

## Organic-walled dinoflagellate cyst production, composition and flux from 1996 to 1998 in the central Strait of Georgia (BC, Canada): A sediment trap study

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### ABSTRACT

Bi-weekly fluxes of dinoflagellate cysts and assemblage composition were recorded from March 1996 to January 1999 in the central part of the Strait of Georgia (BC, Canada). The study period captured the 1997–98 El Niño event, which was characterized locally by increased Fraser River discharge resulting from earlier than usual snowmelt in 1997 and warmer sea-surface temperatures in 1998.

Thirty dinoflagellate cyst taxa were identified in the sediment trap samples. The dinoflagellate cyst flux varied from ~600 to 336,200 cysts m<sup>-2</sup> day<sup>-1</sup>, with an average of 20,000 cysts m<sup>-2</sup> day<sup>-1</sup>. In general, dinoflagellate cyst flux and species composition reflected seasonal variation of water conditions in the Strait of Georgia. Throughout the study period, assemblages were dominated by cysts produced by heterotrophic dinoflagellates, such as *Protoperidineaceae* (*Brigantedinium* spp., *Quinquecuspis concreta*, and *Protoperidinium americanum*). The greatest abundance of cysts of the potentially toxic *Alexandrium* spp. was recorded in the spring of 1996.

Our results demonstrate that cysts produced by heterotrophic dinoflagellates peak in June each year, during or following diatom blooms, as indicated by biogenic silica flux. Cysts produced by autotrophic taxa were most abundant during August–September.

The total annual dinoflagellate cyst flux was lower in 1997 and 1998 than in 1996, mostly due to the bloom of *Alexandrium* spp. in 1996. Warmer sea-surface temperature and the early spring of 1998 had a positive effect on the production of both autotrophic and heterotrophic dinoflagellates as reflected in the cyst fluxes. Cyst assemblages from sediment trap samples were consistent with a cyst assemblage recovered from a core sample at the same site.

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### 1. Introduction

Dinoflagellates are the most diverse group of phytoplankton in coastal/estuarine environments and one of the most important primary producers. They comprise primarily singled-celled organisms (protists) that occur as motile cells with two flagella and characteristic nuclei (Dale, 1996; Fensome et al., 1996). About half of modern dinoflagellate species are heterotrophic, while the other half are autotrophic or mixotrophic (Taylor, 1987; Jacobson and Anderson, 1996). Heterotrophic dinoflagellates are affected most by the distribution of their preferred prey (diatoms), whereas the distribution of autotrophic species depends on the availability of light, sea-surface temperature (SST), salinity (SSS), and dissolved nutrients (e.g. P, N) (Dale, 1996).

Many dinoflagellate species produce resting cysts during sexual reproduction (Pfiester and Anderson, 1987; Taylor, 1987). Resting cysts are non-motile cells that lack flagella and in which metabolic

processes are greatly reduced (e.g. Taylor, 1987). Resting cysts can survive unfavourable environmental conditions and, therefore, have an important role as a seeding source (Matsuoka and Fukuyo, 2000). Cysts sink to the seafloor in the same way as fine particles do (Dale, 1983) and have a mandatory resting period after which they re-establish a motile population (Anderson, 1997). Organic walls of cysts are highly resistant to physical, chemical, and biological degradation, and can become fossilized (Fensome et al., 1996).

Over the last several decades, it has been demonstrated that dinoflagellate cyst assemblages can be used for paleoenvironmental reconstructions. Cyst assemblages in Quaternary sediments may provide information on such environmental signals as SST, SSS, marine productivity, coastal eutrophication, and pollution (e.g. de Vernal et al., 1993; Dale, 1996; de Vernal et al., 1997; Marret and de Vernal, 1997; Rochon et al., 1999; Matsuoka, 1999; de Vernal et al., 2001, 2005; Marret and Scourse, 2002; Marret and Zonneveld, 2003; Pospelova et al., 2002, 2004, 2005; Radi and de Vernal, 2004; Radi et al., 2007; Holzwarth et al., 2007; Marret et al., 2008; Pospelova et al., 2008). These palaeo applications are based on knowledge of dinoflagellate cyst distributions in modern sediments in relation to environmental

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parameters (e.g. Wall et al., 1977; Dale, 1983; Harland, 1983; Dale, 2009). However, cyst assemblages from sediment core samples are deposited over many years, and many ecological signals can be averaged out due to biomixing and/or preservation (Zonneveld et al., 1997). Thus, surface sediment samples often provide insufficient resolution with which to resolve year-to-year cyst ecology and do not provide information on seasonal patterns or rates of dinoflagellate cyst production. Ultimately, the time-resolution of cyst assemblages retrieved from marine sediments limits the application of dinoflagellate cysts as bio-indicators of environmental conditions in the past and present (Pospelova et al., 2006). The patterns of resting cyst production and ecological conditions under which cysts are formed can be studied directly by measuring *in situ* cyst production. The record of dinoflagellate cysts captured by particle-intercepting traps provides unique ecological information on when and how many cysts of certain species are produced; how cyst production relates to water quality; and how water column cyst production relates to assemblages measured in sediments (Dale, 1992; Dale and Dale 1992; Heiskanen, 1993; Montresor et al., 1998; Matsuoka and Fukuyo, 2000). Quantitative measurements from sediment trap material may be limited by resuspension of bottom sediments and by trap efficiency, which depends on the physical configuration and other factors (see e.g. Larsson et al., 1986; Gardner, 2000). Nevertheless, sediment traps provide the most reliable tool for qualitative analysis of seasonal/inter-annual cyst production (Matsuoka and Fukuyo, 2000).

To date, field-based information on dinoflagellate cyst production is limited (Dale and Dale, 1992; Montresor et al., 1998; Harland and Pudsey, 1999; Zonneveld and Brummer, 2000; Godhe et al., 2001; Tanimura and Shimada, 2004; Morquecho and Lechuga-Devéze, 2004; Susek et al., 2005; Fujii and Matsuoka, 2006; Pitcher and Joyce, 2009). Most of the sediment trap studies of dinoflagellate cysts span <9 months (Zonneveld and Brummer, 2000; Harland and Pudsey, 1999; Susek et al., 2005; Fujii and Matsuoka, 2006). Of the longer-term studies, there are only three from coastal environments, these being two-year studies in the Gulf of Naples in the Mediterranean Sea (Montresor et al., 1998),

Bahia Concepcion in the Gulf of California (Morquecho and Lechuga-Devéze, 2004), and Omura Bay in the Western Pacific (Fujii and Matsuoka, 2006). More long-term sediment trap studies of cyst productivity are needed, particularly in coastal waters.

Despite the scarcity of sediment trap studies and the non-uniformity of approaches, such studies have made a significant contribution to dinoflagellate cyst ecology and have clearly demonstrated seasonal trends in cyst production that vary among oceanographic settings. Dinoflagellate cyst diversity and flux demonstrate very strong sensitivity to regional environmental conditions. An understanding of the ecological conditions that trigger encystment is essential for the interpretation of environmental signals left in sediments and should be performed on a regional scale.

Here we present the first study of dinoflagellate cyst production from temperate Pacific coastal waters of North America. The observations provide a high resolution (bi-weekly scale) record over a three-year period, which allows us to describe the seasonal and inter-annual variability of dinoflagellate cyst production in the Strait of Georgia. We document the composition, diversity, abundance and seasonal succession of dinoflagellate cyst taxa, including toxic and potentially toxic species of dinoflagellates, and examine these in relation to changes in freshwater input, SST, SSS, and biogenic silica, based on the availability of such data. Furthermore, we use the record to evaluate, for the first time, the *in situ* response of dinoflagellate flux and species assemblage to a strong El Niño event that is known to have altered seawater salinity, temperature and nutrient flux. Finally, we compare cyst assemblages from sediment trap material and core sediments at the same site.

### 1.1. Regional setting

The Strait of Georgia is a semi-enclosed basin on the west coast of Canada (Fig. 1). The oceanography of this coastal sea, also known as the Salish Sea, is well described by Thomson (1981) and has recently been the topic of a journal issue devoted to physical and chemical processes (e.g., Masson, 2006). Here, we describe only the salient features relevant

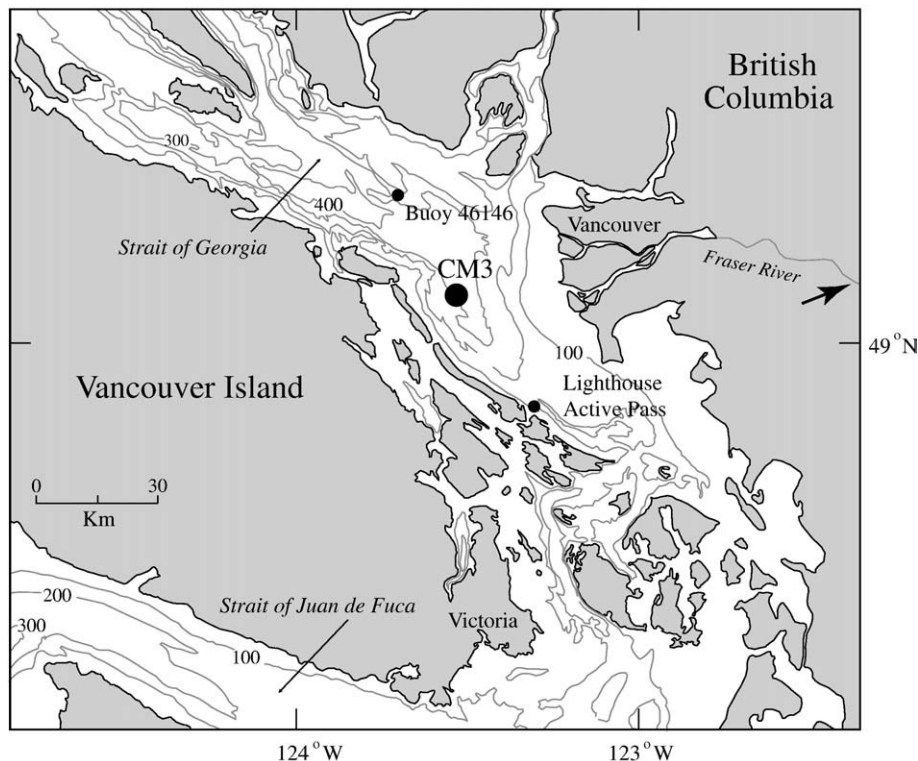


Fig. 1. Map showing the location of sediment trap GSCM-3, local bathymetry, buoy 46146, lighthouse Active Pass in the Strait of Georgia and the direction (the arrow) of the Hope station (49°22'50", 121°27'05").

to the present study. The Strait is approximately 220 km long and 28 km wide, with a total surface area of 6800 km<sup>2</sup>. The average water depth is 155 m, reaching a maximum of 420 m in the central part of the Strait (Thomson, 1981). Most of the exchange with the Pacific Ocean occurs through Juan de Fuca Strait to the south, and the basin-water properties (nutrients, O<sub>2</sub>, SST, SSS) are influenced by those observed on the continental shelf (Johannessen and Macdonald, 2009). Of major local importance, the Fraser River contributes 73% of the total inflow of 158 km<sup>3</sup> yr<sup>-1</sup>, and 64% of the 30 Mt of sediment delivered to the Strait annually (Johannessen et al., 2003). These, together with high precipitation (~600 mm year<sup>-1</sup>; Thomson, 1994), produce a strongly-stratified water column throughout the year, with a turbid plume spanning much of the southern Strait in summer, including at times the location of the sediment trap site (Johannessen et al., 2005). Average SST varies from 13–16 °C in August to 6–7 °C in February; SSS ranges from 24 to 32 (Masson, 2006; Thomson, 1981). Deep basin water is nearly uniform with SST ~8 °C and SSS ~30.5 year-round. The Strait of Georgia is well supplied with nutrients (Masson, 2002) which support high primary productivity (120 to 345 g C m<sup>-2</sup> year<sup>-1</sup> (Stockner et al., 1979; Parsons et al., 1981; Harrison et al., 1983; Antoine et al., 1996)). The phytoplankton composition in the Strait of Georgia is typical for temperate, estuarine coastal waters. Dinoflagellates, particularly heterotrophic species, are the second most abundant group of phytoplankton, following diatoms (Harrison et al., 1983; Radi et al., 2007). There are at least 88 dinoflagellate species in British Columbia's coastal waters, of which 21 are recorded to produce organic-walled cysts (Buchanan, 1961). The spring phytoplankton bloom in the Strait of Georgia usually develops in early March (Harrison et al., 1983), with the greatest abundance of dinoflagellates occurring in the summer (Cattell, 1969).

Aside from their application to paleoceanography, some dinoflagellate species also have the potential to form harmful algal blooms (HABs), which have been observed in the Strait of Georgia. Regionally, HABs have produced paralytic shellfish poisoning (PSP) and domoic acid poisoning (DAP) (Trainer, 2002). Since the beginning of a PSP monitoring program in the late 1940s, toxicity has been detected on the BC coast every year (Taylor and Harrison, 2002), some of it related to dinoflagellate blooms (genus *Alexandrium*) (Prakash and Taylor, 1966). The intensity of such blooms varies over a ~5–7 year cycle and is often highest in El Niño years (Gaines and Taylor, 1985). Practical limitations to monitoring for toxins and phytoplankton can result in the under-reporting of toxic dinoflagellate taxa and bloom occurrences.

Decadal global climate variability, including El Niño-Southern Oscillation, can be viewed as an opportunity to observe how strong changes in SST, SSS, and availability of nutrients affect biological communities, especially at lower trophic levels. Observing the effects of large natural ocean changes has the potential to develop an understanding of how phytoplankton groups are likely to adapt to longer-term environmental change.

Within our observation period, one of the strongest El Niño events of the 20th century was recorded during 1997–98 (Chavez et al., 1999). This event was characterised regionally by high SST, low nutrient concentration, reduced summer coastal upwelling and low primary production. It was accompanied by changes in phytoplankton, zooplankton and higher trophic level organisms (Beamish and Neville, 1999; Whitney and Welch, 2002; Harrison et al., 2004). In the Strait of Georgia, waters were ~0.3 °C warmer than usual during the El Niño (Gower, 2002); freshwater inflow noticeably increased, causing lower surface salinities (Environment Canada); and plankton biomass was reduced (Ocean State Report, 1999).

## 2. Materials and methods

### 2.1. Sediment trap location and collection of samples

Sediment trap samples were collected with a Baker–Milburn sequential particle trap (Baker and Milburn, 1983). The trap is cylindrical

and contains a funnel that tapers to a collecting jar at the bottom that intercepts particles as they fall towards the sea bed. Ten sampling jars are mounted on a carousel that can be programmed to present a new collection jar beneath the funnel at even intervals.

The mooring was deployed in the central part of the Strait of Georgia, 49°06'31" N, 123°29'44" W (Fig. 1), with the trap located at 150 m water depth (200 m above the seafloor, Fig. 2). Details of the GSCM-3 sediment trap, its deployment, field sampling methods, sample handling and geochemical analyses are provided elsewhere (O'Brien et al., 2000; Johannessen et al., 2005). The sampling period spanned 3 years from March, 1996, to January, 1999, with collection intervals of 8–16 days, with an average of 11 days.

Samples were sieved through a 500 μm mesh to remove zooplankton, and one half of each <500 μm sample was analysed for total carbon, organic carbon, total nitrogen, carbonate carbon, and biogenic silica as well as stable isotopes of carbon and nitrogen (Johannessen et al., 2005). The other half of each <500 μm sample, with a dry weight of approximately 1 g, was preserved with HgCl<sub>2</sub> and then stored in plastic cups in the dark at 4 °C (O'Brien et al., 2000) and used for the analyses described in this paper.

Core sediment material was obtained from the site of the GSCM-3 mooring in March, 2008, using a small gravity corer. A subsample of the sediment core was taken from the 28–30 cm depth interval, which approximately represents the depth of material deposited during the years of sediment trap mooring, based on the sedimentation rate at this site, ~2.8 cm year<sup>-1</sup> (Johannessen et al., 2003), although the interval does not represent one age precisely, because of benthic mixing of the sediment.

### 2.2. Palynological sample preparation

Sediment samples were processed in the Paleoenvironmental/Marine Palynology Laboratory at the University of Victoria. The samples were rinsed several times with distilled water to remove HgCl<sub>2</sub>, centrifuged, oven-dried at 40 °C, and weighed with an analytical balance. The samples were subsequently soaked with distilled water for a night, centrifuged, and then processed using a standard palynological technique (Pospelova et al., 2005; Mertens et al., 2009). Marker-grains of a known number of *Lycopodium clavatum* spores (Stockmarr, 1971; Mertens et al., 2009) were added to allow quantitative estimates of the absolute concentrations and fluxes. Sediment samples were treated with cold 10% HCl for 5 min to remove carbonates. After rinsing with distilled water, the samples were sieved through 120 μm and 15 μm mesh sieves to eliminate coarse and fine material. Additions of cold 48% HF for up to 5 days removed the siliceous particles. The residue was treated again with cold 10% HCl, rinsed twice with distilled water, and sonicated for 0.2–0.8 min. The final fraction was collected on 15 μm mesh sieves and transferred to 1.5 mL tubes. Samples were centrifuged at each step. No oxidation was applied to avoid losing fragile protoperidinoic cysts (Dale, 1976; Zonneveld, 1997).

Aliquots of one or two drops were mounted in glycerine gel between glass and cover slides, and sealed to preserve the samples from drying. Dinoflagellate cysts and other organic palynomorphs were identified and counted using light microscopy on a Nikon Eclipse 80i at 60× and 100× oil objectives. All 89 microscope slides and residues are stored in the Paleoenvironmental/Marine Palynology Laboratory, University of Victoria, Canada. Sample Uvic 08-113 was lost due to complications with recovery from the trap, and sample Uvic 08-91 was lost during palynological treatment.

### 2.3. Dinoflagellate cyst analysis

The paleontological taxonomy system used throughout this paper follows Fensome et al. (1993), Lentin and Williams (1993), Head (1996), Zonneveld (1997), Matsuoka and Cho (2000), Head et al.

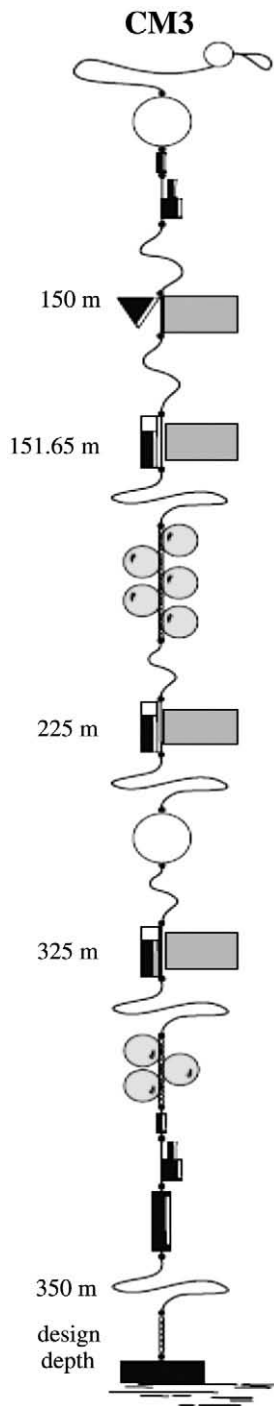


Fig. 2. Mooring design for station GSCM-3.

(2001), and Pospelova and Head (2002). A taxonomic listing of dinoflagellate cysts recovered in this study and cyst-theca nomenclature are provided in Table 1.

On average, 300 cysts per sample were counted; however due to the limited amount of sediment trap material, the count for eight samples was less than 200 cysts per sample. Each cyst was distinguished as either *with* cell content (recently produced) or *without* cell content (remains of cysts that have been hatched).

Cysts were identified to the species level whenever possible. Some of the dinoflagellate cyst taxa were grouped together on the basis of morphological similarities. In particular, *Brigantedinium simplex* and *B. cariacense* are grouped into *Brigantedinium* spp., because archeopyles were often not observed. Cysts of *Polykrikos schwartzii* and *P. kofoidii*

Table 1

Taxonomic citation of dinoflagellate cysts identified in this study. Thecate equivalents are taken from Head (1996), Zonneveld (1997), Head et al. (2001), and Pospelova and Head (2002).

Cyst species (paleontological name)	Dinoflagellate theca (biological name)
	Autotrophic Gonyaulacaceae
Cysts of <i>Alexandrium</i> spp. Halim, 1960 emend. Balech, 1990	<i>Alexandrium</i> spp.
<i>Lingulodinium machaerophorum</i> (Deflandre & Cookson, 1955) Wall, 1967	<i>Lingulodinium polyedrum</i>
<i>Nematospaeropsis labyrinthus</i> (Ostenfeld, 1903) Reid, 1974	<i>Gonyaulax spinifera</i> complex
<i>Operculodinium centrocarpum</i> sensu Wall and Dale, 1966	<i>Protoceratium reticulatum</i>
<i>Spiniferites ramosus</i> (Ehrenberg, 1838) Mantell, 1854	<i>Gonyaulax spinifera</i> complex
<i>Spiniferites</i> spp. Mantell, 1850 emend. Sarjeant, 1970	<i>Gonyaulax</i> complex
	Protoperidiniaceae
Cysts of <i>Pentapharsodinium dalei</i> Indelicato & Loeblich III, 1986	<i>Pentapharsodinium dalei</i>
	Heterotrophic Diplopsalidaceae
<i>Dubridinium</i> spp. Reid, 1977	Diplopsalid group
	Polykrikaceae
Cysts of <i>Pheopolykrikos hartmanii</i> (Zimmermann) Matsuoka & Fukuyo, 1986	<i>Pheopolykrikos hartmanii</i>
Cysts of <i>Polykrikos schwartzii/kofoidii</i> Bütschli, 1873	<i>Polykrikos schwartzii/kofoidii</i>
	Protoperidiniaceae
<i>Brigantedinium</i> spp. Reid, 1977 ex Lentin and Williams, 1993	? <i>Protoperidinium</i> spp.
<i>Brigantedinium cariacense</i> (Wall, 1967) Lentin and Williams, 1993	<i>Protoperidinium avellanum</i>
<i>Brigantedinium simplex</i> Wall, 1965 ex Lentin and Williams, 1993	<i>Protoperidinium conicooides</i>
<i>Echinidinium aculeatum</i> Zonneveld, 1997	<i>Protoperidinium</i> sp. indet.
<i>Echinidinium delicatum</i> Zonneveld, 1997	<i>Protoperidinium</i> sp. indet.
<i>Echinidinium granulatum</i> Zonneveld, 1997	<i>Protoperidinium</i> sp. indet.
<i>Echinidinium</i> spp. Zonneveld, 1997	<i>Protoperidinium</i> sp. indet.
<i>Islandinium</i> ? <i>minutum</i> Head et al., 2001	<i>Protoperidinium</i> sp. indet.
<i>Islandinium</i> ? <i>minutum</i> var. <i>cesare</i> Head et al., 2001	<i>Protoperidinium</i> sp. indet.
<i>Islandinium brevispinosum</i> Pospelova and Head, 2002	<i>Protoperidinium</i> sp. indet.
Cyst of <i>Protoperidinium americanum</i> (Gran et Braarud 1935) Balech, 1974	<i>Protoperidinium americanum</i>
<i>Protoperidinium</i> type 1	<i>Protoperidinium</i> sp. indet.
<i>Quinquecuspis concreta</i> (Reid, 1977) Harland, 1977	<i>Protoperidinium leonis</i>
<i>Selenopemphix nephroides</i> Benedek, 1972 emend. Bujak in Bujak et al., 1980	<i>Protoperidinium subinerme</i>
<i>Selenopemphix quanta</i> (Bradford, 1975) Matsuoka, 1985	<i>Protoperidinium conicum</i>
<i>Votadinium calvum</i> Reid, 1977	<i>Protoperidinium oblongum</i>
<i>Votadinium spinosum</i> Reid, 1977	<i>Protoperidinium claudicans</i>
Cyst type A	<i>Protoperidinium</i> sp. indet.
Cyst type Y	<i>Protoperidinium</i> sp. indet.
Spiny brown	Unknown

are grouped into cysts *P. schwartzii/kofoidii* according to Matsuoka and Cho (2000). Because of the very low abundance and great morphological similarity among species of the genus *Spiniferites*, all taxa except *S. ramosus* were grouped as *Spiniferites* spp.

Species richness (SR) reflects the total number of cyst taxa identified in a trap over the investigated period and was used as a measure of dinoflagellate cyst diversity (see discussion in Pospelova et al., 2002). The relative abundance (%) of cyst taxa in individual samples was calculated by dividing the number of cysts of a given taxa by the total number of cysts in the sample. Mean relative abundance over the annual cycle was calculated, taking collection interval into account. The cyst assemblage collected over the whole 3-year period is referred to in the text as *total cyst assemblage*, while the cyst assemblage collected over a single year is referred to as the *annual assemblage*.

Concentrations of dinoflagellate cysts were calculated by dividing the total number of cysts by the weight of dry sediment (cysts  $g^{-1}$  dry sediment). Fluxes were calculated by dividing the number of cysts collected per square metre by the number of collecting days (cysts  $m^{-2} day^{-1}$ ). The total annual cyst flux is a sum of fluxes multiplied by the number of sampling days in a year. Concentrations and fluxes for other palynomorphs were calculated likewise.

#### 2.4. Environmental data

The monthly average values of SST from buoy 46,146 (Fig. 1) were provided by J.F.R. Gower (personal communication). Information on methodology of the measurements, accuracy and compilation of the *in situ* measurements is documented by Gower (2002). Data on Fraser River flow were obtained from the Archived Hydrometric Data HYDAT (Water Survey of Canada) with daily discharge measured at Hope station (Fig. 1). Data on SSS, measured daily at Active Pass lighthouse (Fig. 1), were obtained from the British Columbia Lighthouse data archive (Fisheries and Oceans Canada).

### 3. Results

#### 3.1. Dinoflagellate cyst composition and relative abundance in sediment trap samples

The sediment trap samples contained well-preserved organic-walled dinoflagellate cysts (Plates I–VII) and other organic palynomorphs (Plate VIII), with 30 dinoflagellate cyst taxa identified, including seven autotrophic and 23 heterotrophic taxa (Table 1 and Appendix A). Dinoflagellate cysts were recovered from all sediment trap samples. The number of dinoflagellate cyst taxa in an individual sample varied from 8 to 25, with an average of 18. The highest values of species richness were usually recorded during spring and summer (Fig. 3).

The total cyst assemblage was dominated by *Alexandrium* spp., *Brigantedinium* spp., *Quinquecuspidata concreta* and cysts of *Protoperidinium americanum*, which constituted 51.2%, 22.8%, 8.8% and 4.7%, respectively (Appendix B). The predominance of cysts of *Alexandrium* spp. was due to an outbreak in the spring and early summer of 1996, when its annual relative abundance reached 78.8%. Cysts of *Alexandrium* spp. constituted only 4.7% and 3.0% in 1997 and 1998, respectively. The total annual assemblages in 1997 and 1998 were strongly dominated by heterotrophic taxa, which contributed 90.1% and 93.1%, respectively. The majority of recorded cysts in the samples belong to the order Protoperidinales.

The relative abundance of dinoflagellate cysts varied considerably from year to year, with the greatest fluctuation occurring in 1996, during the *Alexandrium* spp. bloom mentioned above. The highest relative abundance of the other autotrophic taxa (33.7%) was observed at the end of the summer of 1997 (Fig. 3). The composition of the dinoflagellate cyst assemblage, relative abundance of dino-

flagellate cyst taxa, and the relative abundance of cysts produced by autotrophic and heterotrophic species are provided in Appendix B.

#### 3.2. Dinoflagellate cyst flux and concentration

The flux of organic-walled dinoflagellate cysts during the 3-year record spans three orders of magnitude, with total dinoflagellate cyst flux varying from  $\sim 600$  cysts  $m^{-2} day^{-1}$  (February 1997) to  $\sim 336,200$  cysts  $m^{-2} day^{-1}$  (March–April 1996), with an average of  $\sim 20,000$  cysts  $m^{-2} day^{-1}$ . Due to an outbreak of *Alexandrium* spp. in 1996, the total annual cyst flux was about five times higher in 1996 than in 1997 and three times higher than in 1998 (Table 2). In contrast, the total annual cyst flux of other (excluding cysts of *Alexandrium* spp.) autotrophic taxa was twice as low in 1996 as in 1997 and 1998 (Fig. 3, Table 2). The total cyst flux in 1997 and 1998 was strongly dominated by cysts produced by heterotrophic taxa (Fig. 3). Due to a decrease in cyst production of heterotrophic taxa, the minimum value of total annual flux was recorded in 1997. The highest total fluxes of autotrophic (excluding *Alexandrium* spp.) and heterotrophic taxa were observed in 1998. The total annual fluxes of dinoflagellate cyst taxa over the three year period are provided in Table 2.

The flux of cysts of *Alexandrium* spp. was up to  $\sim 324,700$  cysts  $m^{-2} day^{-1}$  in March–April 1996 (Fig. 3, Appendix A). Cyst production of *Alexandrium* spp. declined drastically in 1997–1998 with a spring and summer peak of only 2600 cysts  $m^{-2} day^{-1}$ . Cyst fluxes of other autotrophic taxa demonstrated marked variability and did not have stable seasonal patterns. Cyst production of autotrophic taxa, excluding cysts of *Alexandrium* spp., varied from 23 to 15,300 cysts  $m^{-2} day^{-1}$  during 1996, with high values recorded in September. In the winter of 1996–1997, this flux was extremely low (not exceeding 1500 cysts  $m^{-2} day^{-1}$ ). During 1997 the highest flux of cysts produced by autotrophic taxa was recorded in August, when this flux was twice that of the highest fluxes of the previous year. Dinoflagellate cyst fluxes of autotrophic taxa were unexpectedly high during the winter of 1997–98 and the following spring, with values from  $\sim 2000$  cysts  $m^{-2} day^{-1}$  to 28,200 cysts  $m^{-2} day^{-1}$ , and averaging 10,600 cysts  $m^{-2} day^{-1}$ . The flux was low for the rest of 1998 (Fig. 3).

The flux of cysts produced by heterotrophic taxa showed consistent seasonal patterns, peaking in spring and early summer in all 3 years. The highest cyst fluxes of heterotrophic taxa always occurred in May–June. In 1998, the highest cyst fluxes (up to 44,800 cysts  $m^{-2} day^{-1}$ ) were 1.5 times higher than in 1996 and 1997 (Fig. 3, Table 2). The lowest cyst fluxes were observed in winter, with the exception of the winter of 1997–1998, when cyst flux was relatively high (up to 26,000 cysts  $m^{-2} day^{-1}$ ).

Fluxes of individual taxa varied seasonally and annually (Table 3). The flux of the most abundant taxon, *Brigantedinium* spp., was lower in 1997 and significantly higher in 1998 (more than doubling the flux) than in 1996. The flux of *Q. concreta* was slightly higher in 1997 than in 1996 and 1998. *P. americanum* flux was markedly lower in 1997 than in 1996, recovering almost completely in 1998. *Islandinium? minutum*, *Echinidinium aculeatum*, and cysts type Y (Plate VI/6) had significantly lower fluxes in both 1997 and 1998. *E. delicatum*, *Echinidinium* spp., and cysts type A (Plate VI-5) had higher fluxes in 1996 and 1998 than in 1997. *Operculodinium centrocarpum*, *Islandinium? var. cesare*, and cysts of *Polykrikos schwartzii/kofoidii* fluxes peaked in 1997. Fluxes of cysts of *Pentapharosodinium dalei*, *Spiniferites* spp., and *Selenopemphix quanta* increased in 1997, reaching the highest values in 1998. Daily average fluxes for the most common species are provided in Appendix A and illustrated in Fig. 4.

Dinoflagellate cyst concentrations ranged from  $\sim 70$  to 29,400 cysts  $g^{-1}$ , with an average of  $\sim 2600$  cysts  $g^{-1}$ . The highest cyst concentrations were recorded in late spring of 1996, due to the outbreak (up to  $\sim 28,400$  cysts  $g^{-1}$ ) of cysts of *Alexandrium* spp. The average dinoflagellate cyst concentration, not including *Alexandrium* spp., was  $\sim 1600$  cysts  $g^{-1}$  (Fig. 3). The concentration of cysts produced by the rest

of the autotrophic species varied from 7 to ~600 cysts  $g^{-1}$  with prominent peaks between August and September. The concentration of cysts produced by heterotrophic species varied from ~60 to 9000 cysts  $g^{-1}$  with the highest values observed in summer. The lowest total concentrations of both autotrophic and heterotrophic taxa occurred during winter (Fig. 3).

### 3.3. Sediment trap records of dinoflagellates producing toxic compounds

Toxic and potentially toxic dinoflagellate cysts and organic remains of the motile dinoflagellates were recorded in the sediment trap samples. These cysts included *Alexandrium* spp., *Lingulodinium machaerophorum* (biological name – *L. polyedrum*), *O. centrocarpum* (biological name – *Protoceratium reticulatum*), *Dinophysis acuminata*, and *D. acuta*.

The cysts of *Alexandrium* spp. (Plate I/1, 2) were recorded in very high concentrations in the spring of 1996. For that year, the cysts of *Alexandrium* spp. comprised ~78% of the assemblage. After the outbreak in 1996, these cysts were found in almost all samples during the study period with an average flux of 500 cysts  $m^{-2} day^{-1}$  (Fig. 3).

Only three specimens of *L. machaerophorum* (Plate I/3) were found over the three-year period. These were observed in samples from May, 1996. In contrast, *O. centrocarpum* was found frequently, with maximum fluxes at the end of summer and beginning of fall. The flux of *O. centrocarpum* peaked at 2300 cysts  $m^{-2} day^{-1}$  in August, 1997.

Thecae of *D. acuminata* (Plate VIII, Fig. 5) were observed, mostly in summer samples. In 1997, the flux of *D. acuminata* increased noticeably, reaching a maximum of 196,000 thecae  $m^{-2} day^{-1}$ . Thecae of *D. acuta* (Plate VIII, Fig. 6) were common during the summers of 1996 and 1997, with highest fluxes (up to ~40,000 thecae  $m^{-2} day^{-1}$ ) recorded at the end of summer. The flux of *D. acuta* declined in 1998.

### 3.4. Other palynomorphs

In addition to dinoflagellate cysts, other palynomorphs (organic-walled microfossils of a size ranging from 5–120  $\mu m$ ) were distinguished and counted. Palynomorph type 1 (Plate VIII) was most abundant, with fluxes up to 1,870,000 specimens  $m^{-2} day^{-1}$  in August 1997 (Fig. 5). The abundance of *Radiosperma corbiferum* and Palynomorph types 1 and 2 increased significantly in the summer of 1997. The flux of Tintinnid? lorica type 2 decreased considerably during 1997, while those of Tintinnid? lorica type 1 and 3 and Rhizopoda all increased in the summer and fall of 1998. The flux of copepod eggs was highest in 1996. All of these organic palynomorphs,

except *D. acuta*, *D. acuminata*, and Tintinnid? lorica type 3, were also found in the sediment sample.

### 3.5. Dinoflagellate cysts in the sediment core sample

Twenty-three dinoflagellate cyst taxa were identified in the sediment core samples, of which five were produced by autotrophic and 18 by heterotrophic taxa. Cysts produced by autotrophic taxa contributed ~9% of the mean relative abundance, the rest comprising heterotrophic taxa. *Brigantedinium* spp. and *Q. concreta* strongly dominated the assemblage, (42% and 34%, respectively; Fig. 3). Cysts of *Alexandrium* spp. constituted ~0.5% of the mean relative abundance (Appendix B). The total cyst concentration in the bottom sediment was comparable (~2,000 cysts  $g^{-1}$ ) to the concentration found in sediment trap samples. The cyst composition and relative abundance of dinoflagellate cyst taxa in this assemblage are provided in Appendix B.

## 4. Discussion

The dinoflagellate cysts caught in sequential sediment traps deployed over a three-year period at 150 m in the Strait of Georgia comprise one of the most detailed temporal records of cyst flux published to date. The resolution of approximately 11 days per sample provides an opportunity to correlate changes in cyst flux and assemblage composition with seasonal changes in major surface water parameters. These data also provide an opportunity to evaluate the changes in dinoflagellate cyst fluxes into the traps that accompany a very strong El Niño event.

### 4.1. Composition of dinoflagellate cyst assemblages and relative abundance

The organic-walled dinoflagellate cysts that accumulated in the sediment trap formed a diverse assemblage, with most of the cysts belonging to widely-distributed, neritic, cold-temperate to temperate taxa (Wall et al., 1977; Dale, 1996). All of the taxa have previously been identified in bottom marine sediments from the Strait of Georgia (Radi et al., 2007). Also contained within the trap collections were dinoflagellate species that had not previously been reported from this area in motile stages. Cysts of *P. dalei* and *P. americanum* were common in sediment trap samples and surface sediments (Radi et al., 2007); but their motile stages are virtually absent in planktonic samples collected from the water samples in the Strait of Georgia (see, e.g. Buchanan, 1961; Cattell, 1969; Taylor and Haigh, 1996 for records of dinoflagellates in the water column). Encountering dinoflagellate species for the first time in sediment trap samples rather than from water samples is common (Dale, 1976; Montrestor et al., 1998; Godhe

**Plate I.** Photomicrographs are bright field images. Scale bar is 10  $\mu m$ . 1–2. Cyst of *Alexandrium* spp. UVic 08-48, slide 1, F25/1, and UVic 08-48, slide 1, E29/1, optical sections. 3. *Lingulodinium machaerophorum*. UVic 08-52, optical Section. 4. *Nematosphaeropsis* spp. UVic 08-87, slide 4, G44/4, optical section. 5–6. *Operculodinium centrocarpum* sensu Wall and Dale (1966). UVic 08-201, slide 2, W24/4, optical section, and UVic 08-75, slide 1, K31/2, dorsal surface.

**Plate II.** Photomicrographs are bright field images. Scale bar is 10  $\mu m$ . 1–2. Cyst of *Pentapharsodinium dalei*. UVic 08-217, slide 1, orientation uncertain. 3–4. *Spiniferites ramosus*. UVic 08-217, slide 1, optical section and dorsal surface. 5–6. *Spiniferites* spp. UVic 08-201, slide 1, O24/3, and UVic 08-217, slide 1, optical sections. (see on page 8)

**Plate III.** Photomicrographs are bright field images. Scale bar is 10  $\mu m$ . 1. *Islandinium? minutum*. UVic 08-56, slide 1, P35/2, orientation uncertain. 2. *Islandinium? minutum* var. *cesare*. UVic 08-48, slide 1, K8/3, optical section. 3. *Brigantedinium simplex*. UVic 08-85, slide 1, F13/3, dorsal surface. 4. *Brigantedinium cariacense*. UVic 08-85, slide 1, M24/1, dorsal surface. 5. *Brigantedinium* spp. UVic 08-56, slide 1, J23/2, dorsal surface. 6. *Dubridinium* spp. UVic 08-85, slide 1, R25/4, dorsal surface. (see on page 9)

**Plate IV.** Photomicrographs are bright field images. Scale bar is 10  $\mu m$ . 1–2. *Echinidinium aculeatum*. UVic 08-56, slide 1, J34/1, dorsal surface and F25/4, optical surface. 3. *Echinidinium delicatum*. UVic 08-82, slide 1, D18/1, optical surface. 4. *Echinidinium granulatum*. UVic 08-49, slide 1, J16/3, dorsal surface. 5. *Pheopolykrikos hartmanii*. UVic 08-70, slide 2, orientation uncertain. 6. *Echinidinium* spp. UVic 08-67, slide 1, J24/2, orientation uncertain. (see on page 10)

**Plate V.** Photomicrographs are bright field images. Scale bar is 10  $\mu m$ . 1–2. Cyst of *Protoperidinium americanum*. UVic 08-81, slide 1, F28/3, dorsal surface and K24/1, optical section. 3–4. *Quinquecuspsis concreta*. UVic 08-57, slide 1, M12/2, dorsal surface and UVic 08-52, slide 1, T35/1, dorsal surface. 5. Cyst of *Protoperidinium* spp., type 1. UVic 08-60, slide 1, D43/1, dorsal surface. 6. Cyst of *Polykrikos schwarzii/kofoidii*. UVic 08-49, slide 1, P40/3, dorsal surface. (see on page 11)

**Plate VI.** Photomicrographs are bright field images. Scale bar is 10  $\mu m$ . 1. *Selenopemphix nephroides*. UVic 08-83, slide 1, U33/1, apical surface. 2. *Selenopemphix quanta*. UVic 08-83, slide 2, D42/4, dorsal surface. 3. *Votadinium calvum*. UVic 08-56, slide 1, K16/2, dorsal surface. 4. *Votadinium spinosum*. UVic 08-217, slide 1, apical surface. 5. Cyst type A. UVic 08-54, slide 1, R15/4, dorsal surface. 6. Cyst type Y. UVic 08-49, slide 1, dorsal surface. (see on page 12)

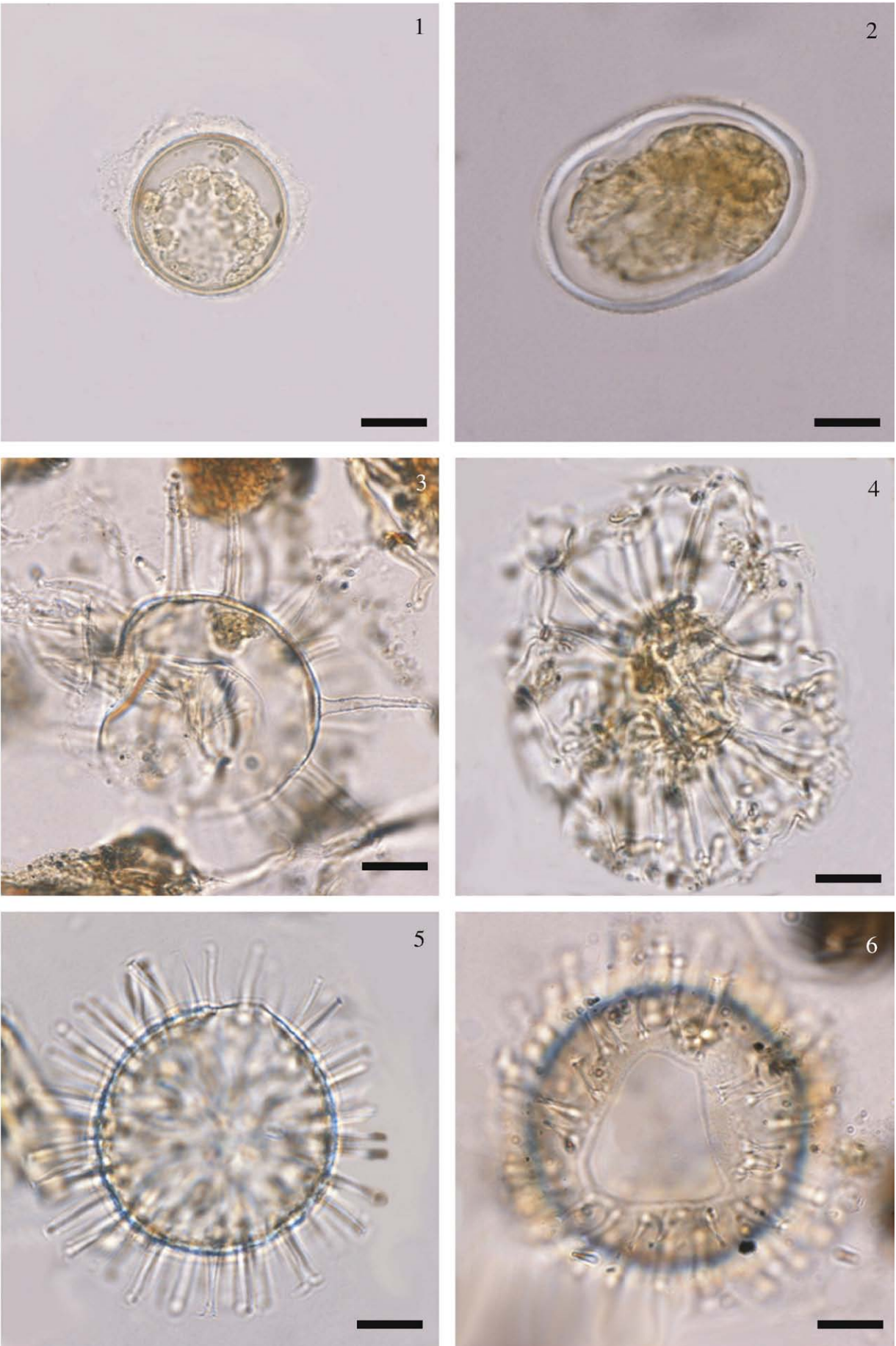


Plate I.

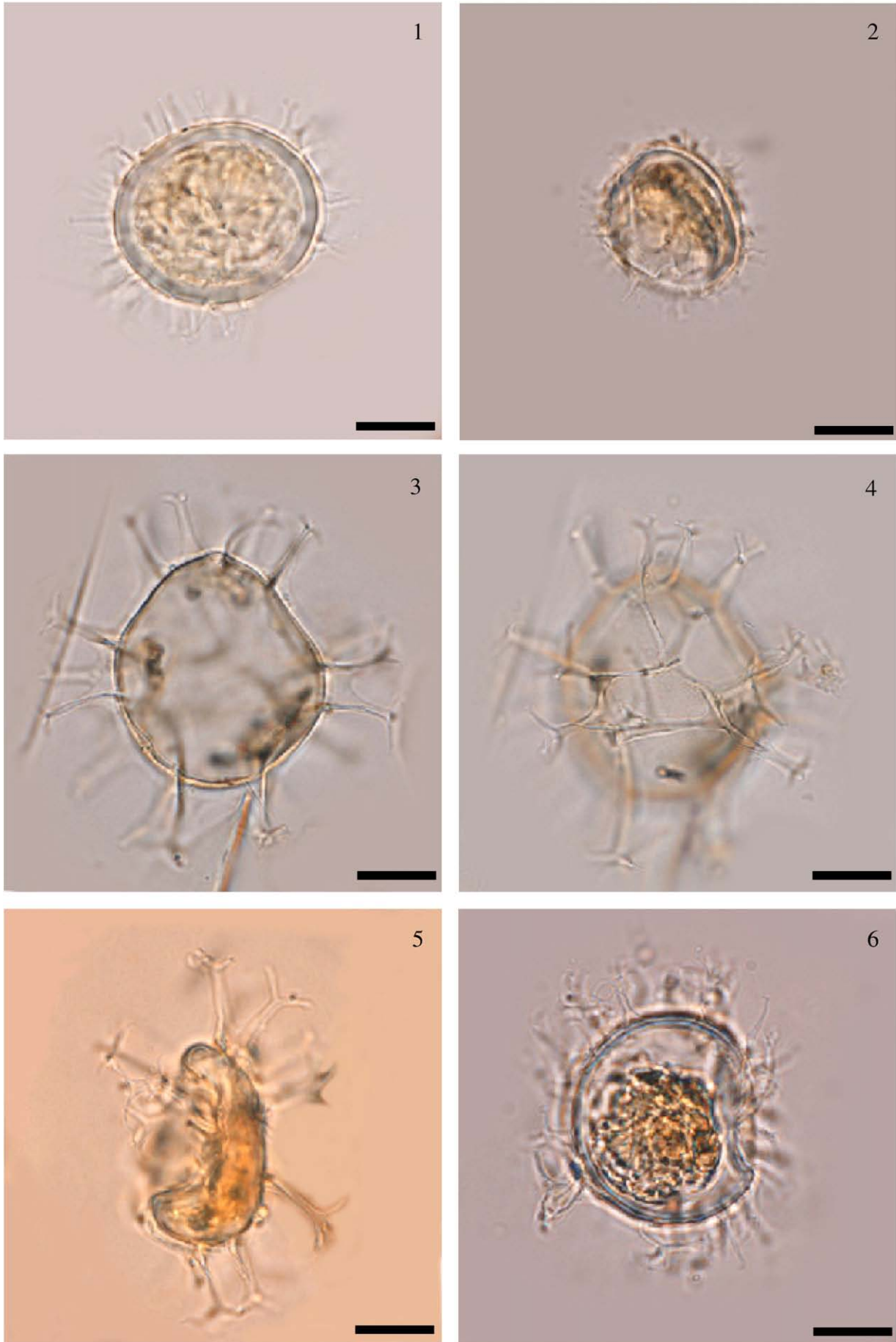


Plate II (see caption on page 22).

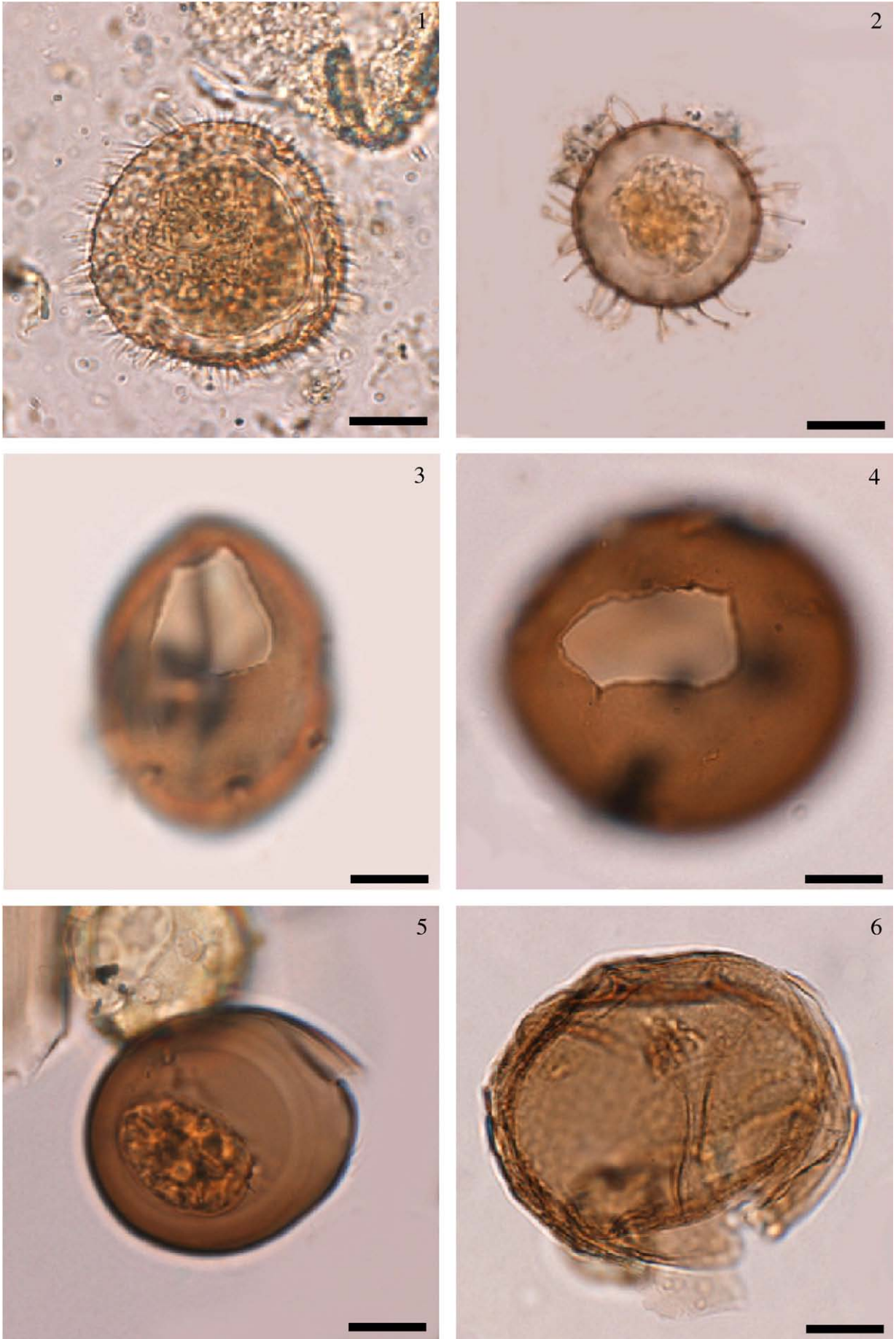


Plate III (see caption on page 22).

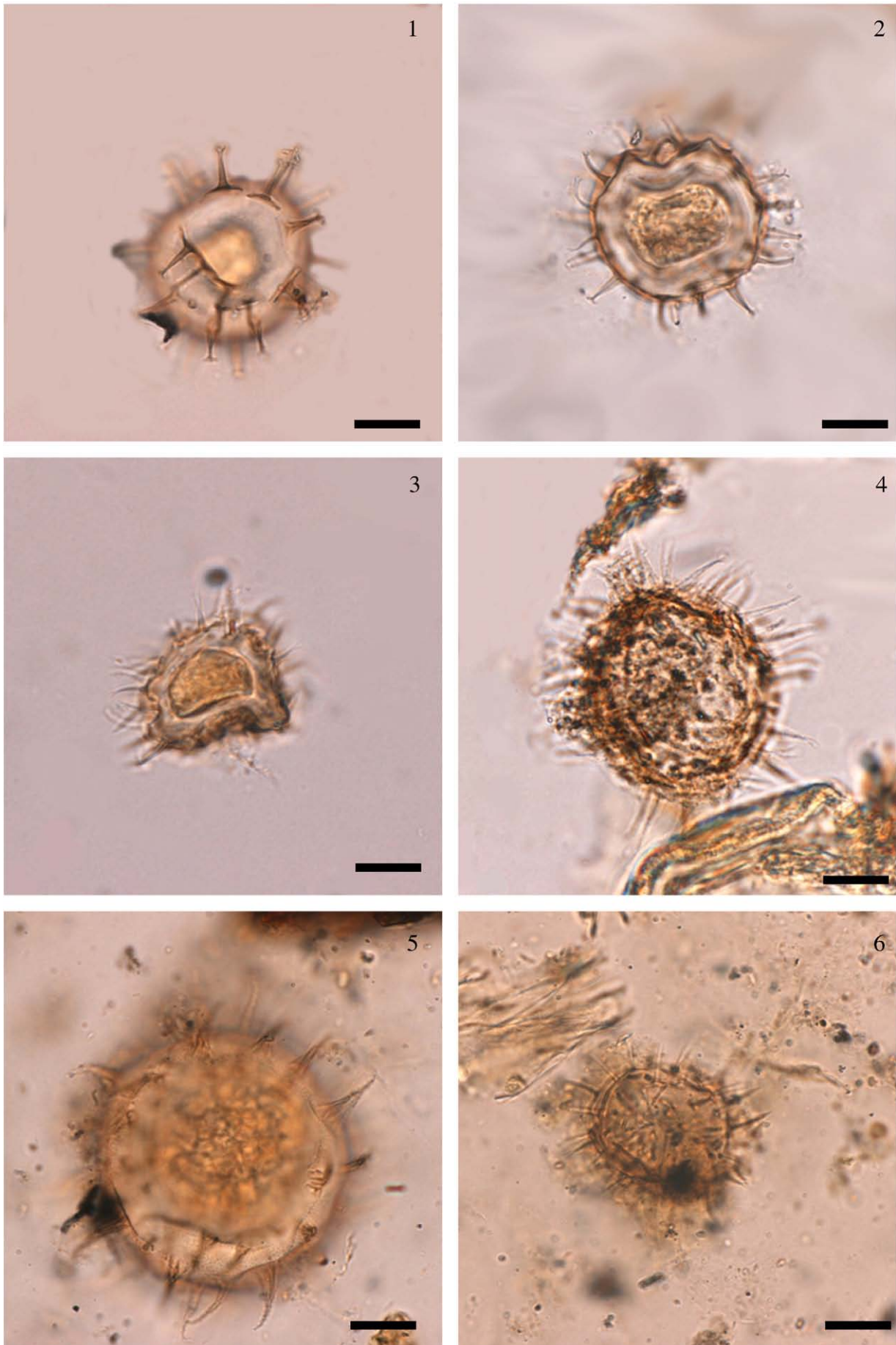


Plate IV (see caption on page 22).

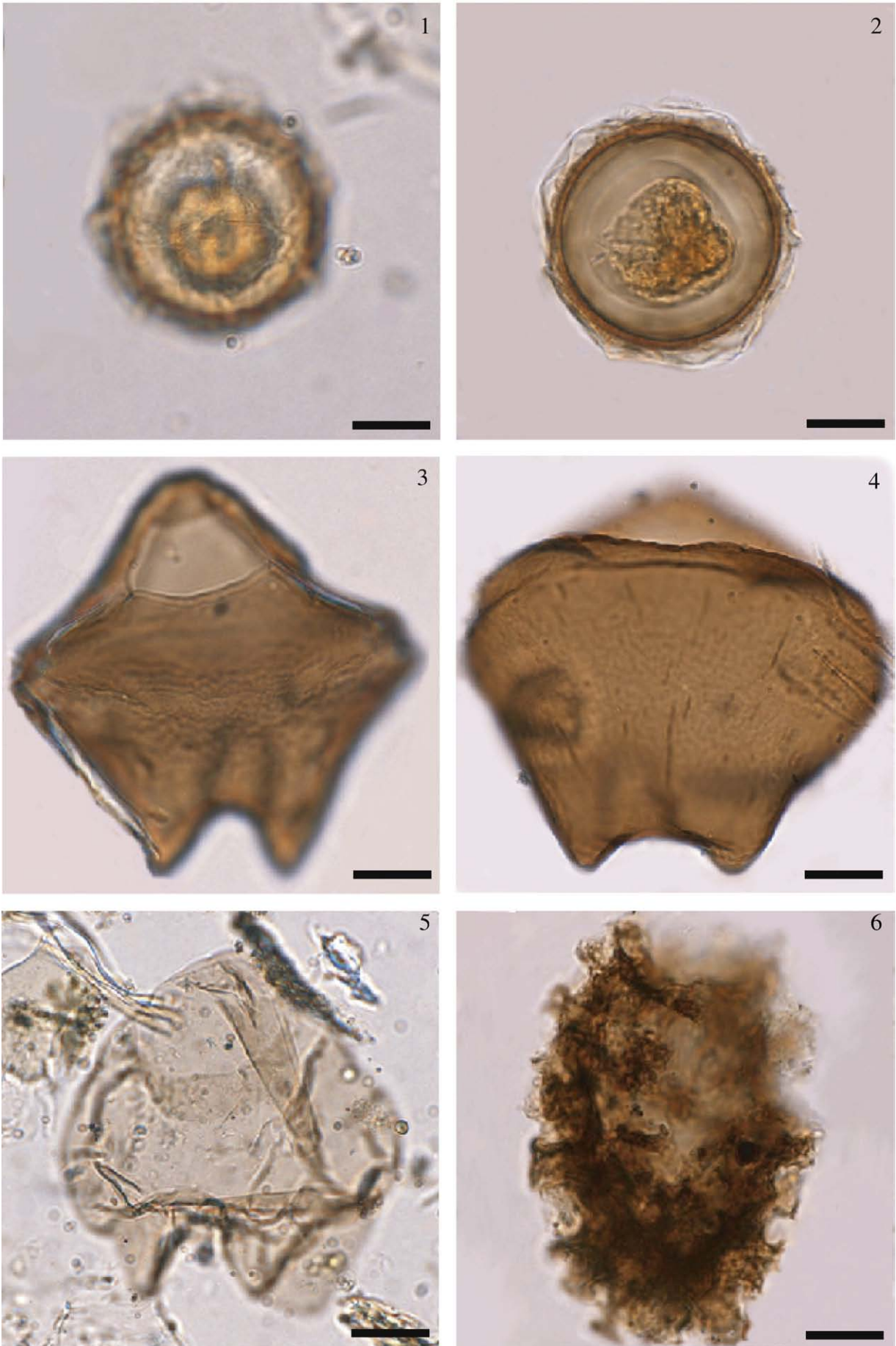


Plate V (see caption on page 22).

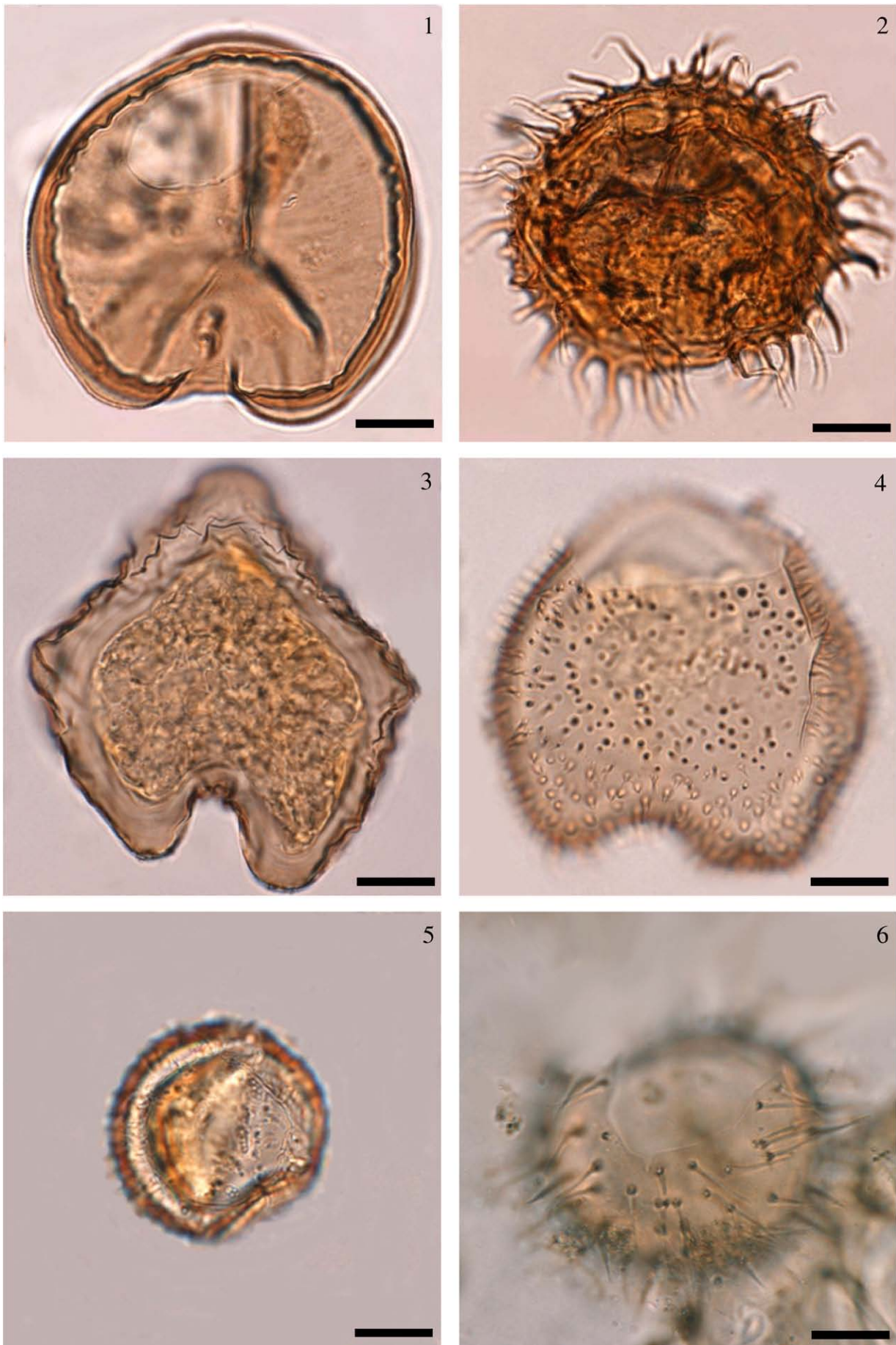
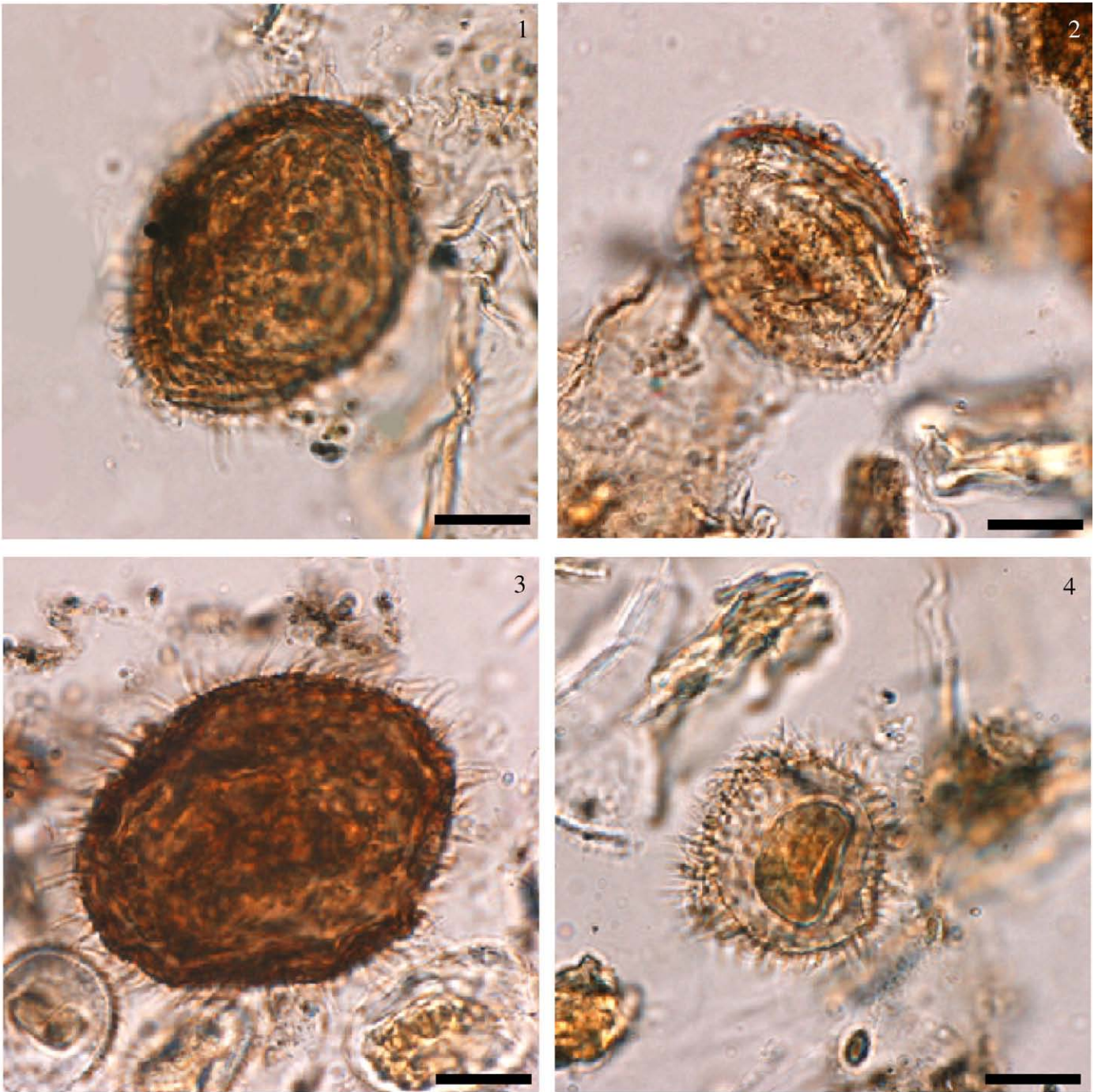


Plate VI (see caption on page 22).



**Plate VII.** Photomicrographs are bright field images. Scale bar is 10  $\mu\text{m}$ . 1–4. Spiny brown cysts.

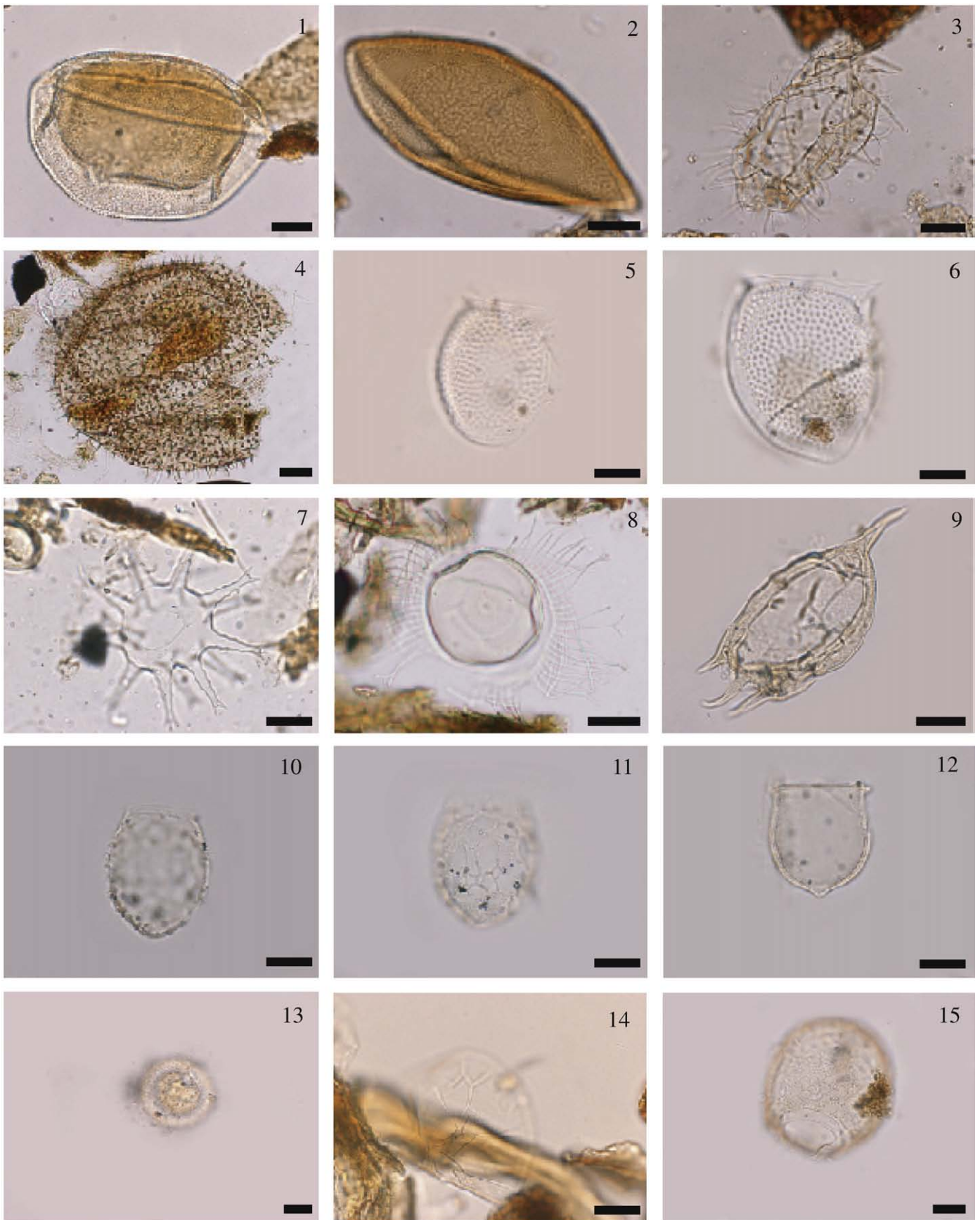
et al., 2001), because the former efficiently integrate sampling over time.

#### 4.2. Seasonal and annual variability of dinoflagellate cyst flux

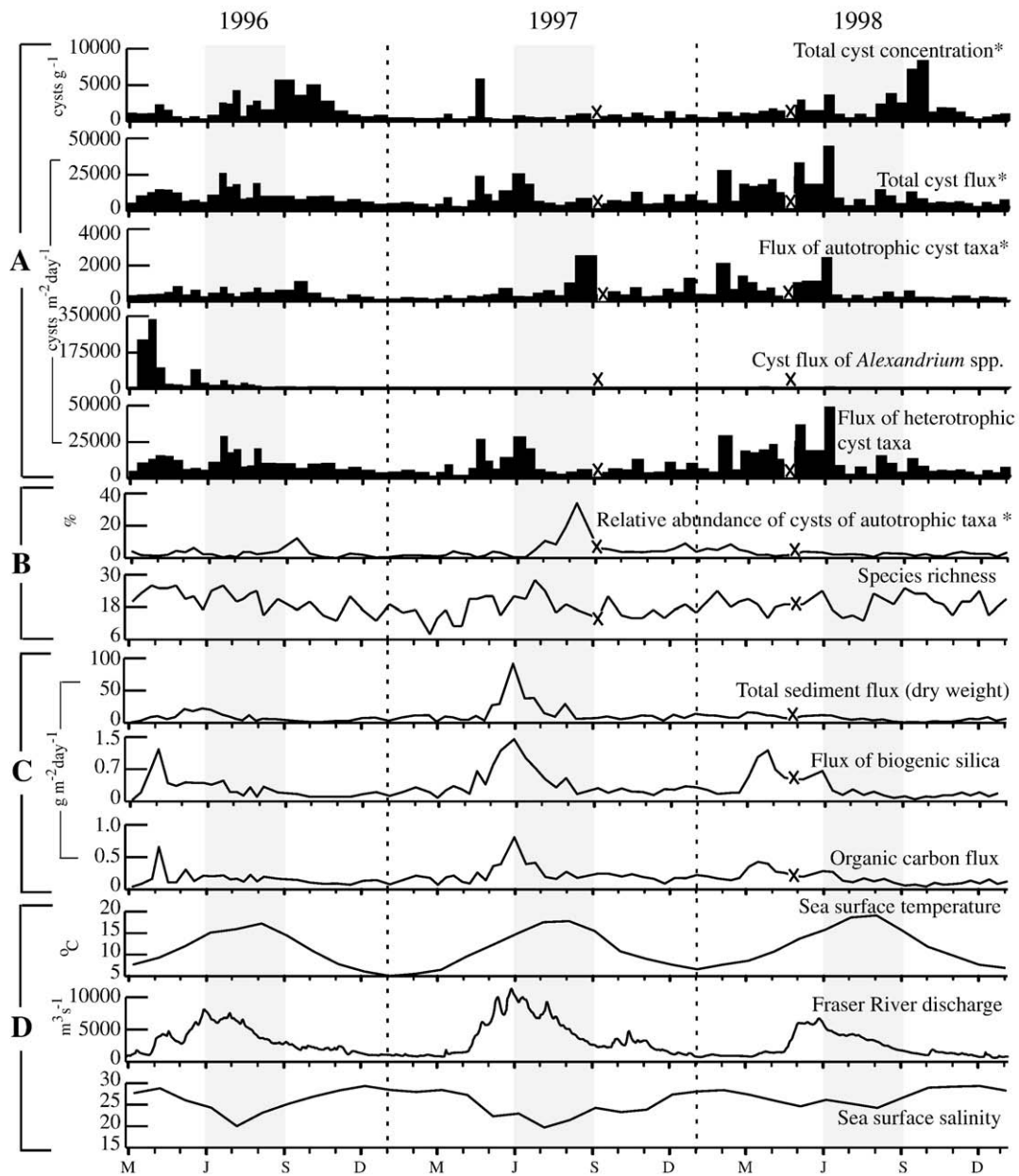
Sediment trap data clearly show seasonal trends in dinoflagellate cyst production and differences in encystment pattern among species. The total cyst flux was lowest in the winter each year, increased in early spring and peaked in late spring or early summer (Fig. 3). This pattern is similar to that observed in the water column of the Strait of Georgia, where motile dinoflagellate stages contribute substantially to the spring bloom and peak in the summer (Cattell, 1969). This pattern is also consistent with previous results on the seasonality of dinoflagellate cyst

production; it has been shown that a dinoflagellate bloom is concomitant or terminated with cyst formation in temperate and cold-temperate environments (Dale, 1976; Heiskanen, 1993; Montreuil et al., 1998; Godhe et al., 2001; Tamelander and Heiskanen, 2004).

Cysts produced by autotrophic and heterotrophic dinoflagellates had different seasonal patterns and annual variations in fluxes. Autotrophic taxa – *O. centrocarpum*, cysts of *P. dalei*, and *Spiniferites* spp. – were present in the samples throughout the year. Although *O. centrocarpum* and cysts of *P. dalei* were recorded year-round, the highest flux for *O. centrocarpum* was recorded at the end of summer and for *P. dalei* in spring (Fig. 4). Heterotrophic cyst taxa had more temporally-restricted production patterns. The most common heterotrophic cyst taxa with fairly regular seasonal patterns were assigned to the following groups:



**Plate VIII.** Photomicrographs are bright field images. Scale bar is 10  $\mu\text{m}$ . 1–4. Copepod eggs. UVic 08-88, slide 1, UVic 08-93, slide 1, UVic 08-49, slide 1. 5. *Dinophysis acuminata*. UVic 08-57, slide 1. 6. *Dinophysis acuta*. UVic 08-49, slide 1. 7. *Hexasterias problematica*. UVic 08-85, slide 1. 8. *Radiosperma corbiferum*. UVic 08-53, slide 1. 9. Rhizopoda. UVic 08-61, slide 1. 10–11. Tintinnid? lorica, type 1. UVic 08-59, slide 1. 12. Tintinnid? lorica, type 2. UVic 08-53, slide 1. 13. Palynomorph type 1. UVic 08-57, slide 1. 14. Palynomorph type 2. UVic 08-133, slide 1. 15. Tintinnid? lorica, type 3. UVic 08-121, slide 1.



**Fig. 3.** Three year time-series of: A. Total dinoflagellate cyst concentration, flux, and fluxes of cysts produced by autotrophic and heterotrophic taxa, as well as flux of cysts of *Alexandrium* spp.; B. Relative abundance of cysts produced by autotrophic taxa and species richness; C. Flux of sediments (dry weight), biogenic silica, and organic carbon; D. Monthly average sea surface temperature and salinity along with daily Fraser River discharge. Gray bands highlight summer seasons (June–August).

spring taxa – *Islandinium? minutum* var. *cesare*; spring and summer taxa – *Brigantidium* spp., *Q. concreta*, *Dubridinium* spp.; summer taxa – *E. aculeatum*, cyst type A; taxa with two peaks in production in fall and spring: *P. americanum*, *E. delicatum*, *Echinidinium* spp., *Selenopemphix quanta*; winter taxa – *S. nephroides* (Fig. 4).

The inter-annual variability of dinoflagellate cyst flux contains the imprint of the 1997–98 El Niño. Here, 1996 is considered to be a normal year followed by two years affected by El Niño. In 1997, the Strait of Georgia was characterized by significantly earlier and higher Fraser River flow (Environment Canada), lower SSS in the summer, and slightly higher SST (Fig. 3). The winter of 1997–98 was warm (Foreman et al., 2001), which resulted in noticeable positive deviations in SST (Fig. 3). Fraser River flow is affected by large-scale climate shifts, as surface air temperature affects snow accumulation and snow melt (Moor, 1991). In 1998 the Fraser River experienced one of the lowest discharges ever recorded due to low snow accumulation during the preceding El Niño winter (Foreman et al., 2001). As a consequence of the low discharge,

the summer SSS in 1998 was higher than in 1996 and 1997 (Fig. 3). Nutrient supply in the Strait of Georgia is affected by variations in Fraser River flow (Harrison et al., 1994) and coastal upwelling (Mackas and Harrison, 1997). Higher than usual SST reduces the upwelling of nutrient-rich water, which results in less nutrition for marine life on the coast (Peña et al., 1999). Compared to 1996, the total annual dinoflagellate cyst flux in years affected by El Niño decreased by five and three times, in 1997 and 1998, respectively (Fig. 3). If the bloom of *Alexandrium* spp. is excluded, the total flux in 1997 was slightly lower than in 1996, followed by a substantial increase in 1998 (Table 2). We also observe that the total cyst flux completely recovered in 1998, driven principally by an increase in the production of heterotrophic taxa. This increase was most likely related to the increased SST and the early warm spring of 1998, which resulted in an expanded production season of dinoflagellates and diatoms.

The exact link between annual changes in dinoflagellate cyst flux at the species level and physical parameters in the Strait is difficult to

**Table 2**

Total annual dinoflagellate cyst flux (cysts  $\times 10^6$  yr $^{-1}$ ). The asterisk (\*) indicates that cysts of *Alexandrium* spp. are not included in the calculations.

	(Mar.1996– Dec.1996)	Jan.1997–Dec.1997 (Mar.1997–Dec.1997)	Jan.1998–Dec.1998 (Mar.1998–Dec.1998)
Days of deployment	(298)	355 (299)	364 (304)
Autotrophic taxa	(9.16)	0.26 (0.24)	0.32 (0.25)
Autotrophic taxa*	(0.08)	0.14 (0.14)	0.18 (0.13)
Heterotrophic taxa	(2.36)	2.26 (2.10)	4.16 (3.49)
Total cyst flux	(11.53)	2.34 (2.52)	4.47 (3.74)
Total cyst flux*	(2.45)	2.41 (2.24)	4.34 (3.62)

establish. Phytoplankton production, including dinoflagellates, depends on a number of biotic and abiotic factors, such as light, nutrients, salinity, temperature, turbulence, and grazing (Harris, 1986). Moreover, in many cases these factors interfere with each other (Harrison et al., 1983), and such interaction becomes particularly complicated in estuarine systems. Our data offer some insight into this rather complicated issue. Table 3 summarizes main annual trends in cyst fluxes of the most common dinoflagellate cyst taxa. The observed, significant drop in the cyst fluxes of *Protoperidinium americanum*, *Brigantedinium* spp., *Alexandrium* spp., *Echinidinium* spp., *E. aculeatum*, *E. delicatum*, *I. minutum*, cyst type A and Y during 1997 (Fig. 4. and Table 3) could have been related to the prolonged period of reduced SSS (six months with SSS below 25). Another factor that might have affected phytoplankton is reduced light penetration in 1997 related to a many-fold increase in the flux of sediment from the Fraser River. An opposite trend is exhibited by *O. centrocarpum*, *Spiniferites* spp. *Q. concreta*, *S. nephroides*, *Dubridinium* spp., *I. minutum* var. *cesare*, spiny brown cysts and cysts of *Polykrikos schwartzii/kofoidii*, whose cyst production was enhanced during the spring-fall of 1997 (Fig. 4 and Table 3). These taxa are known to be tolerant of lower SSS (Marret and Zonneveld, 2003). The production of the autotrophic taxa *Spiniferites* spp. and cysts of *P. dalei* and of the heterotrophic *Echinidinium* spp., *E. delicatum*, *S. nephroides*, *S. quanta* and cyst type A increased in the winter of 1997–98 and spring of 1998 (Fig. 4; Appendix A and B). The increased fluxes of these taxa might have been related to increased SST during the prolonged early spring of 1998.

Patterns in the flux of heterotrophic *Brigantedinium* spp., *Q. concreta* and cysts of *P. americanum* are correlated with the diatom flux, as inferred from the record of biogenic silica in the trap (Figs. 3 and 4). The fluxes of both biogenic silica and cysts produced by heterotrophic dinoflagellates peaked at the end of spring and beginning of the summer in 1996 and 1997 and in early spring in 1998. This result might be anticipated, as heterotrophic dinoflagellate

taxa are ultimately reliant on the availability of preferred prey, such as diatoms, that are controlled by SST. More detailed links among the fluctuations of fluxes/proportions of the individual taxa and specific environmental parameters are not obvious in the dataset.

#### 4.3. Comparison of cyst flux in the Strait of Georgia with other sediment trap studies

The cyst fluxes in the Strait of Georgia average  $\sim 18,000$  cysts  $m^{-2}$  day $^{-1}$ , or 8800 cysts  $m^{-2}$  day $^{-1}$  excluding cysts of *Alexandrium* spp. The highest values (up to 336,200 cysts  $m^{-2}$  day $^{-1}$ ) are comparable to those found in sediment trap studies conducted in Gullmar Fjord on the west coast of Sweden ( $\sim 320,000$  cysts  $m^{-2}$  day $^{-1}$  (Godhe et al., 2001)), Omura Bay, Japan (flux of organic-walled dinoflagellate cysts ranged from 7,300 to 3,770,000 cysts  $m^{-2}$  day $^{-1}$ ; Fujii and Matsuoka, 2006), and in the coastal Mediterranean (maximum flux of organic-walled and calcareous dinoflagellate cysts of 1,700,000 cysts  $m^{-2}$  day $^{-1}$ ; Montrestor et al., 1998).

The seasonal trend of dinoflagellate cyst production in the Strait of Georgia, with its highest cyst flux from early spring to autumn, is similar to that observed in the Gulf of Naples (Montrestor et al., 1998), whereas in sub-tropical Omura Bay the peak in cyst flux was recorded in autumn and winter (Fujii and Matsuoka, 2006). The general trend in autotrophic taxa was similar in Omura Bay to that observed in the Strait of Georgia. In the Gulf of Naples, organic-walled dinoflagellate cyst production by autotrophic taxa was mainly restricted to the warmest months (July–September; Montrestor et al., 1998). However, this peak was caused mainly by the flux of *O. centrocarpum*, which also had the highest flux at the end of summer in the Strait of Georgia. Among the most common heterotrophic taxa from the Strait of Georgia, only two species provide an opportunity for comparison of seasonal patterns in other locations: *S. quanta* in the Gulf of Naples peaked during fall and spring (Montrestor et al., 1998), while *S. nephroides* in Omura Bay peaked in winter (Fujii and Matsuoka, 2006). Both of these species have the same pattern in the Strait of Georgia, despite differences in hydrographical and environmental settings.

#### 4.4. Sedimentary records of potentially toxic dinoflagellates

The most serious problem for managing the risks posed by HABs is the lack of information on the abundance, distribution and population dynamics of harmful algae, both in local waters and elsewhere (Taylor and Horner, 1994). One way to document the seed bank of harmful species of dinoflagellates is to study cysts in dated sediment cores.

**Table 3**

Annual dinoflagellate cyst flux (cysts  $\times 10^3$  m $^{-2}$  year $^{-1}$ ) for the most common taxa. Arrows indicate noticeable changes (increase or decrease) in the cyst flux compared to the flux in 1996.

	Mar.1996–Dec.1996	Jan.1997–Dec.1997 (Mar.–Dec.)	Trend	Jan.1998–Dec.1998 (Mar.–Dec.)	Trend
Cyst of <i>Alexandrium</i> spp.	(9078)	118 (96)	↓	137 (121)	↓
Cyst of <i>Pentapharsodinium dalei</i>	(24)	26 (26)		63 (53)	↑
<i>Operculodinium centrocarpum</i>	(54)	106 (103)	↑	78 (51)	
<i>Spiniferites</i> spp. and <i>S. ramosus</i>	(6)	12 (12)	↑	40 (26)	↑
Total <i>Brigantedinium</i>	(940)	953 (877)	↓	2408 (2059)	↑
Cyst type A	(40)	33 (32)	↓	102 (102)	↑
Cyst type Y	(61)	3 (3)	↓	41 (41)	↓
Cyst of <i>Polykrikos schwartzii/kofoidii</i>	(11)	22 (21)	↑	13 (13)	
Cyst of <i>Protoperidinium americanum</i>	(429)	111 (86)	↓	343 (289)	↓
<i>Dubridinium</i> spp.	(107)	143 (129)	↑	130 (107)	
<i>Echinidinium aculeatum</i>	(63)	42 (40)	↓	37 (31)	↓
<i>Echinidinium delicatum</i>	(61)	29 (26)	↓	158 (148)	↑
<i>Echinidinium granulatum</i>	(7)	5 (5)		3 (2)	↓
<i>Echinidinium</i> spp.	(74)	31 (30)	↓	95 (86)	↑
<i>Islandinium ? minutum</i>	(23)	7 (7)	↓	10 (5)	↓
<i>Islandinium ? minutum</i> var. <i>cesare</i>	(22)	43 (43)	↑	3 (3)	↓
<i>Quinquecupis concreta</i>	(429)	610 (575)	↑	592 (423)	
<i>Selenopemphix nephroides</i>	(27)	37 (35)	↑	44 (32)	↑
<i>Selenopemphix quanta</i>	(12)	15 (15)		64 (57)	↑
Spiny brown	(43)	167 (165)	↑	97 (79)	↑

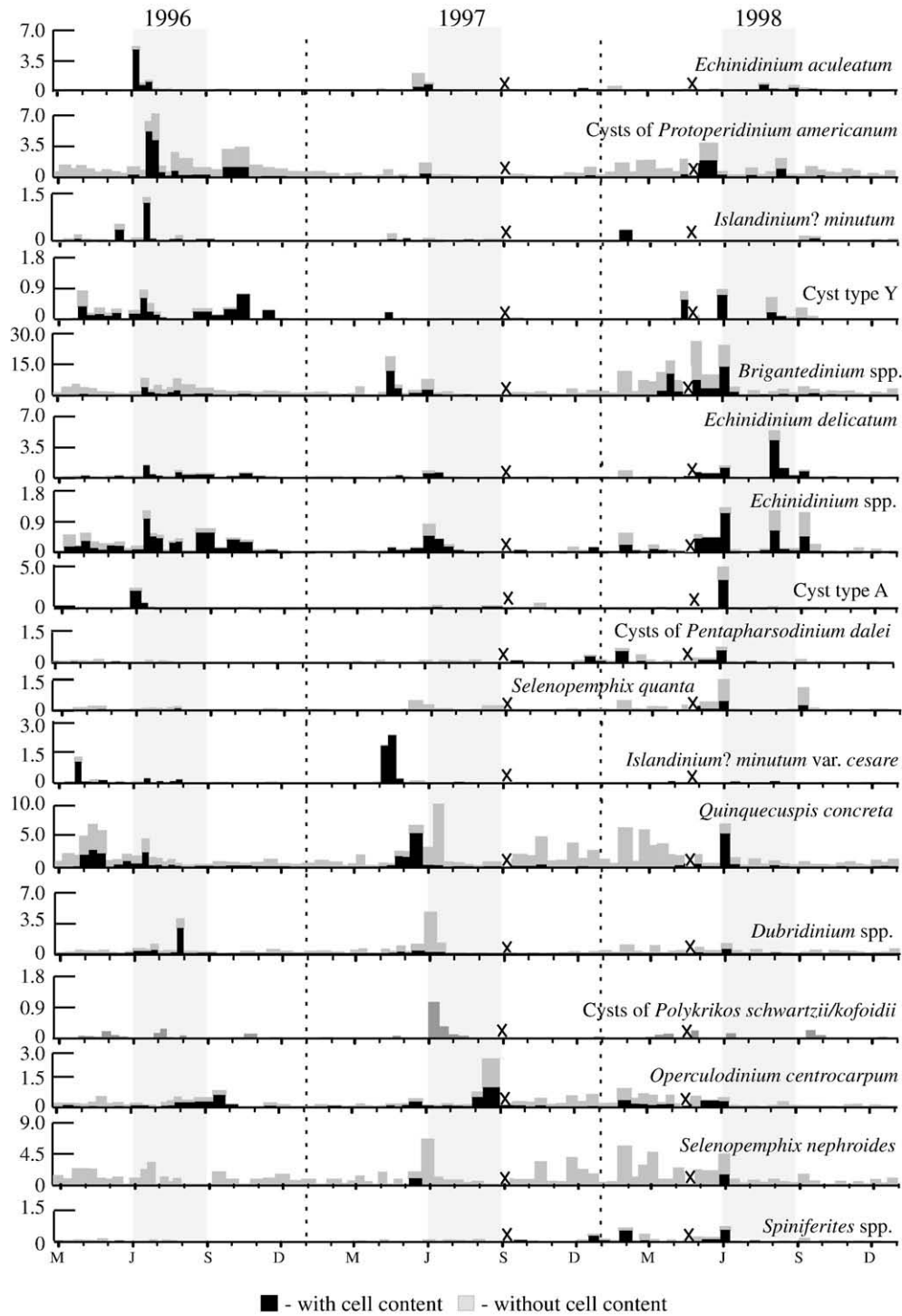


Fig. 4. Average daily cyst flux (cysts  $\times 10^3 \text{ m}^{-2} \text{ day}^{-1}$ ) for the most common taxa, with cell content and without cell content. Gray bands highlight summer seasons (June–August).

This approach could, potentially, document the presence, distribution, and trends in dinoflagellate taxa of concern in the Strait of Georgia.

Most species of the genus *Alexandrium* are toxic, producing saxitoxins that cause paralytic shellfish poisoning (PSP). *Alexandrium* blooms are very common in the Strait of Georgia (Taylor and Harrison, 2002), and these have been directly linked to human illness and fatality through PSP (Prakash and Taylor, 1966). The dominant species of this genus in the Strait of Georgia is *Alexandrium tamarense* (Taylor, 1984). Other toxic species occurring in British Columbia coastal waters include *A. acatenella*, *A. catenella*, and *A. minutum* (Taylor and Harrison, 2002). Some studies suggest that *Alexandrium* spp. is not often found

during surface water sampling, despite its high cyst production rate and common occurrence in sediments and sediment trap samples (Montrestor et al., 1998; Godhe et al., 2001). Thus, detection and monitoring species of genus *Alexandrium* might best be accomplished through sediment trap or surface sediment sampling.

The record of cysts found in sediment traps during our study is consistent with previous studies that show that species of genus *Alexandrium* are common in the Strait of Georgia (Taylor, 1984), and that their blooms usually occur during spring and summer (Taylor and Haigh, 1996). Some planktonic and sediment studies also suggest that blooms of *Alexandrium* spp. coincide with El Niño years (Gaines and

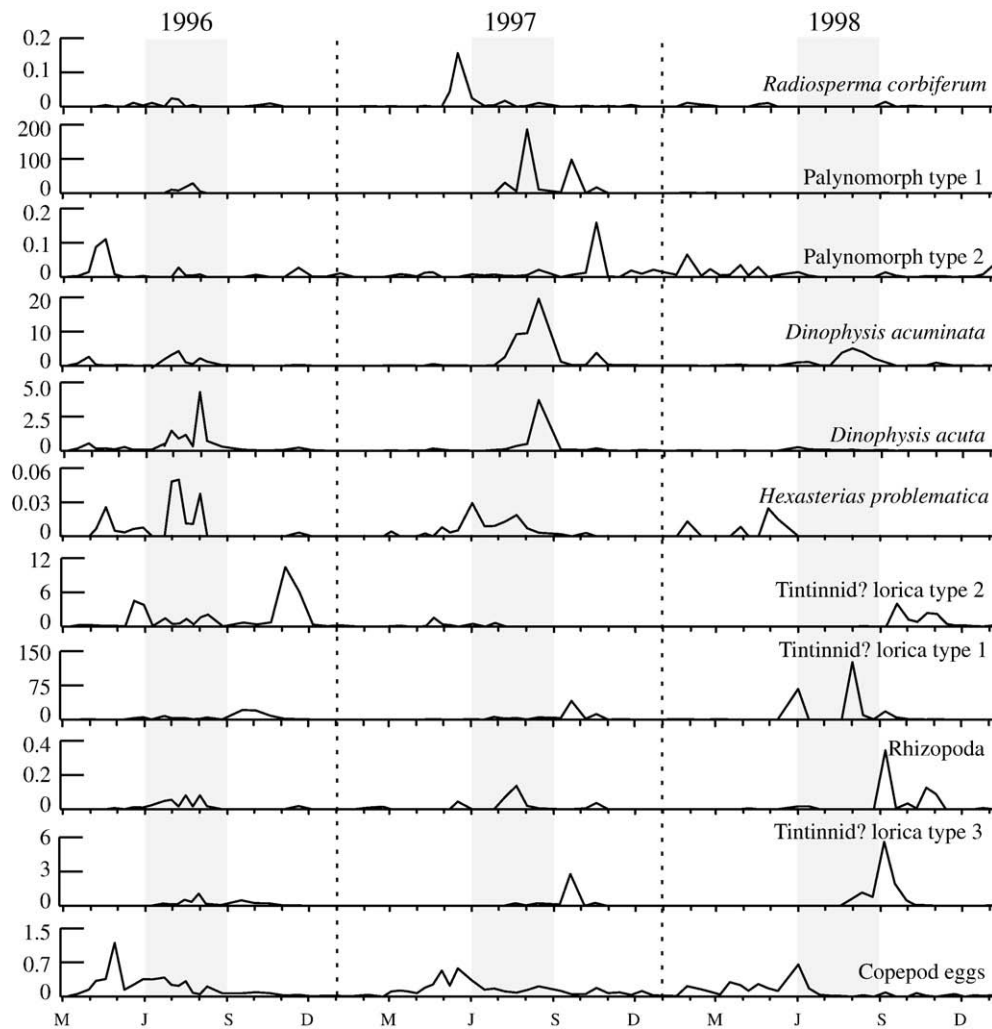


Fig. 5. Average daily flux of selected aquatic palynomorphs (specimens  $\times 10^4 \text{ m}^{-2} \text{ day}^{-1}$ ). Gray bands highlight summer seasons (June–August).

### GSCM-3 sediment trap

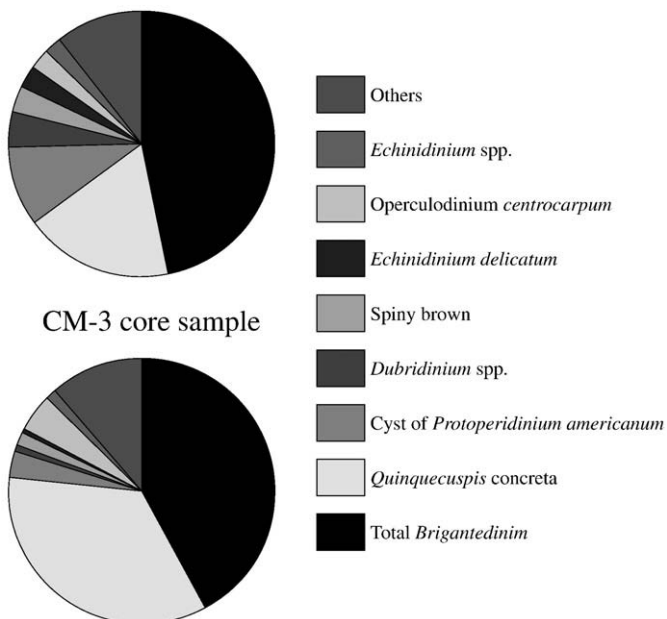


Fig. 6. Relative abundance (%) of most common dinoflagellate cyst taxa from sediment trap GSCM-3 and the core sample CM-3. Cysts of *Alexandrium* spp. are not included in the calculations.

Taylor 1985; Mudie et al., 2002); however, we observed the outbreak of *Alexandrium* spp. in the year preceding El Niño (Fig. 3), implying a weaker link to El Niño-driven hydrographic variability than previously suggested.

*Lingulodinium machaerophorum* (biological name – *L. polyedrum*, synonym – *Gonyaulax polyedra*) has not previously been reported in sediment samples from the Strait of Georgia, but was found in core samples in Saanich Inlet (Mudie et al., 2002). In our sediment trap samples only three specimens were observed. It is possible that *L. machaerophorum* is underrepresented in settling particles, as the planktonic form might not be accompanied by a significant vertical export of cysts (Godhe et al., 2001) or is present in negligible quantities.

*Operculodinium centrocarpum* (biological name – *P. reticulatum*) is a potentially toxic species, producing disulphated polyether yessotoxin and derivatives of yessotoxin (Satake et al., 1997; Eiki et al., 2005). Although *O. centrocarpum* is a common taxon in the northeast Pacific, it has not yet been linked to HABs. In the Strait of Georgia this is the most abundant autotrophic species in almost all samples (Fig. 4; Appendix A and B). It exhibited a strong increase in August 1997, briefly becoming the dominant cyst taxon.

*Dinophysis acuminata* and *Dinophysis acuta* produce okadaic acid, which causes diarrhetic shellfish poisoning (DSP). *D. acuminata* can be misidentified, as it is similar to *D. sacculus*, *D. norvegica*, *D. ovum*, and *D. punctata*. *D. acuta* can be confused easily with *D. norvegica*, which is also toxic. In the Strait of Georgia, *D. acuminata* and *D. acuta* were recorded in the summer, with the highest production rates in July and

August (Fig. 5). The maximum flux occurred in 1997, coincident with the period of decreased SSS (Fig. 3).

#### 4.5. Sediment core sample

The cyst assemblage in the sediment core sample collected from the mooring site was very similar to that in the sediment traps (Appendix B). All species comprising more than 1% of the total assemblage in the sediment trap were present in the core sample, and cysts that were not found in the core sample were rare in the trap. All 30 taxa, with the exception of *L. machaerophorum*, had been reported previously in the Strait of Georgia (Radi et al., 2007). The relative abundance of the most common species was similar in the sediment trap samples and to that observed in the core (Appendix B).

Several features of the Strait of Georgia favour the burial and preservation of dinoflagellate cysts in bottom sediments. The concentration of dissolved oxygen in the bottom water is low (1.5 to 3 ml L<sup>-1</sup>; Masson, 2006), which favours cyst preservation (Zonneveld et al., 1997, 2008). The central basin of the Strait of Georgia, especially off the Fraser Delta, has generally high sedimentation rates (~ 0.28 to ~2.9 cm year<sup>-1</sup>), with ~2.8 cm year<sup>-1</sup> determined at the sediment trap mooring location (Johannessen et al., 2003). Some discrepancies in cyst proportions between sediment trap samples and bottom samples in other studies have been observed (Montrestor et al., 1998; Harland and Pudsey, 1999; Zonneveld and Brummer, 2000) and ascribed to factors such as secondary transport, oxidation of organic fraction, compaction/dilution of bottom sediments, and uncertainty that the age of the core sediments represented the short deployment period of the sediment trap (Harland and Pudsey, 1999; Zonneveld and Brummer, 2000).

The data presented here show a high degree of correspondence in dinoflagellate cyst composition and abundance between trap and core samples. This correspondence suggests that sediment records in the Strait of Georgia may provide a useful proxy for local cyst production. Sediment transport processes are not evenly distributed within the Strait. At the CM-3 site, the bottom sedimentation was estimated to be 4 times the flux measured in the deepest trap at that site (Johannessen et al., 2005), suggesting that advective transport near the bottom was an important process. The correspondence between the cysts caught in the traps and those measured in the bottom sediments at the mooring site, therefore, implies a certain degree of homogeneity within the Strait in the production and export of cysts. Radi et al. (2007) have identified three cyst zones in surface sediments of the studied part of the Strait of Georgia. The sediment trap cyst assemblages are similar to those described by Radi et al. (2007) in the zone in which the mooring was located. Consequently, it appears that sediment cores, properly dated and evaluated for biomixing, might provide reasonable proxy reconstructions of cysts that could be set against long-term changes in environmental parameters in the Strait of Georgia.

#### 4.6. Other palynomorphs

Because the sediment traps were located in highly productive coastal waters and near a large river inflow, other organic palynomorphs were significantly more abundant (by two orders of magnitude) in the samples than were dinoflagellate cysts (Fig. 5). Palynomorphs are discussed briefly below, with reference to changing environmental conditions.

Green algae, *Radiosperma corbiferum*, and Palynomorphs type 1 and 2, probably of algal affinity, had significantly increased fluxes in 1997 (Fig. 5, Plate VIII/8). *Radiosperma corbiferum* is a marine to brackish algae with a distribution primarily controlled by riverine input/SSS (Brenner, 2001). This is consistent with our dinoflagellate cyst results, as its highest fluxes were recorded in the summer during the period of lowest salinity. Palynomorph types 1 and 2 might also prefer low SSS, as their occurrence follows that of *R. corbiferum*.

*Hexasterias problematica* is a brackish water to euryhaline species of Prasinophyceae (Matthiessen et al., 2000) and has been observed in the Arctic in abundance towards a melt-water plume (Mudie, 1992). Our observations for 1997 (Fig. 5, Plate VIII/7) can be understood as a prolonged flux of *H. problematica* supported by a similarly prolonged freshet in the Fraser River (Fig. 3).

Tintinnid? lorica type 2 (Plate VIII/12) flux was low in 1997 (Fig. 5). Tintinnids are heterotrophic organisms that feed on phytoplankton and also are food for larger organisms such as copepods. There are many species of this order, and decreased abundance of Tintinnid? lorica type 2 might reflect decreased availability of its particular food source.

Copepods are the most abundant group of zooplankton in the Strait of Georgia (Harrison et al., 1994). There were fewer copepod eggs (Plate VIII/1–4) in sediment trap samples in 1997 than in the other years (Fig. 5). Copepods feed on phytoplankton and small zooplankton. The decline in copepod eggs during 1997 (Fig. 5) likely reflects the general decrease in plankton biomass in the Strait of Georgia in that year (Ocean State Report, 1999).

*D. acuminata* and *D. acuta* (Plate VIII/5, 6) were abundant in sediment trap samples (Fig. 5), but they were not observed in the sediment core samples, suggesting that these dinoflagellate thecae are easily degraded. Other palynomorphs were well preserved in marine sediments, which implies the possibility to develop at least some palynomorphs for local paleo-environmental reconstructions.

## 5. Conclusions

Here we have presented the first study of organic-walled dinoflagellate cyst production in the temperate coastal waters of North America, and the first *in situ* evaluation of the response of cyst production to an El Niño event. Three years with bi-weekly resolution in the fluxes of dinoflagellate cysts and other palynomorphs were recorded. The length of the record and the high frequency of sampling, which make this data set unique, provided the opportunity to examine the dynamics of dinoflagellate cyst production, including taxa known to produce toxic compounds.

Cyst production in the Strait of Georgia was correlated with seasonal and annual changes in environmental conditions of the water column. An outbreak of *Alexandrium* spp., a species implicated in HABs, was recorded in the spring of 1996. Cysts produced by the other autotrophic taxa were observed year-round, with the highest flux recorded in August and September. Cysts produced by heterotrophic dinoflagellates had strong seasonal patterns with a peak in June, during or following the observed diatom blooms. Strong similarity between seasonal changes in the fluxes of biogenic silica and heterotrophic cyst taxa suggests tight coupling between diatom and heterotrophic dinoflagellate cyst population, reinforcing the conclusion that prey availability is the major control for heterotrophic dinoflagellates. During the years affected by El Niño, the total flux of cysts of autotrophic taxa (with the exception of *Alexandrium* spp.) was higher than that of the non El Niño year. The total cyst flux of heterotrophic taxa was lowest in 1997 and highest in 1998. The unusually warm winter and early spring of 1998 led to the prolonged increased production of both heterotrophic and autotrophic cyst taxa compared to the winter of 1996–97.

In general, the cyst assemblage in a sediment core sample collected at the mooring site agreed with sediment trap assemblages. This important finding indicates that sediments record with reasonable precision the dinoflagellate cyst assemblages exported from the surface layers. Depending on the temporal resolution and degree of bioturbation of the sediment cores, this opens the door to using longer cores to develop cysts as environmental monitors or as proxies for paleoenvironmental reconstruction.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2010.02.003.

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