Order
Cysts of *Protoperidinium americanum*	*Protoperidinium americanum*	Peridiniales
Cysts of *Protoperidinium nudum*	*Protoperidinium nudum*	Peridiniales
Cysts of *Protoperidinium stellatum*	*Protoperidinium stellatum*	Peridiniales
Pyxidinopsis psilata	Unknown	Gonyaulacales
Pyxidinopsis reticulata	Unknown	Gonyaulacales
Quinquecuspis concreta	*Protoperidinium leone*	Peridiniales
Cysts of cf. *Scrippsiella trifida*	*Scippsiella trifida*	Gonyaulacales
Selenopemphix antarctica	Unknown	Peridiniales
Selenopemphix nephroides	*Protoperidinium subinerme*	Peridiniales
Selenopemphix quanta	*Protoperidinium conicum*	Peridiniales
Spiniferites alaskensis	*Gonyaulax* sp.	Gonyaulacales
Spiniferites belerius	*Gonyaulax scrippsae*	Gonyaulacales
Spiniferites bentorii	*Gonyaulax digitale*	Gonyaulacales
Spiniferites bulloideus	*Gonyaulax scrippsae*	Gonyaulacales
Spiniferites cruciformis	*Gonyaulax sp.*	Gonyaulacales
Spiniferites delicatus	*Gonyaulax* sp.	Gonyaulacales
Spiniferites elongatus	*Gonyaulax* sp.	Gonyaulacales
Spiniferites frigidus	*Gonyaulax* sp.	Gonyaulacales
Spiniferites hyperacanthus	*Gonyaulax* sp.	Gonyaulacales
Spiniferites lazus	*Gonyaulax* sp.	Gonyaulacales
Spiniferites membranaceus	*Gonyaulax* sp.	Gonyaulacales
Spiniferites mirabilis	*Gonyaulax spinifera*	Gonyaulacales
Spiniferites pachydermus	*Gonyaulax* sp.	Gonyaulacales
Spiniferites ramosus	*Gonyaulax* sp.	Gonyaulacales
Stelladinium reidii	Unknown	Peridiniales
Stelladinium robustum	Unknown	Peridiniales
Tectatodinium pellitum	*Gonyaulax spinifera*	Gonyaulacales
Trinovantedinium applanatum	*Protoperidinium pentagonum*	Peridiniales
Trinovantedinium variabile	Unknown	Peridiniales
Tuberculodinium vancampoae	*Pyrophacus steinii*	Gonyaulacales
Votadinium calvum	*Protoperidinium oblongum*	Peridiniales
Votadinium spinosum	*Protoperidinium claudicans*	Peridiniales
Xandarodinium xanthum	*Protoperidinium divaricatum*	Peridiniales

Notes: Grey highlighting: heterotrophic or mixotrophic taxa; no highlighting: autotrohic taxa.

3.3. Sedimentation

Part of the differences observed between plankton populations and microfossil contents of deep-sea sediments could be attributed to some lateral transport. The sinking rate of microscopic remains such as dinocysts, or any small size microfossil, is difficult to estimate, but the settling of individual cells or cysts is slow (in the order of meters per day). Incorporation within fecal pellets and marine "snow" particles, which consist of cohesive aggregates of microscopic organic material having a density high enough to sink in the water column, are mechanisms likely to explain the vertical fluxes of pelagic particles over hundreds or thousand of meters (see review by Turner, 2002). The dinocyst assemblages on the sea floor are most probably related to production in the upper part of the water column above the site location, and to subsequent sedimentation within marine snow and fecal pellets. A few trap studies in high productivity areas, comparing assemblages at different depths, indeed suggest that vertical sedimentation of dinocysts is very rapid and that lateral transport is limited (e.g., Zonneveld & Brummer, 2000). However, some lateral transport with surface, intermediate or bottom currents cannot be ruled out, especially in areas of low productivity where any reworking or lateral input can weigh significantly on the "local" assemblages.

3.4. Preservation

Dinocysts are made of highly resistant organic polymers (e.g., Kokinos et al., 1998; Versteegh & Blokker, 2004) and are usually preserved very well in marine sediments, unlike diatoms or foraminifera that are prone to dissolution of opal silica or calcium carbonate, respectively. From this point of view, dinocysts represent an extremely useful proxy of ocean changes in regions of the world's oceans where calcium carbonate dissolution occurs (because of a shallow lysocline and oxidation of organic matter-rich sediments that create a high pCO_2). However, it has been noticed that some taxa may be affected by strong oxidation: laboratory treatments show that acetolysis or strong oxidants may selectively destroy some taxa, in particular *Protoperidinium* species (e.g., Dale, 1976; Marret, 1993; Brenner & Biebow, 2001). In a field experiment, Zonneveld, Versteegh, and deLange (1997, 2001b) classified a number of taxa according to their sensitivity to oxygen availability in bottom waters (Table 3). Selective degradation of the cyst wall of some dinocyst taxa could be a limitation, especially in areas characterized by oxygen-rich bottom waters and low sedimentation rates, preventing rapid burial of the organic matter.

4. RELATIONSHIPS BETWEEN DINOCYST ASSEMBLAGES AND SEA-SURFACE PARAMETERS

Despite uncertainties about the biological affinities of organic-walled dinoflagellate cysts and caveats concerning lateral dispersion and preservation, the distribution of dinocyst assemblages on the sea floor is illustrative of relationships with hydrographical parameters and productivity in surface waters.

On a qualitative or quantitative basis, the species composition of assemblages appears informative at different levels: sea-level changes, biogeography, sea-surface conditions (sea-ice cover duration, temperature, salinity and productivity), hydrological fronts, etc. The pioneering work of Wall et al. (1977) enabled us to view dinocysts as potential paleoceanographical proxies, prompting a number of paleoenvironmental studies. Consequently, numerous studies based on the present-day distribution of dinocysts have allowed for the definition of environmental indices.

Table 3 Organic-Walled Cysts Grouped in Relation to Their Sensitivity to Oxygen Availability in Bottom Waters.

Sensitivity to oxygen	Organic-walled cysts
Extremely sensitive	Cysts from *Protoperidinium* species *Echinidinium* species
Moderately sensitive	*Lingulodinium machaerophorum* *Operculodinium centrocarpum* *Pyxidinopsis reticulata* *Spiniferites* species (*S. bentorii*, *S. mirabilis*, *S. pachydermus*, *S. ramosus*) *Nematosphaeropsis labyrinthus*
Resistant	*Impagidinium species (I. aculeatum, I. paradoxum, I. patulum, I. plicatum, I. Sphaericum)* *Operculodinium israelianum* Cysts of *Pentapharsodinium dalei* *Polysphaeridium zoharyi*

Source: Data collected from Zonneveld et al. (2001b).

In the early 1980s, Turon (1980) and Harland (1983) were the first to produce distribution maps of dinocysts on the sea-floor. Harland (1983) published the relative abundance of 42 taxa for the North Atlantic Ocean and adjacent seas, initiating an international interest. Since the 1980s, numerous studies from around the world have permitted the definition of distribution patterns at regional levels, and have led to the determination of relationships between cyst assemblages and sea-surface conditions (e.g., Matsuoka, 1985; Baldwin, 1987; Bint, 1988; Dodge & Harland, 1991; Edwards & Andrle, 1992; Mudie, 1992; de Vernal et al., 1994; Sun & Mcminn, 1994; Ellegaard, Christensen, & Moestrup, 1994; Marret, 1994a; Matthiessen, 1994; Mudie & Harland, 1996; Marret & de Vernal, 1997; Sonneman & Hill, 1997; Zonneveld, 1997; Harland et al., 1998; Rochon et al., 1999; Godhe, Karunasagar, Karunasagar, & Karlson, 2000; Persson, Godhe, & Karlson, 2000; Vink et al., 2000; Grosfjeld & Harland, 2001; Mudie & Rochon, 2001; Zonneveld et al., 2001a; Cho, Kim, Moon, & Matsuoka, 2003; Debenay et al., 2003; Morquecho & Lechuga-Devèze, 2003; Azanza et al., 2004; Kawamura, 2004; Orlova, Morozova, Gribble, Kulis, & Anderson, 2004; Radi & de Vernal, 2004; Sangiorgi, Fabbri, Comandini, Gabbianelli, & Tagliavini, 2005; *cf.* Table 1).

4.1. Nearshore vs. Offshore Distribution, Sea-Level and Continentality Indices

The study of Wall et al. (1977) illustrated a biogeographic zonation reflecting the distance to the shore based on the identification of inner neritic, outer neritic and oceanic taxa. Thus, the species composition of assemblages and the relative abundance of taxa have been used as indicators of sea level, assuming that lateral and down-slope transports are minimal and that preservation bias is negligible. The

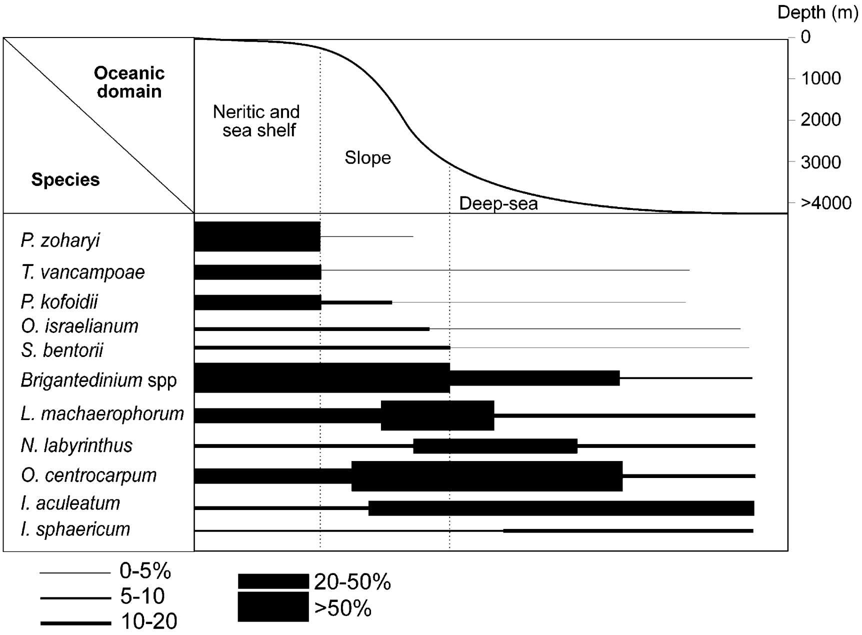

Figure 4 Relative abundance vs. water depth of the most common dinocyst taxa in temperate to equatorial regions (40°N to 40°S). Data compiled from Dale et al. (2002), Marret and Zonneveld (2003), and de Vernal et al. (2005).

schematic profile in Figure 4 clearly shows that some taxa have a specific distribution in the oceanic domain, hence they are commonly used to assess sea-level changes and to make biogeographical reconstructions (e.g., Morzadec-Kerfourn, 1992; Harland & Long, 1996; Marret, Scourse, & Austin, 2004b). However, the relationship between sea level and dinocyst assemblages is indirect, and reflects a combination of many parameters that often characterize nearshore–offshore gradients, notably the turbulence, water mass stratification and nutrient availability. Because these gradients are changing along frontal zones and upwellings, dinocysts should be used cautiously as a sea-level indicator.

Dinocysts are relatively abundant in estuarine environments, which are generally characterized by stratified waters and strong salinity gradients because of dilution with freshwater discharge. Estuarine regions play an important role in the global carbon cycle as they procure nutrient enrichment that triggers high primary productivity. In low latitude environments, deep-sea fans are ideal archives for past environments and land–ocean interaction records. River discharge events in past deep-sea sediments can be appraised by: (1) increase of freshwater algae flux (i.e., *Pediastrum*, *Botryococcus*); (2) increase of neritic or lagunal species (such as *Tuberculodinium vancampoae* and *Polysphaeridium zoharyi*) in the case of West African sequences; (3) higher ratio of the terrestrial vs. marine palynomorph content; (4) occurrence peaks of old palynomorphs reworked from sedimentary outcrops. Pollen grains are commonly found in marine sediments. Along continental margins, pollen concentration is high

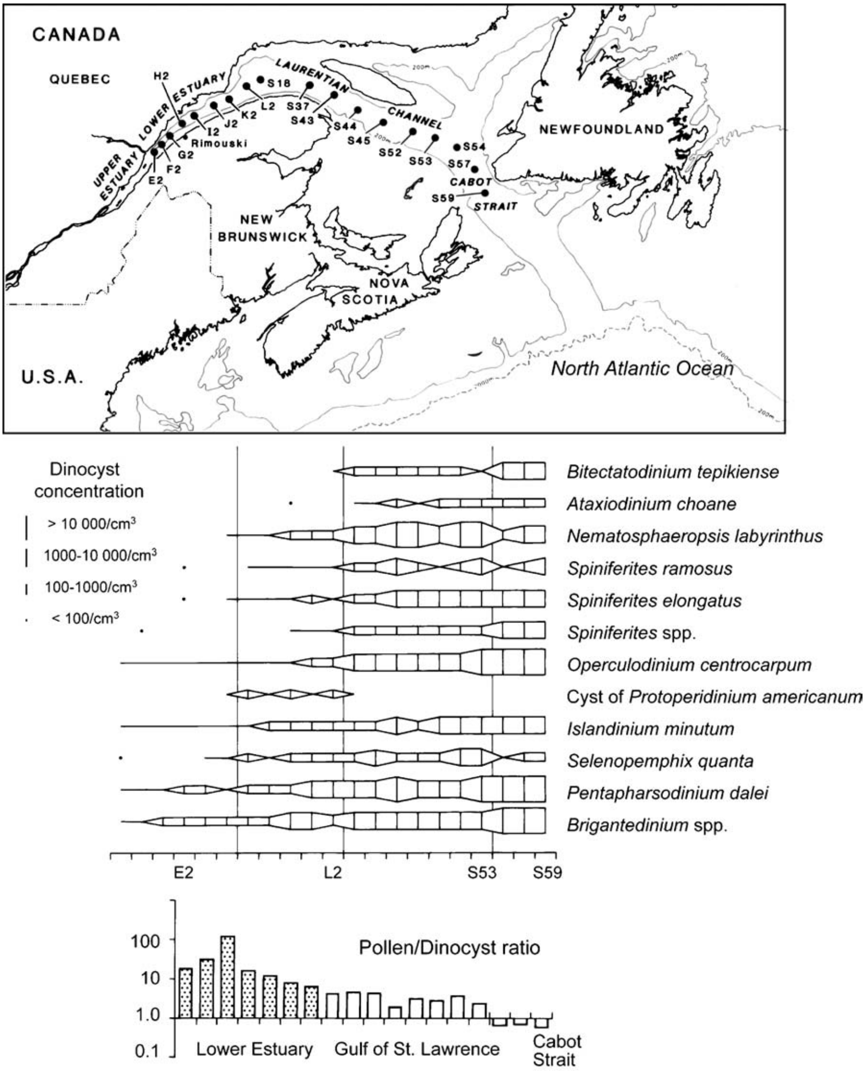

Figure 5 Concentrations of the most common dinocyst taxa (middle panel) and ratio of pollen vs. dinocyst concentration (lower panel) from the lower St. Lawrence Estuary to the Cabot Strait at the edge of the Atlantic Ocean, where sea-surface salinity in August ranges from 24 (E2) to 31 (S59). The figure is redrafted with permission from de Vernal and Giroux (1991).

and decreases rapidly toward open oceanic environments. Transport mechanisms involve eolian and fluvial processes, and pollen flux is often considered to be an indicator of the dynamics of the transport mechanism (e.g., Melia, 1984; Hooghiemstra & Agwu, 1986; Dupont & Agwu, 1991; Dupont, 1999; Dupont & Wyputta, 2003). The (pollen+spores)/dinocyst (or P/D) ratio enables the qualification of the origin of the organic flux, i.e. terrestrial vs. marine, with values tending to zero toward the open ocean (de Vernal & Giroux, 1991; see Figure 5). This "continentality" index reflects the proportion of terrestrial microfossils transported by rivers or in the atmosphere, although production at the source, storage and reworking, differential preservation of both terrestrial and marine palynomorphs may also influence this ratio.

4.2. Salinity

Dinocysts are found from freshwater to hypersaline environments, with only a few species occurring within a restricted salinity range (e.g., Wall et al., 1977; Dodge & Harland, 1991; de Vernal et al., 1994; Dale, 1996; Marret & Zonneveld, 2003). Oceanic taxa, such as *Impagidinium*, are only found where fully saline conditions occur, whereas most of the taxa seem to be euryhaline. However, brackish environments, such as the Baltic Sea, the Black sea and other Central Asian seas, contain assemblages characterized by a high morphological variability and very low diversity (less than eight taxa) (Dale, 1996; Mudie, Aksu, & Yasar, 2001a; Mudie, Harland, Matthiessen, & de Vernal, 2001b; Marret, Leroy, Chalie, & Gasse, 2004a). The cruciform shape of the cyst body typical in these regions, or the process length, had been initially attributed to low salinity or environmental stress by Wall and Dale (1973). Mudie, Rochon, Aksu, and Gillespie (2002) attempted to associate morphotypes of *Spiniferites cruciformis* with a specific salinity range; although the relationship was unclear, they observed that extreme morphotypes (i.e., the most and the least developed processes) seemed to be dominant at the extremities of the salinity range. Lewis and Hallett (1997) documented that *L. machaerophorum*, a euryhaline species, may develop shorter processes with low saline conditions, although all shapes have been found with a constant salinity. Other species, such as *Operculodinium centrocarpum* (Nehring, 1994, 1997) or cysts of *Gonyaulax baltica* (Ellegaard et al., 2002), also present considerable variations in process length that have been attributed to low saline conditions. However, the relationship between variations of processes and salinity is not clearly demonstrated on a quantitative basis for many species, and other environmental factors such as turbulence, temperature or density may affect the development of the cysts and their morphological attributes (Kokinos & Anderson, 1995; Zonneveld & Susek, 2006; Lewis, personal communication).

In areas characterized by a large amplitude gradient of salinity such as estuaries and continental margins, a relationship can be established between the assemblages of dinocysts and sea-surface salinity. This can be shown on a qualitative basis, in the Estuary and Gulf of St. Lawrence for example (*cf.* de Vernal & Giroux, 1991; Figure 5). This has been illustrated using multivariate analyses, in the northwest North Atlantic, for example (e.g., de Vernal et al., 1994; Rochon et al. 1999). However, although quantitative relationships between dinocyst assemblages and salinity are clear in some marine environments, they cannot be extrapolated unequivocally on a hemispheric or global scale.

4.3. Sea-Surface Temperature and Seasonality

Dinocysts are found in marine sediment from polar to tropical environments. In general, the diversity of species decreases from the tropics to the poles, although the dinocyst concentration can be very high in Arctic seas and subpolar seas (e.g., de Vernal et al., 2001, 2005a). More than 60 taxa have been recorded in the Northern Hemisphere, but only 10 to 12 taxa are common in the Arctic seas. They include opportunistic or ubiquitous taxa, such as *Operculodinium centrocarpum* and *Brigantedinium* spp. They also include a few taxa that seem adapted to particularly cold conditions (notably *Impagidinium pallidum*, cyst of *Polykrikos* sp. Arctic morphotype, *Islandinium* spp.). In the southern hemisphere also, there is a gradient of decreasing diversity toward the pole where a few taxa seem to characterize cold conditions (*Selenopemphix antarctica* in particular; Marret & de Vernal, 1997). From high to low latitudes, the increase in the number of species is related to increased temperature (Figure 6). The relative abundance of many taxa also varies in relation with sea-surface temperatures (SST), either annually or seasonally (Edwards & Andrle, 1992; Marret, 1994a; Marret & Zonneveld, 2003). Multivariate analyses further support the determining influence of SST in taxa and assemblage distribution, both at regional or hemispheric scales (e.g., Marret, 1994a; Marret & Zonneveld, 2003; Marret et al., 2001a; Rochon et al., 1999; de Vernal et al., 1994, 1997, 2001, 2005a; Radi & de Vernal, 2004).

The existence of a relationship between SST and dinocyst assemblages is unquestionable. However, this relationship is most probably season-dependent. In high latitudes, the bloom of dinoflagellates, which is often followed by encystment, most frequently occurs during summer after the diatom bloom (e.g., Matthiessen et al., 2005). Therefore, it can be assumed that dinocyst assemblages are mainly related to summer SSTs. However, dinoflagellates and their cyst population also appear dependent upon the temperature changes over the annual cycle. The overall life cycle of dinoflagellates and cyst production can take place over a few weeks to over a few months, depending upon the taxon. In polar seas where the ice-free season is very short, only the species having the ability to form cysts in a short time can develop. The seasonal constraint is low in intertropical environments, but possibly plays an important role on determining the abundance of taxa in temperate regions. Actually, the distribution of dinocyst assemblages in the North Atlantic and adjacent subpolar and polar seas suggests a relationship between dinocyst assemblages and the seasonality, as expressed by the difference between the coldest and warmest months (e.g., de Vernal et al., 1994, 2001; Rochon et al., 1999). For example, some taxa, such as *Bitectatodinium tepikiense*, apparently require a high summer temperature but tolerate freezing winter conditions, whereas many other thermophilic taxa do not tolerate a wide amplitude temperature gradient from winter to summer (e.g., *Impagidinium aculeatum* or *Spiniferites mirabilis*). Seasonality is also probably a parameter that plays a major role in dinoflagellate distribution, ecology and cyst production (Figure 7).

4.4. Sea-Ice Cover

Biogeographical distribution of dinocysts shows that some taxa have affinities for polar environments, and some may be used as sea-ice indicators. In their study, Matthiessen et al. (2005) presented a general review of Arctic taxa and their ecological significance. Only two cyst-forming species are known to dwell in the

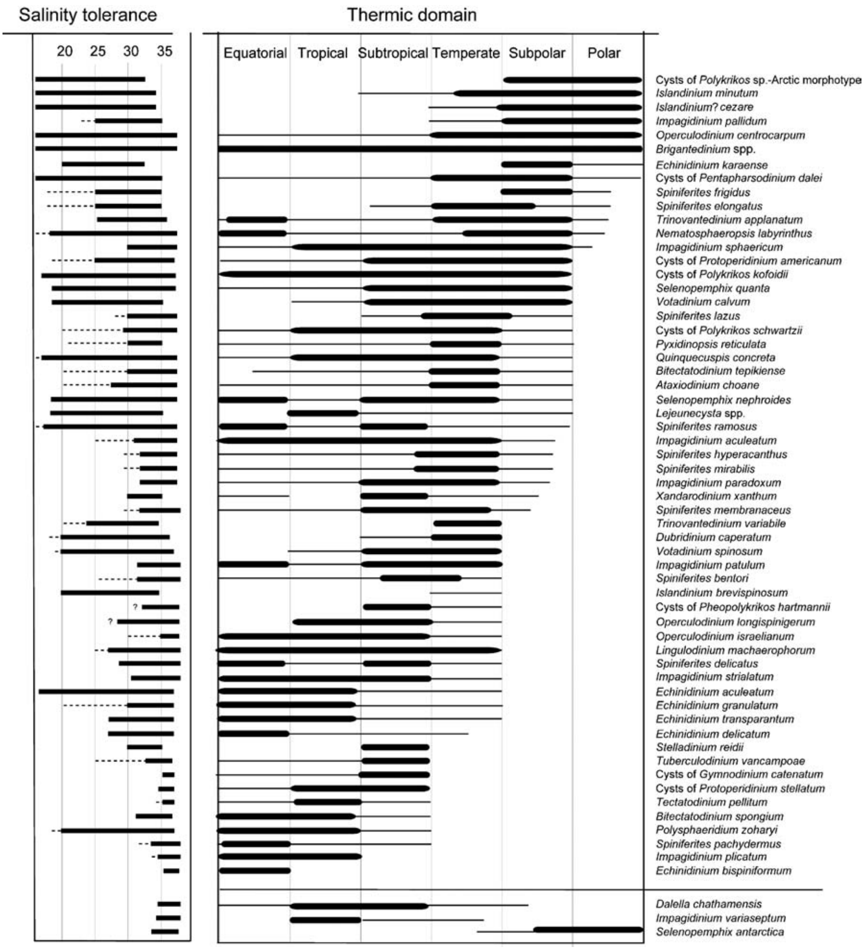

Figure 6 Diagram showing the known distribution of the main dinocyst taxa in surface sediments according to bioclimatic domains and their salinity tolerance. The compilation was made from Marret and Zonneveld (2003), Radi and de Vernal (2004) and de Vernal et al. (2005a). Note that *Dalella chathamensis*, *Selenopemphix antarctica* and *Impagidinium variaseptum* are taxa exclusively reported to occur in the Southern Ocean. A few taxa also seem to occur exclusively in middle- to high latitudes of the northern Hemisphere: *Polykrikos* sp. — Arctic morphotype, *Spiniferites elongatus*, *Spiniferites frigidus*, and *Trinovantedinium variabile*.

ice-pack environment, *Polarella glacialis* and *Peridiniella catenata*. However, their cysts were not recovered in sediment. The sea-floor sediments of areas characterized by multiyear perennial pack-ice are usually barren of dinocysts (e.g., Rochon et al., 1999; de Vernal et al., 2005a). Nevertheless, there are a few dinocyst taxa that are known to occur in sediments of areas marked by seasonal sea-ice. In both hemispheres, and especially in Arctic and subarctic seas, *Islandinium* species are often abundant (e.g., Pienkowski-Furze, 2004; de Vernal et al., 2005a). *Selenopemphix antarctica* is also characteristic of seasonal sea-ice cover, but its occurrence is

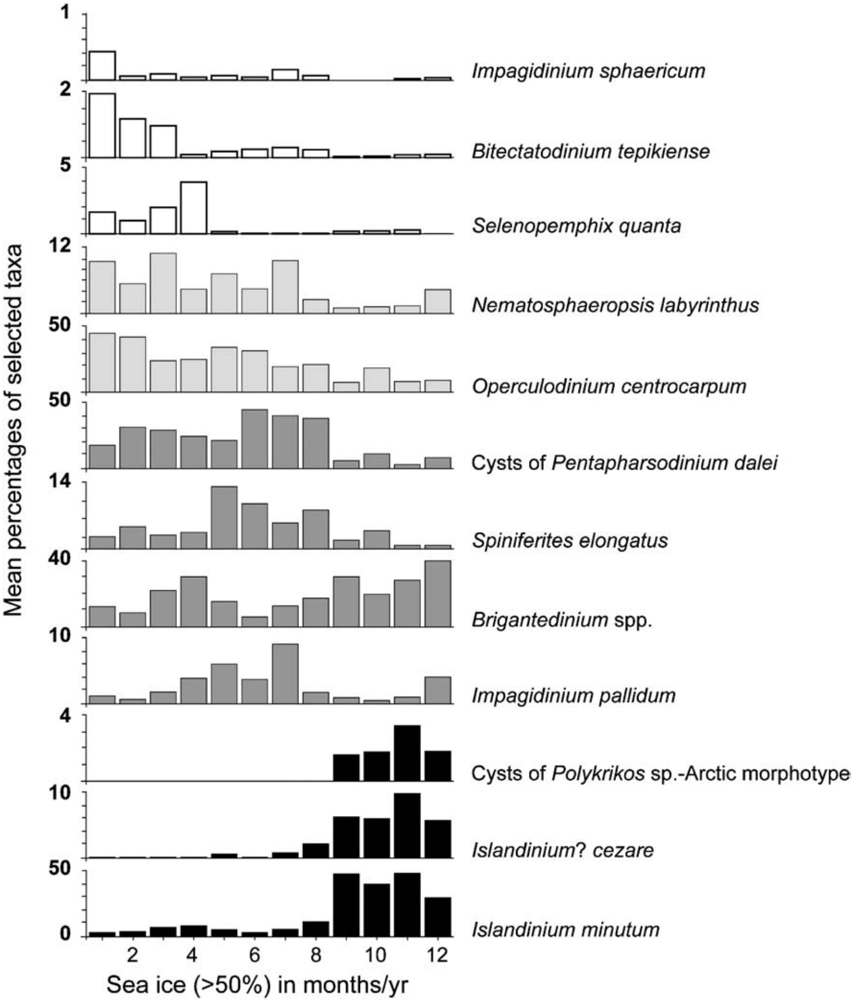

Figure 7 Mean percentage of selected dinocyst taxa vs. sea-ice extent in months per year with more than 50% of ice concentration. The compilation was made from the North Atlantic and Arctic Ocean database (*cf.* de Vernal et al., 2001).

restricted to the circum Antarctic Ocean (Marret & de Vernal, 1997; de Vernal et al., 2001). Similarly, the cyst of *Polykrikos* sp. — Arctic morphotype exclusively occurs in ice-covered marine environments of the Northern Hemisphere. Many other taxa appear tolerant to sea-ice cover and may occur in high proportions in sea-ice environments. This is particularly the case of the ubiquitous taxa *Operculodinium centrocarpum* and *Brigantedinium* spp. Other taxa such as *Pentapharsodinium dalei*, *Spiniferites elongatus-frigidus* and *Impagidinium pallidum* have affinities for subarctic environments and often characterize areas of winter sea-ice (e.g., de Vernal et al., 2001; Figure 7).

4.5. Productivity, Upwelling and Polynyas

Dinocyst assemblages that include both phototrophic and heterotrophic taxa seem to reflect the trophic characteristics of the upper water mass (e.g., Devillers & de Vernal, 2000). Paradoxically, high productivity areas such as upwellings or polynyas are usually characterized by the dominance of heterotrophic dinocysts (e.g., Lewis, Dodge, & Powell, 1990; Hamel et al., 2002; Radi & de Vernal, 2004). This can be attributed to competition among primary producers, diatoms being dominant in high nutrient contexts because they reproduce at a much faster rate (up to eight cell divisions per day) than dinoflagellates (about one division per day). Therefore, in upwellings and polynyas, diatoms are advantaged in as much as nutrients are not limiting. In these environments, heterotrophic dinoflagellates feeding on diatoms can be very abundant. The main dinocyst taxa commonly used for reconstructing the strength of upwelling regimes belong to the heterotrophic *Protoperidinium* group. The ratio Protoperidiniaceae/Gonyaulacaceae (P/G) was first documented by Lewis et al. (1990) to illustrate changes in the upwelling intensity along the Peruvian margins. This ratio has been broadly used and adapted, with the inclusion of heterotrophic species such as *Polykrikos* (Marret, 1994a) or *Echinidinium* (Esper, Versteegh, Zonneveld, & Willems, 2004) species, to look into past variations of upwelling systems along the west African margin (Susek, Zonneveld, Fischer, Versteegh, & Willems, 2005).

Over the last decade, a number of studies have documented qualitatively and quantitatively the cyst distribution in recent sediments from many high productivity regions such as NW European shelves (Dale, 1996; Nehring, 1997; Grosfjeld & Harland, 2001; Marret & Scourse, 2002; Marret et al., 2004b), Arctic and subarctic areas (de Vernal et al., 2001; Hamel et al., 2002), and coastal upwelling areas from the west African margin, NW America, the Peruvian margin and the Arabian Sea (e.g., Marret, 1994b; Blanco, 1995; Biebow, 1996; Zonneveld, 1997; Zonneveld et al., 2001a; Dale, Dale, & Jansen, 2002; Marret & Zonneveld, 2003; Radi & de Vernal, 2004; Sprangers, Dammers, Brinkhuis, Van Weering, & Lotter, 2004; Joyce, Pitcher, du Randt, & Monteiro, 2005; Susek et al., 2005). In general, dinocyst assemblages from high productivity environments are dominated by heterotrophic taxa (Figure 8). However, the species composition of assemblages differs from one site to another in relation to latitude (Table 4), and shelf areas from the northeast North Atlantic and North Pacific that are not under upwelling influence contain high proportions of autotrophic gonyaulacoid taxa (*Operculodinium centrocarpum*, *Spiniferites* species), accompanied by cysts of *Pentapharsodinium dalei* (e.g., Voronina et al., 2001; Marret & Zonneveld, 2003; Radi, Pospelova, de Vernal, & Vaughn, 2007).

The relationship between productivity and dinocyst assemblages has been analyzed statistically using regional data sets (e.g., Devillers & de Vernal, 2000; Radi & de Vernal, 2004, 2006). The results suggest that quantitative reconstruction would be feasible with an accuracy comparable to the uncertainty of estimates from satellite observations. To date, however, only qualitative estimates of past productivity are available based on dinocyst fluxes, P/G ratios or percentages of indicator species. For example, studies of marine sequences collected from high productivity regions of the South Atlantic Ocean have allowed the identification of periods of

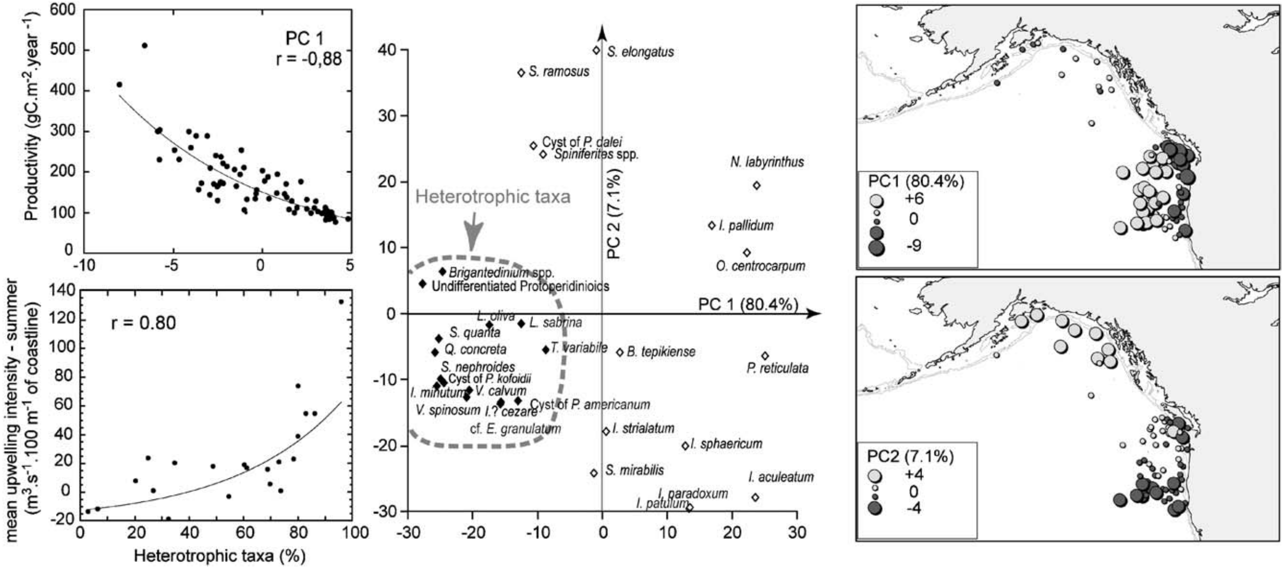

Figure 8 Illustration of the relationships between dinocyst assemblages, heterotrophic taxa, productivity and upwelling in the northeast North Pacific (with permission from Radi & de Vernal, 2004). Right: Maps showing the geographical distribution of principal component 1 and 2 (PC1 and PC2) scores (right panels). Middle: Ordination of taxa on the axes of PC1 and PC2; white diamonds represent cysts of autotrophic taxa and black diamonds represent cysts of heterotrophic taxa. Left: Relationship between the percentages of heterotrophic taxa and productivity and mean upwelling intensity (UI) in summer (average over June, July, August and September; UI can be generated only at coastal sites; the coefficient of correlation is calculated based on a logarithmic relationship). Relationship between PC1 and the annual primary productivity (the coefficient of correlation is calculated based on a logarithmic relationship).

Table 4 Classification of Dinocyst Taxa in Upwelling and River Induced-Upwelling Systems of the Eastern Sides of the Atlantic, Pacific Oceans and Arabian Sea Based on Their Relative Abundance in Recent Sediments.

Hydrological context	Region	Taxa
Seasonal coastal upwelling	Northeastern Pacific	*Brigantedinium* spp., *O. centrocarpum*, Cysts of P. dalei, *P. reticulata*, S. quanta, S. *nephroides*
	NW Africa and Iberia	*L. machaerophorum*, *Protoperidinium* spp., *P. schwartzii*
	Somalia/Arabian Sea	*Brigantedinium* spp. with *Echinidinium* spp.
	West equatorial Africa	*Brigantedinium* spp., *S. nephroides, P. kofoidii, L. machaerophorum, O. israelianum, N. labyrinthus, S. delicatus, S. ramosus, S. membranaceus*
Permanent coastal upwelling	SW Africa (Benguela)	*Brigantedinium* spp. with *Echinidinium* spp., *O. centrocarpum, P. americanum, S. quanta, N. labyrinthus, S. pachydermus*
River-induced upwelling with cells of coastal upwelling	Off Congo River	*O. centrocarpum, S. delicatus, Brigantedinium* spp.
	Off SW Africa	*Brigantedinium* spp., with *Echinidinium* spp., *O. israelianum, P. kofoidii, P. schwartzii, P. americanum, S. quanta, T. applanatum*

Source: Data collected from Zonneveld et al. (2001a), Dale et al. (2002), Marret and Zonneveld (2003), Radi and de Vernal (2004), Sprangers et al. (2004).

enhanced upwelling regime concurrent with increased atmospheric circulation strength during glacial stages (e.g., Marret, 1994b; Dupont, Marret, & Winn, 1998; Holl, Zonneveld, & Willems, 2000). An example from the east equatorial Atlantic Ocean is illustrated in Figure 9. It shows the similarity between the cyst concentration and flux variability, and the export productivity based on TOC and foraminiferal assemblages over the last climatic cycle (Struck, Sarnthein, Westerhausen, Barnola, & Raynaud, 1993; Marret, 1994b).

4.6. Environmental Quality and Eutrophication

Increasing numbers of studies are using dinocysts to characterize eutrophication and/or human-induced impacts on fjords, harbors, or bays (Lewis & Hallett, 1997;

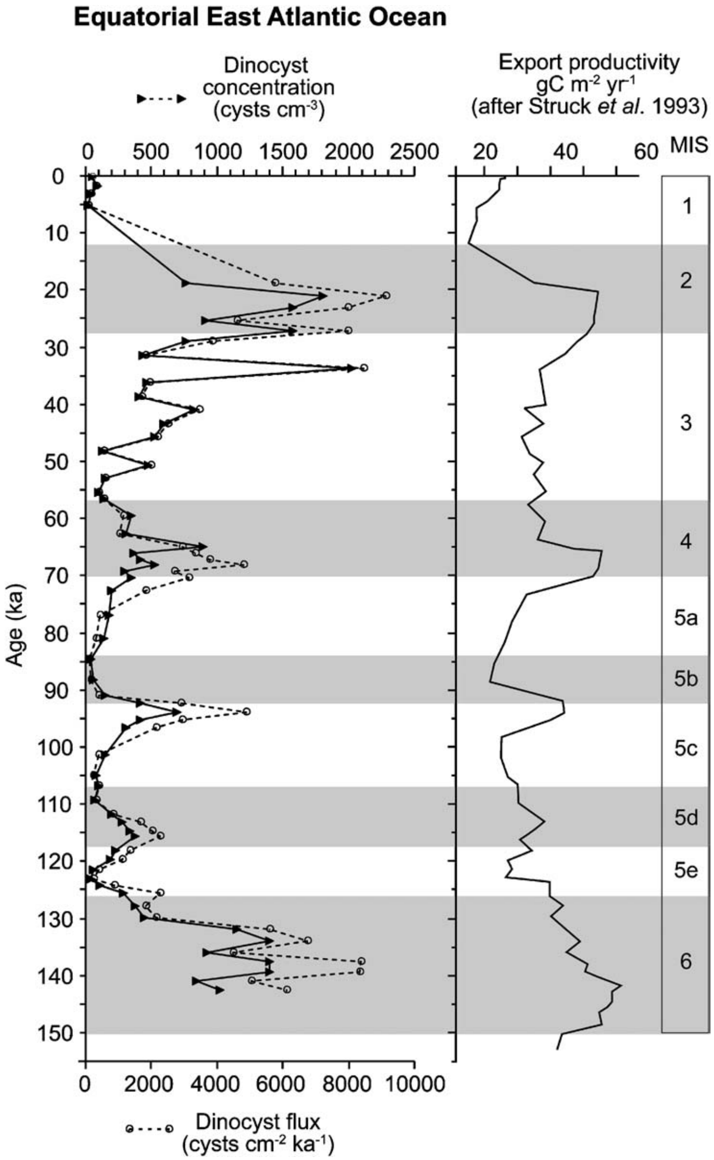

Figure 9 Comparison of dinocyst concentration and flux curve with quantified export productivity from site GIK16772, Gulf of Guinea (Marret, 1994b).

Thorsen & Dale, 1998; Dale, Thorsen, & Fjellså, 1999; Matsuoka, 1999; Dale, 2001; Dale & Dale, 2002; Pospelova, Chmura, Boothman, & Latimer, 2002; Harland, Nordberg, & Filipsson, 2004; Sangiorgi & Donders, 2004; Brenner, 2005). In particular, increased abundance of *L. machaerophorum* in sediments has been used as an indicator of eutrophication in European fjords and lochs, in association with increased levels of nutrients due to human activities. As shown above, it seems clear that dinocyst assemblages reflect the trophic characteristics of surface waters. However, whether they allow us to distinguish human-induced eutrophication from natural variations in productivity is another matter, and one which would certainly require more investigation.

Beyond the relationship between productivity and dinocyst assemblages, some studies have examined the links that could be established with nutrients, including phosphate, silica and nitrate (Devillers & de Vernal, 2000; Radi et al., 2007). The analyses suggested some relationships between distribution of dinocysts and nutrients, especially nitrate. However, the relationships are regional and cannot be extrapolated on a hemispheric scale. Moreover, they remain unclear due to the interdependency of nutrient content in water and hydrographical parameters.

4.7. Red Tides and Harmful Algal Blooms (HAB)

Although HAB and red tides are natural phenomena that have occurred throughout geological times, their increased frequency over the last two decades has become a concern for the public health and economic resources (Hallegraeff, Anderson, & Cembella, 2003). The bloom-species group is dominated by dinoflagellates, with approximately 200 taxa (or 10% of the total number) creating toxic blooms or red tides (Smayda & Reynolds, 2003), and of these only 3% are reported to be harmful (60 taxa). The majority seems to be photosynthetic, with the exception of *Noctiluca* and *Dinophysis*. Red tides usually occur when one non-toxic bloom-forming species proliferates in huge numbers (up to 20 million cells per liter), generating anoxic conditions and a discoloration of water (red or brown). For instance, a luminescent red tide is caused by *Lingulodinium polyedrum* (cyst producer). During HABs, toxins are released and affect at different levels the marine ecosystem and the food web (see Table 5).

An explanation for a global increase in HABs has been attributed to four main causes: (1) increased scientific awareness of toxic species; (2) increased use of coastal waters for fisheries and shellfish farms; (3) occurrence of algal blooms due to cultural eutrophication and/or unusual climatic conditions; (4) transport of cysts from toxic species either in ship ballast or from translocation of shellfish stocks from one region to another one (Hallegraeff et al., 2003).

The viability of cysts in sediments raises the question of "seed" banks that could generate toxic blooms. Laboratory experiments and field observations document that some cyst taxa may still germinate after a number of years. For instance, McQuoid et al. (2002) managed to generate a viable population of *Lingulodinium polyedra* from 20- to 55-year old cysts collected in the Koljö Fjord (Sweden). Mizuchima and Matsuoka (2004) successfully germinated cysts of *Alexandrium* species that were at least eight years old. Monitoring eutrophication and/or bloom events in coastal regions and estuaries would require a survey of dinocyst records from high sedimentation rate cores covering the last few decades.

Among HAB taxa, only a few species produce organic-walled cysts that are recovered in sediment, and very few studies have thus provided evidence of past "red tides." Thorsen and Dale (1998) suggested that the increase in cysts of *Gymnodinium catenatum* is related to climate warming in Skagerrak-Kattegat.

Table 5 List of Some Dinoflagellate Species that Produce Toxins.

Paralytic shellfish poisoning (PSP)	Diarrhetic shellfish poisoning (DSP)	Neurotoxic shellfish poisoning (NSP)	Ciguatera fish poisoning
Alexandrium catenella[1]	*Dinophysis acuminata,*	*Karenia brevis* (Florida)	*Gambierdiscus toxicus*
Alexandrium minutum[1]	*Dinophysis acuta*	*K. papilionaceae*	*Ostreopsis siamensis*
Alexandrium tamarense[1]	*Dinophysis fortii*	*K. selliformis*	*Coolia monotis*
Gymnodinium catenatum[1]	*Dinophysis norvegica*		
Pyrodinium bahamense[1]	*Prorocentrum lima*	*K. bicuneiformis* (New Zealand)	

Note: Data collected from Hallegraeff et al. (2003). It is of note that the only species that yield known dinocysts in the sedimentary record with unquestionable taxonomical affinities are *Gymnodinium catenatum* and *Pyrodinium bahamense* (cyst name *Polysphaeridium zoharyi*).

[1] Cyst-forming species.

5. THE DEVELOPMENT OF QUANTITATIVE APPROACHES FOR THE RECONSTRUCTION OF HYDROGRAPHIC PARAMETERS BASED ON DINOCYSTS

5.1. A Brief History

Dinocysts can be used as proxies for various environmental parameters because the species occurrence, taxa abundance and assemblage distribution show relationships with sea-surface temperature, seasonality, salinity, sea-ice cover, as well as with productivity, and possibly nutrients (*cf.* Section 4). On this basis, quantitative approaches were developed or adapted for the reconstruction of past oceanographical conditions using dinocyst data. The earliest attempts for quantitative reconstructions of paleoceanographical conditions based on dinocyst data were made by Edwards, Mudie, and de Vernal (1991), Mudie (1992) and Edwards and Andrle (1992). They were based either on indices (for example, the relative abundance of thermophilous *Impagidinium* species vs. more ubiquitous taxa) or on the Imbrie and Kipp (1971) transfer function. These early studies were done using compilations of the few dinocyst data available in the literature. They showed the potential of dinocysts for estimating past oceanographical parameters and proposed regressions for the calculation of winter temperature, summer temperature or salinity (Edwards et al., 1991; Mudie, 1992). The development of standardized databases with respect to laboratory procedures and taxonomy (e.g., de Vernal et al., 1994, 1997) made it possible to apply the best analogue method of Guiot (1990), which allows the simultaneous reconstruction of several oceanographical parameters. The best analogue approach was then used to quantitatively reconstruct sea-surface temperature in summer and winter, salinity and sea-ice cover for several late Quaternary sequences of high latitudes, in the North Atlantic (e.g., de Vernal, Guiot, & Turon, 1993; de Vernal et al. 1994, 2001; de Vernal, Hillaire-Marcel, & Bilodeau, 1996; Rochon, de Vernal, Sejrup, & Haflidason, 1998; Eynaud et al., 2002; Levac, 2001), Arctic and subarctic seas (Levac & deVernal, 1997; Levac, de Vernal, & Blake, 2001; Voronina et al., 2001; de Vernal et al., 2005a; de Vernal, Hillaire-Marcel, & Darby, 2005b), the northeastern North Pacific (de Vernal & Pedersen, 1997; Marret, de Vernal, Pedersen, & McDonald, 2001b) and of the Southern Ocean (Marret et al., 2001a). Alternative methods based on regression techniques (e.g., de Vernal et al., 1994; Marret et al., 2001a) or neural network approaches (e.g., Peyron & de Vernal, 2001) were also tested and have yielded comparable results. The advantages and limitations of each transfer function approach used for quantitative paleoceanographic reconstruction are discussed in depth by Guiot and de Vernal (Chapter XIII, this volume). Reference dinocyst databases are under development and various approaches are currently being tested, not only to reconstruct SSTs, salinity and sea-ice, but also primary productivity.

5.2. A Few Caveats

One of the advantages of dinocyst compared to other paleoceanographic proxies is the possibility of simultaneously reconstructing various parameters, such as salinity or sea-ice in addition to temperature. This is possible because of the wide range of dinoflagellate occurrence with respect to hydrographic conditions, and because the reference databases include data from epicontinental and estuarine settings in addition to open ocean, which results in various combinations of salinity vs. temperature, or summer vs. winter temperature. However, in some marine environments, co-variance does occur among the above-mentioned parameters. In the open North Atlantic Ocean, there is generally co-variance of seasonal SSTs and of SST vs. salinity. Similarly, there is a relationship between sea-ice cover and SSTs. Also, large differences between summer and winter SSTs often characterize near-shore areas, epicontinental seas and estuaries as the result of low thermal inertia in surface waters due to the stratification of a buoyant low salinity surface layer. Therefore, depending upon the marine setting, there is interdependency between hydrographic parameters (salinity, stratification, seasonal SSTs) and it is not always obvious to assess which is the one that is the most determinant and best reconstructed. Nevertheless, the overall reconstructions from dinocysts provide an integrated picture of the diverse hydrographical conditions, including situations that are not represented by proxies occurring exclusively in open ocean environments.

Another caveat concerns the influence of nutrient availability and the structure of plankton populations on the dinoflagellate and cyst assemblages, which could possibly interfere in the relationships with hydrographical conditions. As shown by assemblages in polynyas and upwelling areas (*cf.* Section 4.5), there is a relationship between dinocyst assemblages and productivity, which can be the most determinant parameter at regional scales. Moreover, it should be stressed that the differences in the assemblages of the Pacific and Atlantic Oceans could be due to differences with respect to nutrient limitations.

Because of the above mentioned caveats, regression-based techniques such as the Imbrie and Kipp (1971) method or artificial neural networks have to be used with much caution. The relationship between assemblages and a given parameter, and the equation describing this relationship, may differ significantly depending upon the initial calibration data set. The problem is not as acute with the modern analogue technique, which does not assume any relationship but simply supposes that identical assemblages should be the result of identical abiotic and biotic conditions. However, by using the modern analogue technique, spatial autocorrelation may possibly result in an underestimation of the prediction error (Telford, 2006; see discussion by Guiot and de Vernal, Chapter XIII, this volume).

The analogue techniques and their variants appear more appropriate than calibration approaches. However, they can also yield ambiguous results. One potential problem concerns false analogues, notably when assemblages are characterized by the dominance of ubiquitous taxa. This is why the accompanying taxa, which often have more narrow environmental tolerances than ubiquitous taxa, are more heavily weighted through logarithmic transformation prior to statistical comparison of assemblages (*cf.* de Vernal et al., 2001). Another issue concerns non-analogue situations, which are relatively frequent when dealing with some interval of the past, such as the LGM (*cf.* de Vernal et al., 2005a). In such cases, the distance between the best modern analogue and the fossil assemblages can be used to define a confidence level to estimate the reliability or quality of reconstructions.

6. THE USE OF DINOCYSTS IN PALEOCEANOGRAPHY

The use of dinocysts in paleoceanography is relatively recent. Until the mid-1960s, the biological affinities of dinocysts were unknown. Dinocysts were associated with hystrichospheres. They were used as biostratigraphical markers but virtually ignored in the fields of paleoecology and paleoceanography. Moreover, the study of dinocysts is usually more time consuming than that of other proxies, such as planktonic foraminifera because of treatments involving repeated chemical (HCl, HF) and mechanical (wet sieving) manipulations prior to any observation. It should also be mentioned that the taxonomy of modern dinocysts is still under development, with new species and new morphotypes being regularly described during the course of surface sediment analyses for the development of reference databases.

During the 1980s and 1990s, the development of modern databases led to an improvement in the understanding of dinocyst distribution in relation to environmental parameters, which permitted their use as proxies in paleoceanography. As mentioned above, and further illustrated by a few examples below, dinocysts appear useful in documenting various aspects of changes in the ocean, notably productivity variations at low latitudes and sea-surface temperature, salinity and sea-ice at high latitudes.

In the tropical and equatorial domains of the Atlantic Ocean, dinocyst studies in late Quaternary cores have provided insight into the variability of a number of past sea-surface parameters in relation to climate changes. Periods of enhanced oceanic upwelling, in particular during glacial stages, were characterized by increased productivity and a higher abundance of dinocysts (see Figure 9). Along the SW African coasts, dinocyst assemblages in marine cores have yielded evidence for a coupling between sea-level changes and nutrient-enrichment induced by coastal upwellings and/or river discharges (Marret, 1994b; Holl et al., 2000; Vink et al., 2001; Dupont et al., 1998; Marret, Scourse, Versteegh, Jansen, & Schneider, 2001c; Shi, Schneider, Beug, & Dupont, 2001).

In the Southern Ocean, investigations of dinocysts allowed for the reconstruction of past SST in the Chatham Region, notably at DSDP Site 594, which is a well-studied late Quaternary record off the coast of New Zealand (e.g., Marret et al., 2001a; Wells & Okada, 1997). This record has provided evidence for large amplitude SSTs changes following the glacial–interglacial cycles based on several proxies, including foraminiferal assemblages. At this site, the dinocyst-based SST reconstructions yielded results coherent with those obtained using planktonic foraminifera (Figure 10), with, however, larger amplitude of temperature variations. Dinocyst-based estimates tend to indicate colder conditions during the isotope stage 2 and higher SSTs during isotope stage 5 than foraminifera. These discrepancies might result from different sensitivity of dinoflagellates and planktonic foraminifera toward seasonal temperatures.

In the mid to high latitudes of the North Atlantic and adjacent polar and subpolar seas, many studies were done based on dinocysts to document late Quaternary changes of SSTs, sea-ice cover and salinity. As an example, the studies of de Vernal et al. (1996), Rochon et al. (1998) and Grosfjeld et al. (1999) have shown very extensive sea-ice cover along the southeastern Canadian margin and along the Scandinavian coast during the Younger Dryas. As another example, an in-depth study of the LGM suggests that the northern North Atlantic was characterized by sea-surface conditions much different from the modern ones: sea-ice cover was more extensive, salinity was lower, and SSTs apparently recorded much larger winter to summer amplitudes (*cf.* de Vernal et al., 2000, 2005a). The reconstruction of the North Atlantic SSTs at LGM based on dinocysts shows significant discrepancies with estimates based on planktonic foraminifera (*cf.* CLIMAP, 1976; Kucera et al., 2005; de Vernal et al., 2006). These discrepancies are evidence of the complexity of the biotic responses to climate changes, and most probably result from a combination of factors, including salinity and water mass stratification, seasonality, nutrient concentrations and productivity, in addition to mean summer temperature.

7. CONCLUDING REMARKS

Dinocysts are paleoceanographical proxies that are complementary to other microfossils in many respects:

1. They are composed of refractory organic matter. Thus, their preservation is not affected by dissolution processes, which can be a problem in the case of siliceous microfossils because of under-saturation of the water in opal silica, and in the case of calcareous remains below the lysocline. However, dinocysts can be sensitive to oxidation.
2. Dinoflagellates are ubiquitous and their cysts are particularly abundant in epicontinental seas and along continental margins, whereas the open ocean

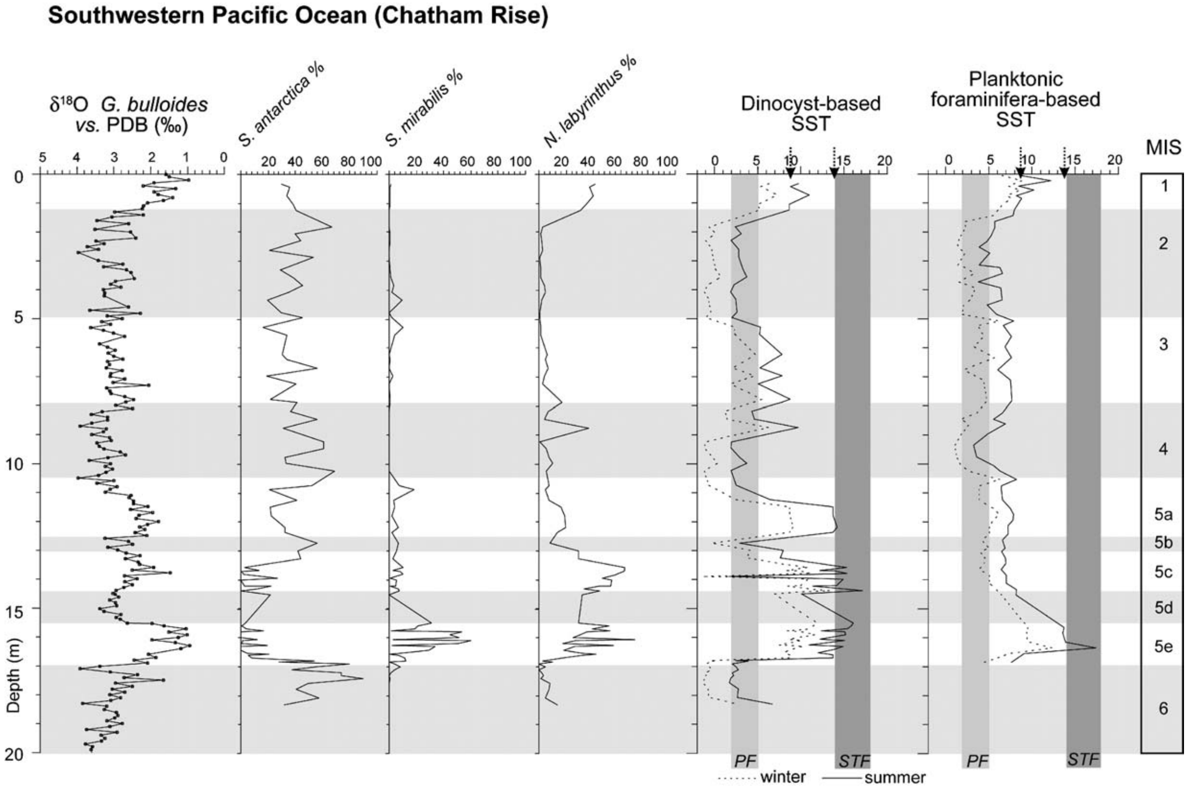

Figure 10 Comparison of winter and summer dinocyst-based (with permission from Marret et al., 2001a) and foraminifera-based SSTs (Wells & Okada, 1997) from site DSDP 594, southwest Pacific The percentages of a subantarctic taxon (***Selenopemphix antarctica***) and of cool temperate and warm temperate taxa (***Nematosphaeropsis labyrinthus*** and ***Spiniferites mirabilis***, respectively) are illustrated. Vertical shaded bands correspond to the thermic domains of the polar and subtropical fronts (PF = Polar front and STF = Subtropical Front). Arrows indicate present-day winter and summer SST at the site.

areas are often marked by low cyst concentrations. It is thus believed that dinocysts are very useful proxies in neritic areas, on sea floor slopes and rises, but that they are of more limited use in central gyre areas of the open ocean domain.

3. Dinocyst assemblages show a relatively high species diversity in polar seas and constitute one of the rare tracers for the paleoceanographical investigations and sea-ice cover reconstruction in the Arctic and circum-Antarctic seas.
4. Dinocysts are abundant nearshore where wide amplitude gradients of salinity and large seasonal contrasts of temperature, due to stratification of the upper water mass, are recorded. They can provide information on hydrographical parameters, such as salinity and seasonal SSTs. From this point of view, they are complementary to micropaleontological tracers such as coccoliths or planktonic foraminifera that are more stenohaline and restricted to the open ocean domain.
5. Recent developments suggest that dinocysts could be used to quantitatively reconstruct productivity in the ocean and upwelling intensity.

Our understanding of dinocysts as paleoceanographical tracers is still developing. Nevertheless, the investigations made over the last decades have clearly shown that dinocysts are a useful proxy for documenting the changes of biotic (trophic character) and abiotic (seasonal temperature, salinity, sea-ice) conditions in surface waters, especially in the continental margins domain.

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