



Research paper

High-resolution sediment trap study of organic-walled dinoflagellate cyst production and biogenic silica flux in Saanich Inlet (BC, Canada)

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ABSTRACT

Dinoflagellate cyst fluxes and assemblage composition were investigated from November 2007 to February 2010 in Patricia Bay, Saanich Inlet (BC, Canada). Samples were collected using a sediment trap deployed at ~97 m water depth. The sampling interval ranged from 0.5 to 19.5 days, allowing for a high-resolution study of dinoflagellate cyst production in relation to measured environmental parameters. Ninety-six samples were collected and a total of 42 dinoflagellate cyst taxa were identified. The dinoflagellate cyst flux was very high and ranged from ~149,000 to ~2,400,000 cysts $m^{-2} day^{-1}$, with an average of ~777,000 cysts $m^{-2} day^{-1}$. Seasonal and interannual variation in cyst assemblage was recorded. It reflects changes in environmental parameters such as sea-surface temperature, sea-surface salinity, solar insolation, river discharge, and biogenic silica flux. Fluxes of cysts produced by autotrophic dinoflagellates, particularly *Spiniferites* spp. and *Spiniferites bentonii*, were greatest during winter. Spring dinoflagellate cyst assemblages were dominated by *Brigantedinium* spp. and *Quinquecuspis concreta*. In summer the assemblages were characterized by an increase of cysts produced by heterotrophic dinoflagellates, in particular by *Echimidinium delicatum*, *E. cf. delicatum*, *Votadinium spinosum* and cysts of *Protoperidinium minutum*. Multivariate statistical analysis performed on the data supports the observed seasonal trends, where winter taxa are associated with low sea-surface temperatures, low salinity, and high Cowichan River discharge, whereas summer taxa are associated with warmer sea-surface temperatures, higher solar insolation and increased biogenic silica flux. The cyst assemblage from nearby surface sediment was shown to be very similar to an annual average sediment trap assemblage.

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1. Introduction

Dinoflagellates are one of the most important groups of primary producers in coastal and estuarine systems, with over 2500 known species worldwide (Hoppenrath et al., 2009). Approximately half of all dinoflagellate species are heterotrophic (Dale, 2009), and therefore also contribute to the microzooplankton community. Dinoflagellates are predominately single-celled protists, and display a high degree of diversity both in their motile stage (Sarjeant et al., 1987) and cyst stage. Motile cells have two flagella and characteristic nuclei (Dale, 1996; Fensome et al., 1996a). The cell wall of the motile stage is commonly composed of a cellulose-like substance and is readily degraded, thus they are rarely found in the sedimentary record. Approximately 13–16% of living dinoflagellate species produce resting cysts, a dormant stage, that is formed after sexual reproduction (Head, 1996). The formation of cysts has a variety of potential ecological

functions including survival through adverse environmental conditions (Sarjeant et al., 1987; Dale, 1983), seeding source for the motile population (Dale, 1977; Anderson and Morel, 1979; Anderson, 1984), species dispersal (Sarjeant et al., 1987), and increased genetic recombination (Anderson, 1984). Once produced, cysts have a mandatory dormancy period ranging from days to months, however they can remain viable in the sediment for many years if favorable conditions for excystment are not reached (Dale, 1983).

Most organic-walled cysts are highly resistant to physical, chemical and biological degradations (Dale, 1996; Fensome et al., 1996a) and are prominent in the sedimentary record from the Jurassic onwards (Fensome et al., 1996b). Over the last few decades cyst assemblages have been developed as tools used in paleoenvironmental reconstructions to determine past sea-surface temperature (SST), sea-surface salinity (SSS), primary productivity, eutrophication, pollution, and sea-ice coverage (e.g. de Vernal et al., 1994, 2001; Dale, 1996; Matsuoka, 1999; Rochon et al., 1999; Marret and Zonneveld, 2003; Pospelova et al., 2004, 2008; Holzwarth et al., 2007; Radi et al., 2007; Zonneveld et al., 2009; Verleye and Louwye, 2010). However, the reliability of such paleoenvironmental reconstructions depends crucially on understanding modern cyst ecology and distribution in relation to environmental parameters.

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The spatial distribution of dinoflagellate cysts in recent marine sediments has been well documented in some regions (e.g. Marret and Zonneveld, 2003). Cyst assemblages and abundances in surface sediments are commonly compared to physical, chemical and environmental parameters of the upper water column, which are then used to demonstrate different aspects of cyst ecology (Zonneveld et al., 2010). However, surface sediments are typically deposited over many years making it difficult to resolve year-to-year and seasonal changes in cyst ecology and rates of dinoflagellate cyst production (Pospelova et al., 2010). In addition, according to Zonneveld et al. (2007), surface sediment can be subjected to aerobic degradation, resulting in a different cyst assemblage than was originally produced in the water column.

Coastal sediment traps provide an ideal tool to measure *in situ* cyst production and determine the ecological and environmental conditions under which dinoflagellate cysts are produced. Recording individual cyst taxa in a trap as a function of time along with the physical, chemical and biological parameters in the upper water column allows for a better ecological understanding of the relationship between environmental parameters and cyst production. In sediment traps where *in situ* preservatives (i.e. MgCl₂, formaldehyde, or supersaline solution) are used to inhibit bacterial degradation and grazing, the potential for the preservation of sensitive palynomorphs (organic-walled microfossils 5–120 µm in size) is increased. Thus sensitive palynomorphs may be found in trap material when they might otherwise be absent or found in lower numbers in the sedimentary record. Short deployment periods which limit the time in which material is exposed to degrading factors, also enhances the probability of finding higher abundances of sensitive palynomorphs in traps, compared to the sediment. Documenting the assemblages of other palynomorphs such as copepod eggs, tintinnid loricae, and microforaminiferal linings, in addition to dinoflagellate cysts, allows for an enhanced understanding of the relationships between various planktonic organisms.

The use of sediment traps can provide additional insights if used on a multi-year basis and with sufficiently short sampling intervals. Multi-year sediment trap studies are necessary to record seasonal and year-to-year changes in phytoplankton production, including cyst-producing dinoflagellates. This is especially important in coastal regions where local environmental parameters (i.e. river discharge), can vary significantly from year to year. In regions where upper water parameters may change rapidly due to atmospheric or oceanic events such as winter storms, extreme precipitation events, temperature fluctuations and renewal events, short sampling intervals can help to detect the influence of abrupt shifts in environmental parameters on cyst production.

At present there are very few high-resolution sediment trap studies of organic-walled dinoflagellate cysts in coastal waters where both seasonal and year-to-year cyst production are recorded. There are only five coastal sediment trap studies where sampling was conducted over a multi-year time period: the Gulf of Naples, Mediterranean Sea (Montresor et al., 1998); Bahia Concepcion, Gulf of California (Morquecho and Lechuga-Deveze, 2004); Omura Bay, West Japan (Fujii and Matsuoka, 2006); Namaqua shelf, Benguela upwelling system (Pitcher and Joyce, 2009); and the Strait of Georgia, Eastern Pacific (Pospelova et al., 2010). Average sampling intervals in these five studies ranged from 11 to 26 days.

Our present work utilizes material collected from a sediment trap located in Saanich Inlet over a two and a half year period. The sediment trap, a part of the VENUS (Victoria Experimental Network Under the Sea) project, has an important capability of adjustable sampling intervals. This is the first long-term study where the average sampling interval was one week in duration, and where many sampling intervals were less than three days in duration. Since Saanich Inlet represents a highly productive estuarine system with well-understood hydrographic conditions, we are in a unique position to investigate dinoflagellate cyst production in relation to changing

environmental parameters. Diatoms are one of the main primary producers in Saanich Inlet (Sancetta and Calvert, 1988; Hobson and McQuoid, 2001). Although individual diatoms frustules were not counted or identified, biogenic silica flux was used as a proxy for diatom production in this study, since diatoms are known to be the major contributors of biogenic silica in the inlet (Sancetta and Calvert, 1988; Sancetta, 1989a).

We aim to document seasonal and annual variations in the production of individual dinoflagellate cyst taxa and biogenic silica, search for a causal relationship with the most important environmental parameters, and compare trap assemblages to the surface sediment assemblage. Our work also lays the grounds for future high-resolution paleoenvironmental studies using temporal dinoflagellate cyst records from laminated sedimentary cores collected in the inlet.

2. Regional setting

Saanich Inlet is a fjord-type inlet located on southeastern Vancouver Island, British Columbia (Fig. 1). It is 25.7 km in length and varies in width from 0.4 to 7.6 km (Gucluer and Gross, 1964). While exceeding depths of 200 m in the central basin, a sill located at the mouth of the inlet reaches shallower depths of ~75 m, restricting deepwater circulation (Gargett et al., 2003).

In a typical estuarine system a major river will supply freshwater at the head of the estuary where the brackish surface layer flows oceanward, promoting normal estuarine flow (Gargett et al., 2003). However, Saanich Inlet is an inverse estuary where the dominant freshwater source is supplied from outside of the inlet, from the Cowichan and Fraser Rivers. Cowichan River flows into Cowichan Bay northwest of Saanich Inlet, and provides the main source of freshwater to the inlet during fall and winter (Fig. 1). Maximum Cowichan River discharge values of 400 m³ s⁻¹ were recorded during the study period (Water Survey of Canada, 2010), following large precipitation events in fall and winter. SSS inside the inlet is strongly influenced by the Cowichan River, reaching lowest values (~13–22 psu) following maximum river discharge rates. During summer the main source of freshwater is supplied from the Fraser River. The Fraser River reaches peak discharge rates (>9000 m³ s⁻¹) in May or June during the spring freshet when snowmelt is at its maximum. Thus, during most of the year the dominant freshwater source is from the mouth of the inlet, from the Cowichan River in fall and winter, and from the Fraser River during summer (Fig. 2). During the study period SSS ranged from 13 to 30 psu, and SST varied from 3 °C in winter to 21 °C in summer (J.F.R. Gower, personal communication).

A combination of weak estuarine circulation, low vertical mixing rates, particle-retention, and high primary production act to promote anoxic bottom water during most of the year in the central basin (Timothy and Soon, 2001; Gargett et al., 2003; Grundle et al., 2009). Periodic deepwater renewal events in summer and fall (Anderson and Devol, 1973; Gargett et al., 2003) and possibly in the spring (Manning et al., 2010) bring dense, oxygenated, nutrient-rich water over the sill and into the inlet. These intrusions of nutrient-rich water, have been linked to the spring/neap tidal cycle and have been observed to cause periodic phytoplankton blooms (Takahashi et al., 1977; Parsons et al., 1983). The periodic influx of nutrients causes “mini-blooms,” when nutrients might otherwise be limiting and acts to promote high primary productivity throughout the year (Grundle et al., 2009).

Saanich Inlet is characterized by surface stratification and low vertical mixing due to weak winds and tidal currents, creating stable conditions conducive for phytoplankton growth (Timothy and Soon, 2001). There is high spatial variability of primary productivity in the inlet with highest average yearly production at the mouth, a consequence of nutrient input from Satellite Channel, which acts to promote phytoplankton growth (Takahashi et al., 1977; Parsons et al., 1983; Hobson and McQuoid, 2001; Timothy and Soon, 2001; Gargett et al., 2003; Grundle et al., 2009). Timothy and Soon (2001) and Grundle

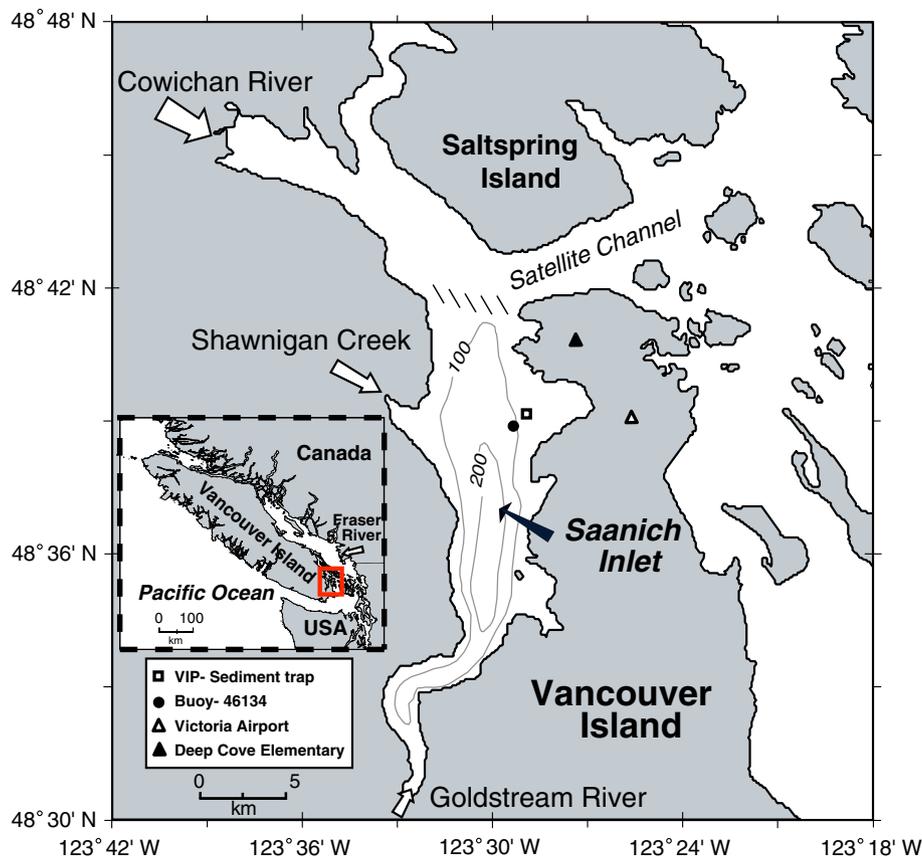


Fig. 1. Map of Saanich Inlet showing the location of the sediment trap, buoy 46134, the Victoria International Airport, and Deep Cove Elementary School. The 100 m and 200 m bathymetric contours are shown in Saanich Inlet only. Diagonal lines outside Saanich Inlet represent the approximate location of the sill. Inset shows study area in relation to Vancouver Island, British Columbia, Canada.

et al. (2009) report that primary production at the mouth of the inlet is ~1.5 times greater compared to the head of the inlet during the growing season (spring, summer, and fall). The average annual estimate for primary production at the mouth of the inlet is $1.6 \text{ g C m}^{-2} \text{ day}^{-1}$, whereas at the head of the inlet the estimate is $1.1 \text{ g C m}^{-2} \text{ day}^{-1}$ (Timothy and Soon, 2001).

3. Materials and methods

3.1. Sample collection

Samples were collected using a Technicap sediment trap (model PPS 4/3–24S), mounted to the VENUS Instrument Platform (VIP) in Patricia Bay, Saanich Inlet (Table 1). The trap is cylindrical in shape and is designed for collecting particles in high sedimentation regimes (Technicap, 2010). The trap mouth has a collecting area of 0.05 m^2 and is located ~2 m above the seafloor. A honeycomb baffle was placed over the trap during the third to fifth deployments (October 2008–February 2010), to prevent fish and other large organisms from entering. The sediment trap was specially adapted to connect to the VIP for power connection and communication, allowing the trap to be remotely operated. The trap was rotated on command allowing the length of the sampling interval to be controlled by the investigators. Approximately every six months the trap was recovered during routine maintenance cruises where the sediment trap samples were collected, and the trap subsequently redeployed.

The sampling period in this study covers a two and a half year interval from November 1, 2007 to February 18, 2010, during which 96 samples were collected. Sampling intervals range from 0.5 to 19.5 days with an average interval of one week. Sampling intervals of

the shortest duration were not required for this study, but resulted from parallel projects that used the same trap. Gaps in the record occurred when either the trap became clogged or it was out of the water during biannual recovery of the samples (see Fig. 2). A large gap in the sampling record occurred from June 2008, when the sediment trap accidentally clogged until September 2008 when the trap was recovered.

All 96 sediment trap samples were preserved in supersaline (5 M NaCl) solution *in situ* to inhibit bacterial degradation and prevent grazing. Upon recovery an additional 5 M NaCl solution was added. Each sediment trap sample was split into four aliquots, ranging from 1/8 to 1/4 of the entire sample. One aliquot was used for palynological analysis and was sieved through a $500 \mu\text{m}$ mesh to remove zooplankton. The fraction $<500 \mu\text{m}$ was used for further analysis. A second aliquot was used for biogenic silica analysis. The results from both are discussed in this paper. In addition to sediment trap samples, one surface sediment sample was collected from Patricia Bay near the sediment trap location on September 25, 2009. The sample was suctioned from the upper ~1.5 cm of the seafloor using a remotely operated vehicle (Remotely Operated Platform for Ocean Science or ROPOS) (Canadian Scientific Submersible Facility, 2010).

3.2. Palynological sample preparation and microscopy

Recovery of dinoflagellate cysts and other organic palynomorphs such as copepod eggs, microforaminiferal linings, tintinnid loricae, and oligotrich ciliate cysts, was achieved using a standard palynological processing technique (Pospelova et al., 2005). Samples were rinsed 2–3 times to remove salt residue, oven dried at $40 \text{ }^\circ\text{C}$, and weighed analytically. One to two tablets of exotic marker grain

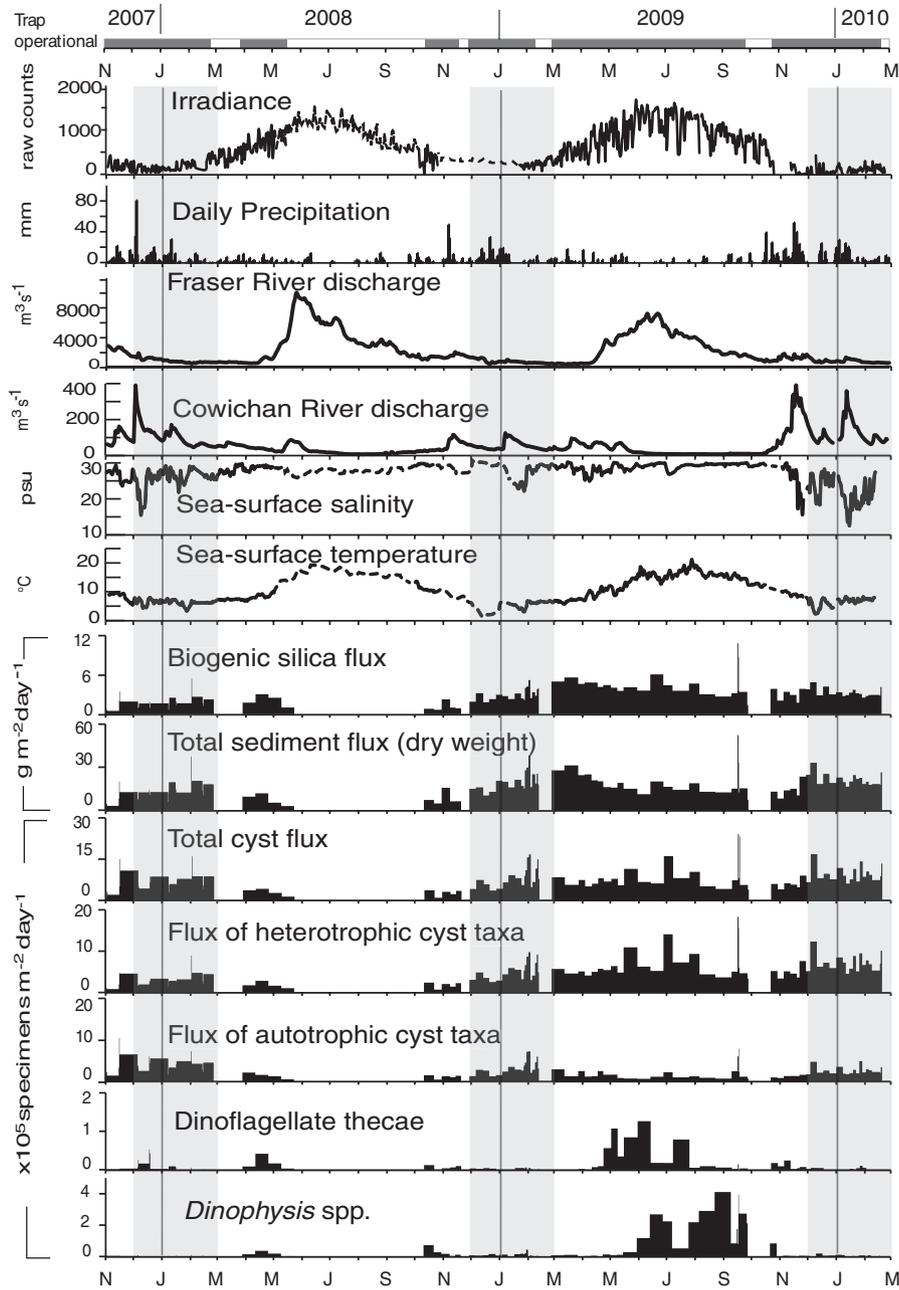


Fig. 2. Daily average irradiance, precipitation, SSS, SST, Fraser River and Cowichan River discharge, as well as sediment trap fluxes for biogenic silica, total sediment (dry weight), total cysts, heterotrophic cyst taxa, autotrophic cyst taxa, dinoflagellate thecae and *Dinophysis* spp. A dashed curve indicates missing measurements for irradiance, SSS and SST. The bar located at the top of the figure shows when the sediment trap was not operational (white). Gray bands lengthwise across the figure highlight winter seasons (December–February).

Lycopodium clavatum (Stockmarr, 1971; Mertens et al., 2009) were added prior to sample treatment in order to determine absolute dinoflagellate cyst fluxes. The samples were treated with room temperature 10% HCl to remove carbonates, rinsed with distilled water, sieved through a 120 μm mesh and captured on a 15 μm mesh

to remove both coarse and fine fractions. Siliceous material was digested using room temperature 48–50% HF for 2–3 days followed by a second 10% HCl treatment to remove precipitated fluorosilicates. Finally, the samples were rinsed with distilled water, sieved, gently sonicated for up to 30 s and collected on a 15 μm mesh. One to

Table 1
Mooring site information and time of deployment.

Sediment Trap	Date range	Site ID	Latitude (N)	Longitude (W)	Water depth (m)
Deployment 1	2007-09-12 to 2008-02-25	VIP-06	48° 39' 5"	123° 29' 10"	96
Deployment 2	2008-02-27 to 2008-09-27	VIP-07	48° 39' 4"	123° 29' 10"	96
Deployment 3	2008-09-28 to 2009-02-12	VIP-08	48° 39' 4"	123° 29' 11"	97
Deployment 4	2009-02-15 to 2009-09-26	VIP-09	48° 39' 4"	123° 29' 11"	97
Deployment 5	2009-09-30 to 2010-02-17	VIP-10	48° 39' 5"	123° 29' 10"	96

two drops of the residue were mounted in glycerin jelly between a slide and cover slip. Dinoflagellate cysts were counted and identified using a Nikon Eclipse 80i transmitting light microscope at 600× and 1000× magnifications. Up to 558 cysts were counted per sample, with an average of 372 cysts per sample. A minimum of 300 cysts were counted per sample, with the exception of one sample (UVic 09-409) where only 217 cysts were counted. All samples and slides are stored at the Paleoenvironmental Laboratory, University of Victoria, Canada.

3.3. Identification of dinoflagellate cysts and other palynomorphs

Dinoflagellate cysts were identified according to the paleontological taxonomy system described in publications by Fensome et al. (1993), Lentin and Williams (1993), Head (1996), Zonneveld (1997), Rochon et al. (1999), Head et al. (2001), Pospelova and Head (2002), Matsuoka et al. (2009), Hoppenrath et al. (2010), Ribeiro et al. (2010), and Verleye et al. (2011). Wherever possible cysts were identified to the species level. Due to morphological similarities some cyst taxa were grouped together. *Brigantedinium* spp. consists of *Brigantedinium cariacense*, *Brigantedinium simplex*, and other round brown cysts where archeopyles were not always observed due to unfavorable orientations or folding. *Spiniferites* spp. includes all species of *Spiniferites* except *Spiniferites bentorii*, *Spiniferites elongatus*, *Spiniferites mirabilis*, and *Spiniferites membranaceus*. *Selenopemphix quanta* and cysts of *Protoperdinium nudum* were grouped together as these two cyst species show a high degree of morphological similarity. Cysts of *Polykrikos kofoidii* and *Polykrikos schwartzii* were named according to the nomenclature of Matsuoka et al. (2009). Where cysts did not conform to previously published descriptions, cyst types were assigned. Cyst type A has been previously identified by Pospelova et al. (2006), Radi et al. (2007) and Pospelova et al. (2008) and is also illustrated in Pospelova et al. (2010) and Krepakevich and Pospelova (2010). Cyst type L is likely the cyst of *Protoperdinium mendiolae*, as illustrated in Kawami (2008). Cyst type D has a light to medium brown spherical central body and a smooth cell wall, with hollow acuminate processes ending in a sharp point (Plate V). Central body diameter ranges from 30 to 40 μm and the process length varies from 8 to 13 μm, but are similar in length on a single specimen. Processes are evenly distributed. An intact archeopyle has yet to be observed for cyst type D. Other spiny brown cysts of unknown affinity were grouped in the spiny brown category. A list of all dinoflagellate cyst taxa recorded in this study and their corresponding biological affinities are provided in Table 2.

Dinophysis spp. were grouped together as distinguishing morphological features were not always observed. Cysts of cf. *Biecheleria* spp. are similar in morphology to *Biecheleria baltica* (Moestrup et al., 2009), previously named *Woloszynskia halophila sensu Kremp et al. (2005)*. In this study cysts of cf. *Biecheleria* spp. have an average body diameter of 20–30 μm, although during one sampling interval (November 2, 2007–November 3, 2007) the body diameter was as small as 8 μm. Processes are numerous, evenly distributed, and are 2–3 μm in length. Very few cysts of cf. *Biecheleria* spp. without cell content were recorded in the trap or sediment samples. Future studies to determine the cyst-theca relationship and phylogenetics are required to properly identify this cyst. Although this palynomorph is most likely a dinoflagellate cyst, since this has yet to be confirmed, they were not included in the dinoflagellate cyst counts for this study.

Five tintinnid loricae and two oligotrich ciliate cyst types were recorded in this study (Plate VII). Possible genera were assigned when possible. Tintinnid loricae cf. *Acanthostomella novegica*, cf. *Helicostomella* spp., and cf. *Ptychocylis* spp. were identified according to the descriptions in Hada (1937). Tintinnid loricae types A and B may be agglutinated loricae. However, since the samples in this study were treated with HCl and HF, any agglutinated bodies would have dissolved, making identification more difficult. Oligotrich ciliate cysts cf. *Cyrtostrombidium*

boreale and cf. *Strombidium* spp. were identified based on the descriptions in Kim et al. (2002) and Montagnes et al. (2002), respectively.

3.4. Environmental data

Hourly SSS and SST data collected from buoy 46134 in Patricia Bay (Fig. 1) were provided by J.F.R. Gower (personal communication). For plotting purposes daily averages were computed (Fig. 2). Daily discharge rates of the Fraser River (08MF005) and Cowichan River (08HA011) were obtained from the Archived Hydrometric Database (Water Survey of Canada, 2010; Lynne Campo, personal communication). Precipitation, air temperature, wind speed, and cloud cover recorded at the Victoria International Airport were obtained from Environment Canada (2010). Solar insolation data recorded at Deep Cove Elementary School was obtained from the University of Victoria School-based Weather Station Network (Weaver and Wiebe, 2006; Edward Wiebe, personal communication). The seasons are defined as follows: winter – December to February, spring – March to May, summer – June to August, and fall – September to November.

3.5. Biogenic silica analysis

One aliquot of each sediment trap sample was used for biogenic silica analysis. All samples were rinsed 3–4 times with distilled water to remove salt residue from the sediment, freeze-dried at –80 °C for 3–5 days, weighed analytically, sub-sampled, and then powdered. Biogenic silica content was analyzed at the Pacific Center for Isotopic and Geochemical Research (PCIGR) located at the University of British Columbia. The standard wet-alkaline procedure was used where H₂O₂ and HCl were added to remove diluting phases such as organics and carbonates, and to expose opal surfaces to dissolution. The resulting supernatant was then analyzed for dissolved silica using molybdate-blue spectrophotometry (Mortlock and Froelich, 1989). Percent opal can be calculated from the following equation: %OPAL = 2.4 × % Si_{OPAL} (Mortlock and Froelich, 1989), which takes into account a correction for a relatively constant water content of ~10% in diatomaceous silica. Biogenic silica flux in units of g m⁻² day⁻¹ was determined by multiplying %OPAL by the average sediment flux obtained from two aliquots.

3.6. Statistical analyses

Statistical analyses were performed on dinoflagellate cyst relative abundances and fluxes using CANOCO 4.5 for Windows (ter Braak and Smilauer, 2002). Detrended Correspondence Analysis (DCA) was used to test the nature of the variability of the dinoflagellate cyst assemblages. The length of the first gradient in standard deviation units determines whether the assemblage shows unimodal variation (length > 2) or linear variation (length < 2). The length of the first gradient in this dataset was determined to be 1.7 standard deviations, signifying linear variation within the study area. This indicates the dataset can be further analyzed using the Redundancy Analysis (RDA) for direct analyses. RDA allows for the detection of correlation between dinoflagellate cyst assemblages and environmental parameters and was performed on both relative abundance and flux datasets. Environmental parameters used in the analyses include SSS, SST, solar insolation, cloud cover, wind speed, precipitation, biogenic silica flux, and discharge from the Cowichan and Fraser Rivers. Samples with a sampling interval of less than one day were excluded from statistical analyses for the following reasons: (1) some of the environmental parameters were only available as daily averages, (2) a change in river discharge would not be felt instantaneously in Saanich Inlet, thus the time lag may be too great to be adequately captured during the short time intervals, and (3) there is a high variability in flux magnitudes during short intervals that may not be caused by changing environmental parameters (see Section 5.1 for a further

Table 2

Taxonomic citation of dinoflagellates identified in this study. Thecate equivalents are taken from Head (1996), Zonneveld (1997), Head et al. (2001), Pospelova and Head (2002), Matsuoka et al. (2009), Hoppenrath et al. (2010), Ribeiro et al. (2010) and Verleye et al. (2011).

Cyst species (Paleontological name)		Dinoflagellate theca (Biological name)
	<i>Autotrophic</i>	
	Gonyaulacaceae	
–		<i>Alexandrium</i> spp.
<i>Impagidinium</i> spp.		<i>Gonyaulax</i> sp. Indet.
<i>Nematosphaeropsis labyrinthus</i>		<i>Gonyaulax spinifera</i> complex
<i>Operculodinium centrocarpum sensu</i>		<i>Protoceratium reticulatum</i>
Wall and Dale, 1966		
<i>Spiniferites elongatus</i>		<i>Gonyaulax spinifera</i> complex
<i>Spiniferites bentorii</i>		<i>Gonyaulax spinifera</i> complex
<i>Spiniferites membranaceus</i>		<i>Gonyaulax spinifera</i> complex
<i>Spiniferites mirabilis</i>		<i>Gonyaulax spinifera</i> complex
<i>Spiniferites</i> spp.		<i>Gonyaulax</i> complex
–	Protoperidiniaceae	
		<i>Pentapharsodinium dalei</i>
	<i>Heterotrophic</i>	
	Diplopsalidaceae	
<i>Dubridinium</i> spp.		Didlopsalid group
–	Polykrikaceae	
–		<i>Polykrikos kofoidii</i>
–		<i>Polykrikos schwartzii</i>
–		<i>Polykrikos hartmanii</i>
	Protoperidiniaceae	
<i>Brigantedinium</i> spp.		? <i>Protoperidinium</i> spp.
<i>Brigantedinium cariacense</i>		<i>Protoperidinium avellanum</i>
<i>Brigantedinium simplex</i>		<i>Protoperidinium conicoides</i>
<i>Echinidinium aculeatum</i>		<i>Protoperidinium</i> sp. indet.
<i>Echinidinium delicatum</i>		<i>Protoperidinium</i> sp. indet.
<i>Echinidinium</i> cf. <i>delicatum</i>		<i>Protoperidinium</i> sp. indet.
<i>Echinidinium granulatum</i>		<i>Protoperidinium</i> sp. indet.
<i>Echinidinium</i> spp.		<i>Protoperidinium</i> sp. indet.
<i>Islandinium brevispinosum</i>		<i>Protoperidinium</i> sp. indet.
<i>Islandinium?</i> <i>minutum</i>		<i>Protoperidinium</i> sp. indet.
<i>Islandinium?</i> <i>minutum</i> var. <i>cesare</i>		<i>Protoperidinium</i> sp. indet.
–		<i>Protoperidinium americanum</i>
–		<i>Protoperidinium minutum</i>
–		<i>Protoperidinium nudum</i>
–		<i>Protoperidinium oblongum</i>
<i>Protoperidinium</i> spp.		<i>Protoperidinium</i> spp. indet.
<i>Quinquecuspis concreta</i>		<i>Protoperidinium leonis</i>
<i>Selenopemphix undulata</i>		<i>Protoperidinium</i> sp. indet.
<i>Selenopemphix quanta</i>		<i>Protoperidinium conicum</i>
<i>Trinovantedinium applanatum</i>		<i>Protoperidinium pentagonum</i>
<i>Trinovantedinium variabile</i>		<i>Protoperidinium</i> sp. indet.
<i>Votadinium calvum</i>		<i>Protoperidinium oblongum</i>
<i>Votadinium spinosum</i>		<i>Protoperidinium claudicans</i>
	Indeterminant	
Cyst type A		? <i>Protoperidinium</i> sp. indet.
Cyst type D		? <i>Protoperidinium</i> sp. indet.
Cyst type L		? <i>Protoperidinium</i> sp. indet.
Spiny brown		? <i>Protoperidinium</i> sp. indet.

discussion). The statistical significance of each variable was determined using a Monte Carlo permutation test, with 499 unrestricted permutations. Environmental variables with a *P*-value less than 0.05 were deemed to be significantly related to species data.

In order to quantitatively compare the similarity of the dinoflagellate cyst assemblages from the Patricia Bay surface sediment sample to the average yearly sediment trap sample, the Euclidean distance was calculated using species relative abundances from surface sediments from the Northeast Pacific. The following datasets were used: the NE Pacific dinoflagellate cyst database ($n = 188$) (Pospelova et al., 2008 and references there within), surface sediment samples collected from southern Vancouver Island ($n = 38$) (Krepakevich and Pospelova, 2010), and one surface sample from Patricia Bay, Saanich Inlet (this study). The shorter the Euclidean distance, the more similar the two samples are in their species composition and relative abundances.

4. Results

All 96 sediment trap samples contained well-preserved organic-walled dinoflagellate cysts and other palynomorphs (Plates I–VII). A total of 42 dinoflagellate cyst taxa were identified, including 10 autotrophic and 32 heterotrophic taxa. An average of 25 cyst taxa were recorded in each sample, with a minimum of 16 and a maximum of 32 taxa.

4.1. Relative abundance of dinoflagellate cysts in sediment trap samples

During the study period the cyst assemblages were dominated by cysts produced by heterotrophic taxa – *Brigantedinium* spp., *Quinquecuspis concreta*, cysts of *Protoperidinium americanum*, cyst type L, and cysts of *Protoperidinium minutum*, with the exception of winter 2007/08 which was dominated by *Spiniferites* spp. and *S. bentorii*

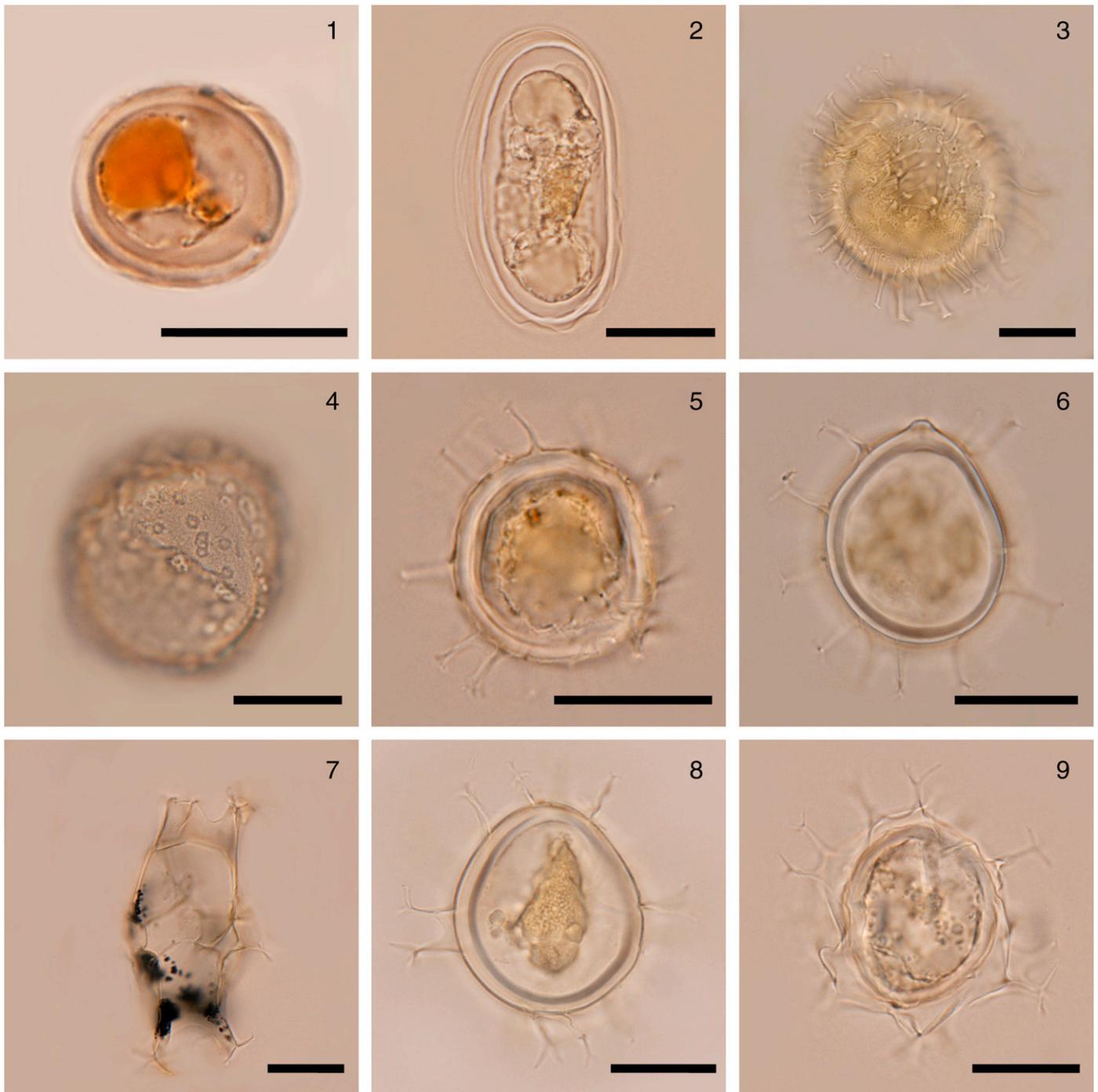


Plate I. Bright-field photomicrographs. 1–2. Cyst of *Alexandrium* spp., UVic 09-175, slide 1, R36/4 and UVic 09-647, slide 1, K32/2; optical sections. 3. *Operculodinium centrocarpum* sensu Wall and Dale (1966), UVic 09-649, slide 2, J51/2; orientation uncertain. 4. *Operculodinium centrocarpum* var. *truncatum*, UVic 09-088, slide 1, W33/2; orientation uncertain. 5. Cyst of *Pentapharsodinium dalei*, UVic 09-649, slide 2, S37/0; optical section. 6. *Spiniferites bentorii*, UVic 09-096, slide 1, T37/0; optical section. 7. *Spiniferites elongatus*, UVic 09-092, slide 1; orientation uncertain. 8–9. *Spiniferites* spp., UVic 09-096, slide 1, V28/4 and UVic 09-407, slide 1, Y33/2; optical sections. Scale bars are 20 μ m.

(Fig. 3). The relative abundance of dinoflagellate cysts varied seasonally and annually (Fig. 3). During winter the cyst assemblages were dominated by *Spiniferites* spp., *Brigantedinium* spp., and *S. bentorii*. During the spring the relative abundance of cyst type D, *Q. concreta*, and *Brigantedinium* spp. increased (Fig. 3). In the summer the dominant cyst taxa were *Brigantedinium* spp., cysts of *P. minutum*, *Q. concreta*, *Spiniferites* spp., *Echinidinium* cf. *delicatum* and *E. delicatum* (Fig. 3). The relative abundance of the most dominant cyst taxa, particularly *Spiniferites* spp., *Brigantedinium* spp., and *Q. concreta* show the greatest year-to-year variability.

Cyst assemblages from three winter seasons and two spring seasons can be compared. Winter 2007/08 was dominated by cysts produced by autotrophic dinoflagellates (57%), whereas winters 2008/09 and 2009/10 were dominated by cysts produced by heterotrophic dinoflagellates (61% and 74%, respectively). During winter of 2007/08 the relative abundance of *Spiniferites* spp. was much higher, comprising an average of 39% of the total assemblage, compared to winter 2008/09 and winter 2009/10, where *Spiniferites* spp. were less dominant comprising 24%, and 18%, respectively. The winters of 2008/09 and 2009/10 were dominated by *Brigantedinium*

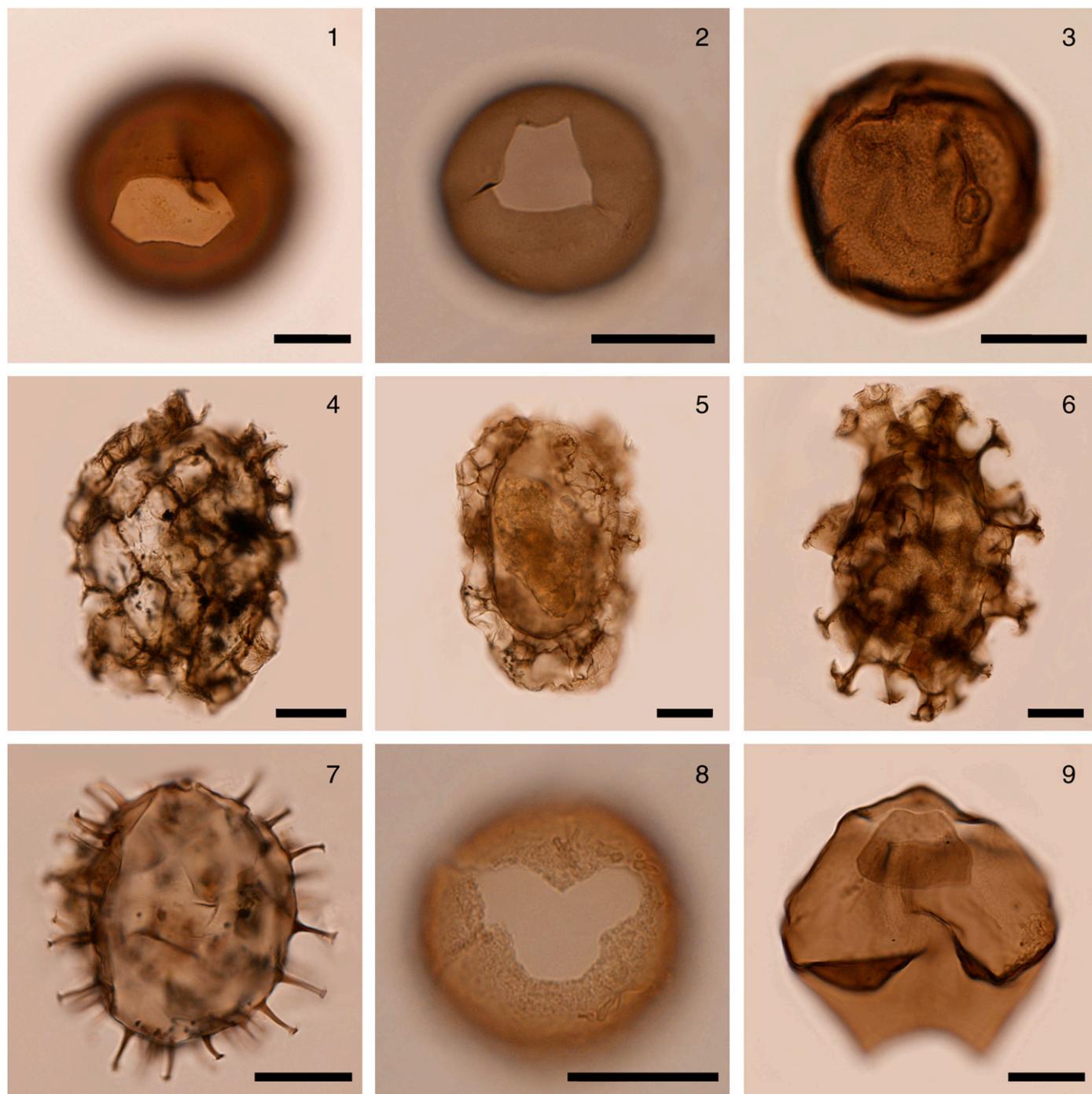


Plate II. Bright-field photomicrographs. **1.** *Brigantedinium cariacense*, UVic 09-649, slide 2, O42/2; dorsal surface. **2.** *Brigantedinium simplex*, UVic 09-392, slide 1, J28/2; dorsal surface. **3.** *Dubridinium* spp., UVic 09-404, slide 1, T51/3; dorsal surface. **4–5.** Cysts of *Polykrikos kofoidii* sensu Matsuoka et al. (2009), UVic 09-175, slide 1, V29/3 and 09-154, slide 1, E40/4; orientations uncertain. **6.** Cyst of *Polykrikos schwartzii* sensu Matsuoka et al. (2009), UVic 09-400, slide 1, Q46/4; orientation uncertain. **7.** *Trinovantedinium variabile*, UVic 09-183, slide 1, U32/4; dorsal surface. **8.** Cyst of *Protoperidinium americanum*, UVic 09-649, slide 2, L34/1; dorsal surface. **9.** *Quinquecuspis concreta*, UVic 09-177, slide 1, W47/4; dorsal surface. Scales bar are 20 μm .

spp. comprising up to 32% and 35%, respectively. Cyst type L increased in abundance during fall 2008 and winter 2008/09, comprising up to 18%. During both spring 2008 and 2009 the relative abundance of cysts produced by heterotrophic cyst taxa increased over the previous winters. Spring 2009 consisted of a greater percentage of cysts produced by heterotrophic taxa (79%) compared to spring 2008 (58%), due to the relative increase in *Brigantedinium* spp., *Q. concreta*, and cyst type L and a relative decrease in *Spiniferites* spp. (Fig. 3). In summer 2009 cysts produced by heterotrophic dinoflagellates strongly dominated with an average relative abundance of 81%.

Cysts of *P. minutum* and *Brigantedinium* spp. were the most dominant taxa during the summer season.

4.2. Dinoflagellate cyst fluxes

During the two and a half year sampling period the flux of dinoflagellate cysts ranged from $\sim 149,000$ cysts $\text{m}^{-2} \text{day}^{-1}$ (May 2008) to $\sim 2,400,000$ cysts $\text{m}^{-2} \text{day}^{-1}$ (September 2009) with an average of $\sim 777,000$ cysts $\text{m}^{-2} \text{day}^{-1}$. Total cyst fluxes of over $1,000,000$ cysts $\text{m}^{-2} \text{day}^{-1}$ ($n=19$) were recorded in all seasons,

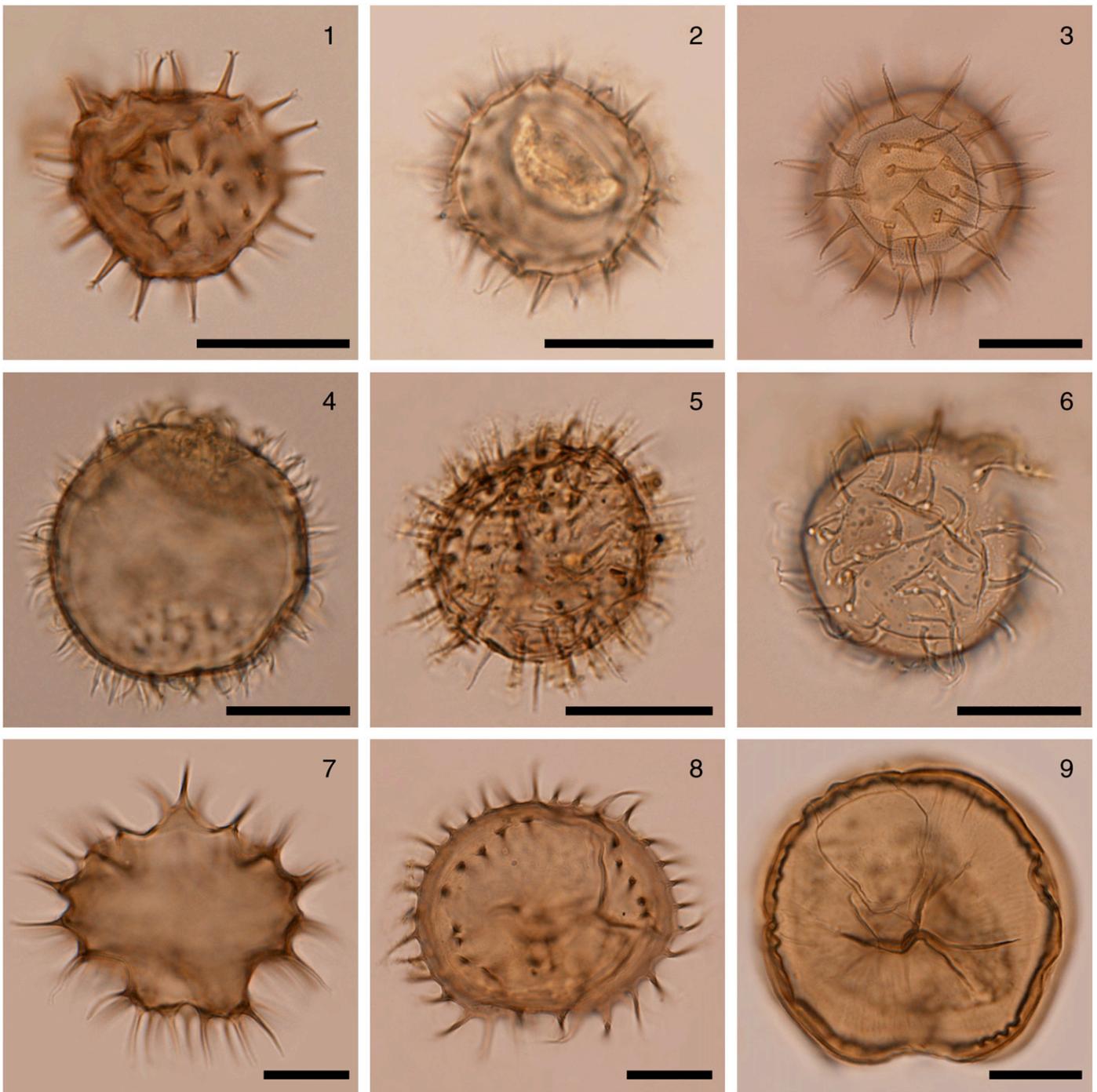


Plate III. Bright-field photomicrographs. 1. *Echinidinium aculeatum*, UVic 09-096, slide 1, U38/0; orientation uncertain. 2. *Echinidinium delicatum*, UVic 09-397, slide 2, P48/1; orientation uncertain. 3. *Echinidinium granulatum*, UVic 09-644, slide 1, V48/2; orientation uncertain. 4–6. *Echinidinium* spp., UVic 09-409, slide 1, Y38/3, optical section; UVic 09-184, slide 1, H25/3, dorsal surface; UVic 09-177, slide 1, V52/3, dorsal surface. 7. Cyst of *Protoperidinium nudum*, UVic 09-655, slide 1, V46/3; dorsal surface. 8. *Selenopemphix quanta*, UVic 09-394, slide 1, L53/1; antapical surface. 9. *Selenopemphix undulata*, UVic 09-153, slide 1, T48/2; apical surface. Scale bars are 20 μm .

and fluxes over $2,000,000 \text{ cysts m}^{-2} \text{ day}^{-1}$ ($n=2$) were only recorded in September 2009. The highest total cyst fluxes were recorded when the sampling interval was two days or less in duration.

There is no noticeable seasonal trend in total dinoflagellate cyst flux, however seasonal trends are observed when cysts produced by autotrophic and heterotrophic taxa are analyzed separately (Fig. 2). The flux of cysts produced by autotrophic taxa was greatest during winter, especially during winter 2007/08. The flux of cysts produced by heterotrophic taxa increased during spring, reaching maximum values during summer, and remained high throughout the fall (Fig. 2).

Cyst fluxes of most individual taxa varied seasonally and annually. Fluxes of *Spiniferites* spp. and *S. bentorii* were approximately three times higher in winter 2007/08 in comparison to the rest of the sampling period (Fig. 4). The cyst flux of *P. americanum* was higher in winter 2007/08 and winter 2009/10 compared to winter 2008/09. Conversely, the cyst flux of cyst type L increased in winter of 2008/09 compared to winters 2007/08 and 2009/10. The flux of *Dubridinium* spp. was low throughout most of the sampling period, except during fall 2009 where the flux increased and remained high throughout the winter. Cyst fluxes of individual taxa on average were higher in spring

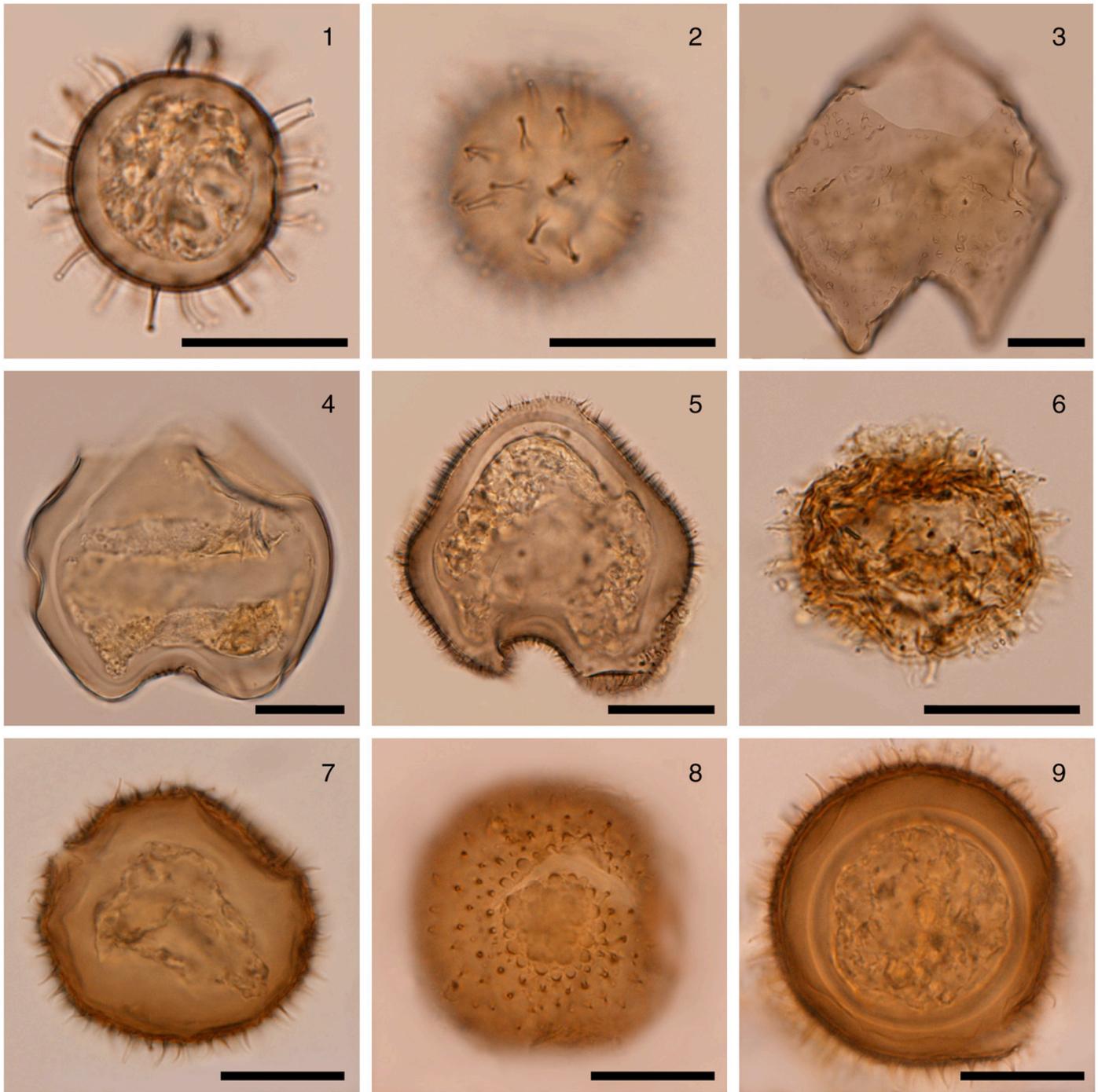


Plate IV. Bright-field photomicrographs. **1–2.** *Islandinium?* *minutum* var. *cesare*, UVic 09-391, slide 1, W44/1; optical section and dorsal surface. **3.** Cyst of *Protooperidinium oblongum*, UVic 09-179, slide 1, V37/0, dorsal surface. **4.** *Votadinium calvum*, UVic 09-179, slide 1, T41/2, dorsal surface. **5.** *Votadinium spinosum*, UVic 09-402, slide 1, U43/4; optical section. **6.** Cyst type A, UVic 09-175, slide 1, T43/4; dorsal surface. **7–9.** Cyst type L, UVic 09-096, slide 1, V27/4, optical section and UVic 09-646, slide 1, U39/1, dorsal surface and optical section. Scale bars are 20 μ m.

of 2009 than in spring 2008 with *Q. concreta*, *Brigantedinium* spp., *S. quanta*, *Alexandrium* spp., and *Votadinium calvum* recording the greatest increases (Fig. 4).

The flux of dinoflagellate cysts with cell content compared to those without cell content varied seasonally for most taxa (Fig. 4). Cysts of *Pentapharsodinium dalei* and *Alexandrium* spp. were exceptions, as almost all cysts counted contained cell content throughout the sampling period. During winter *Spiniferites* spp., *S. bentorii* and *Operculodinium centrocarpum* showed an increase in the number of

cysts containing cell content. In spring the flux of cysts with cell content increased for cyst type D, *Q. concreta*, *Brigantedinium* spp., *Echinidinium granulatum*, *E. cf. delicatum* and *Selenopemphix undulata*. In summer the flux of cysts with cell content reached maximum values for *E. delicatum*, *E. cf. delicatum*, *Votadinium spinosum*, cysts of *P. minutum*, and *Protooperidinium* spp.

The flux of dinoflagellate thecae also shows seasonal trends (Fig. 2). Few dinoflagellate cysts encased in a theca were found during winter. During spring both the flux of dinoflagellate thecae and the

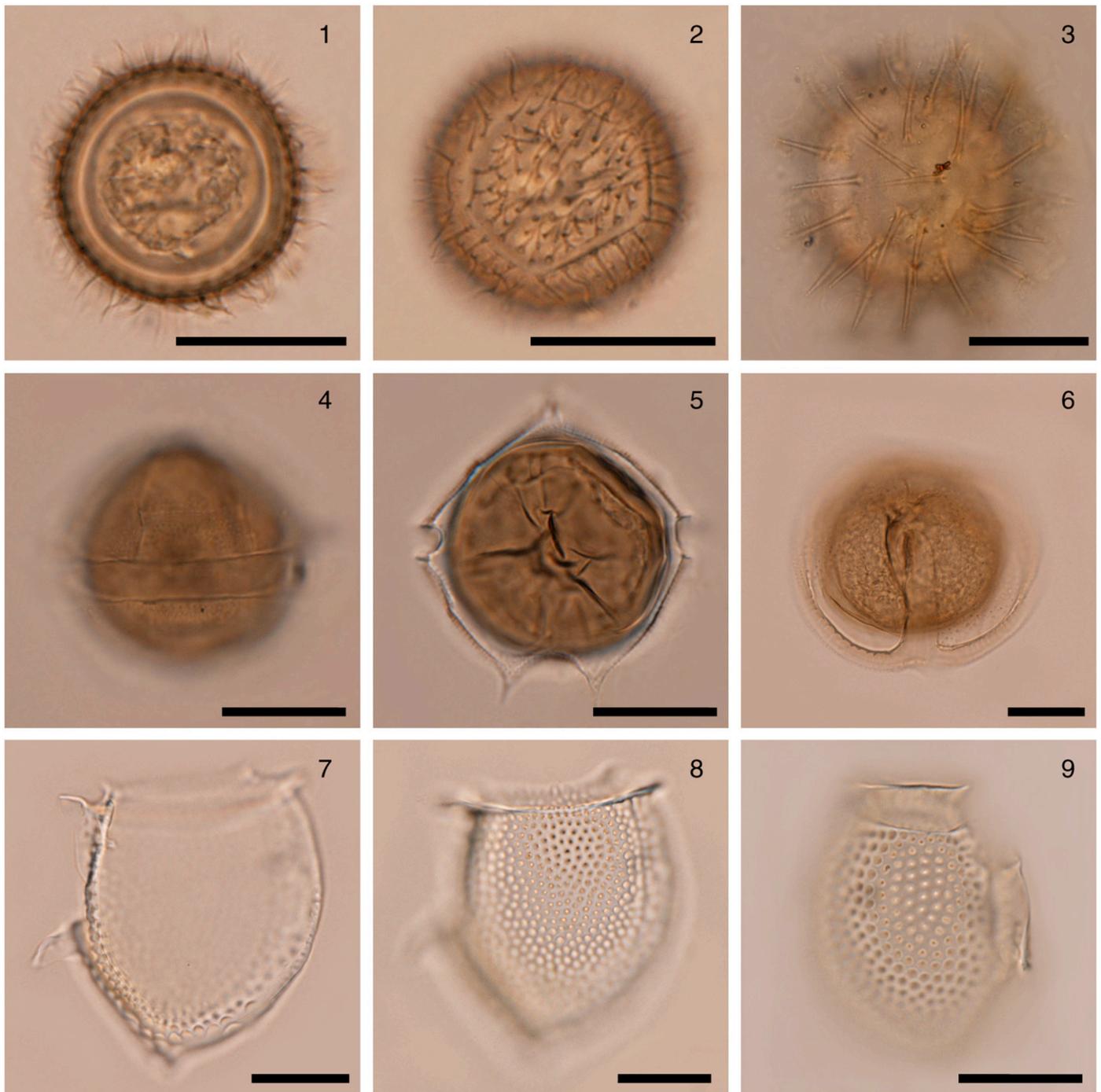


Plate V. Bright-field photomicrographs. **1–2.** Cysts of *Protoperidinium minutum*, UVic 09-404, slide 1, X30/3; optical section and uncertain orientation. **3.** Cyst type D, UVic 09-153, slide 2, W36/2; uncertain orientation. **4–5.** Cyst encased in a theca of *Protoperidinium* spp., UVic 09-405, slide 1, W48/3; dorsal surface and optical section. **6.** Cyst encased in a theca of *Diplopsalidaceae*, UVic 09-397, slide 2, N23/2; antapical surface. **7–8.** *Dinophysis novegica*, UVic 09-402, slide 1, N45/4. **9.** *Dinophysis acuminata*, UVic 09-402, slide 2, R34/3. Scale bars are 20 μm .

flux of dinoflagellate cysts encased in a theca increased, reaching peak values in late April and remaining high until the end of July. The flux of *Dinophysis* spp. did not show a dramatic increase until early summer, where their highest values were recorded in late summer to early fall.

4.3. Other palynomorphs

Other palynomorphs were counted in addition to dinoflagellate cysts (Fig. 5). The most dominant palynomorphs identified were tintinnid

loricae, oligotrich ciliate cysts, cysts of cf. *Biecheleria* spp., copepod eggs, and microforaminiferal linings. The lowest flux of tintinnid loricae occurred during winter. In spring 2008 fluxes of tintinnid lorica type B and cf. *Acanthostomella novegica* increased significantly. Spring 2009 recorded a slight increase in tintinnid lorica type B compared to the previous winter. In general all tintinnid lorica taxa increased in May–June 2009, remaining high throughout the summer and declining through the fall. Cf. *Helicostomella* spp. and cf. *Ptychocyclus* spp. were almost exclusively found from late spring to late summer (Fig. 5). Oligotrich ciliate cysts show less pronounced seasonal trends, however cf. *Cyrtostombidium boreale*

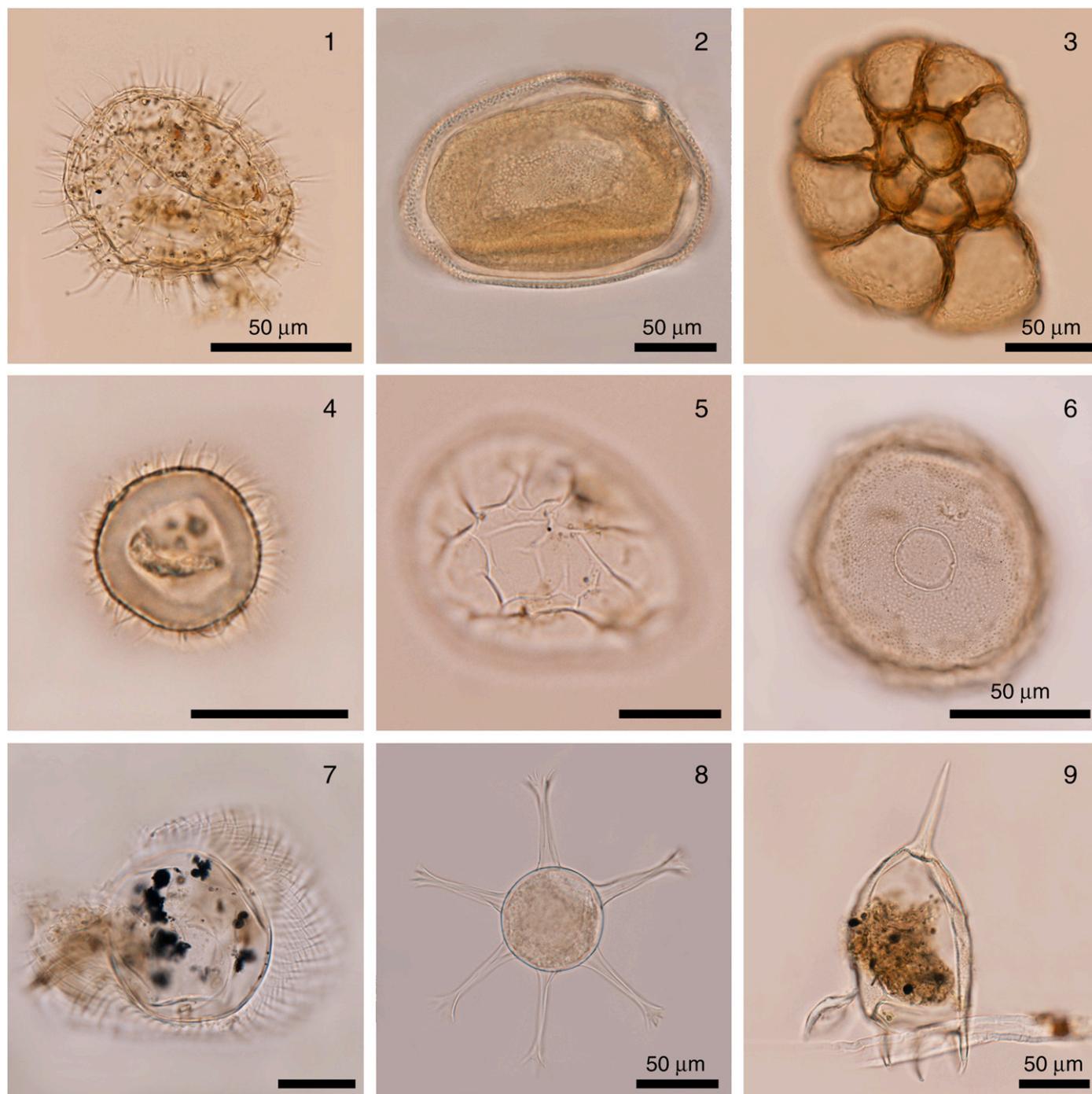


Plate VI. Bright-field photomicrographs. 1–2. Copepod eggs, UVic 09-184, slide 1, K27/0 and UVic 09-646, slide 1, V36/2. 3. Trochiserial microforaminiferal organic lining, UVic 09-394, slide 1, M47/2. 4. Cyst of cf. *Biecheleria* spp., UVic 09-096, slide 1, X49/0. 5. Palynomorph type 3, UVic 09-184, slide 1, O42/4. 6. *Halodinium minor*, UVic 09-402, slide 1, T50/3. 7. *Radiosperma corbiferum*, UVic 09-395, slide 1, H50/3. 8. *Hexasterias problematica*, UVic 09-397, slide 2, P31/3. 9. *Keratella* spp., UVic 09-088, slide 1, Q52/1. Scale bars are 20 µm unless otherwise specified.

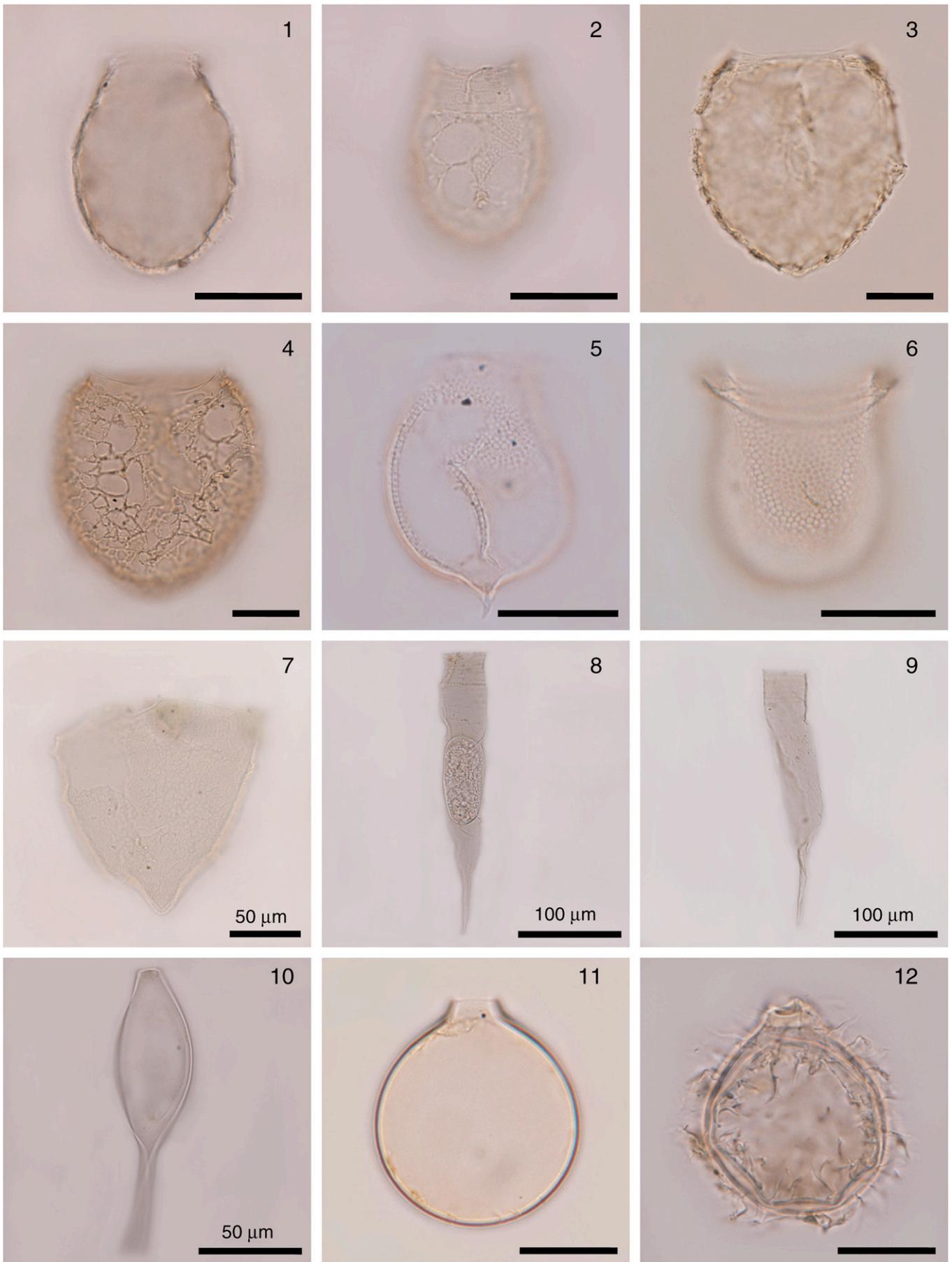
increases in early spring, early summer and late fall of 2009, while cf. *Strombidium* spp. shows a moderate increase in late summer 2009.

Total fluxes of copepod egg envelopes and microforaminiferal linings show a high degree of variability. The flux of copepod eggs was generally highest in spring and summer 2009. The flux of microforaminiferal linings was slightly higher during winter. Cysts of cf. *Biecheleria* spp. commonly contained cell content and were abundant in all samples (Fig. 5). Fluxes on average were highest during winter 2007/08, although an outbreak was recorded in June 2009. *Keratella* spp. were almost exclusively found in

winter. Fluxes of palynomorph type 3 and *Halodinium minor* were highest during winter, whereas *Hexasterias problematica* and *Radiosperma corbiferum* were most common during late spring to early summer.

4.4. Biogenic silica flux

Average biogenic silica fluxes were lowest during winter, and increased during spring. In spring 2009 the biogenic silica flux increased reaching a peak in mid-March, while it slowly declined



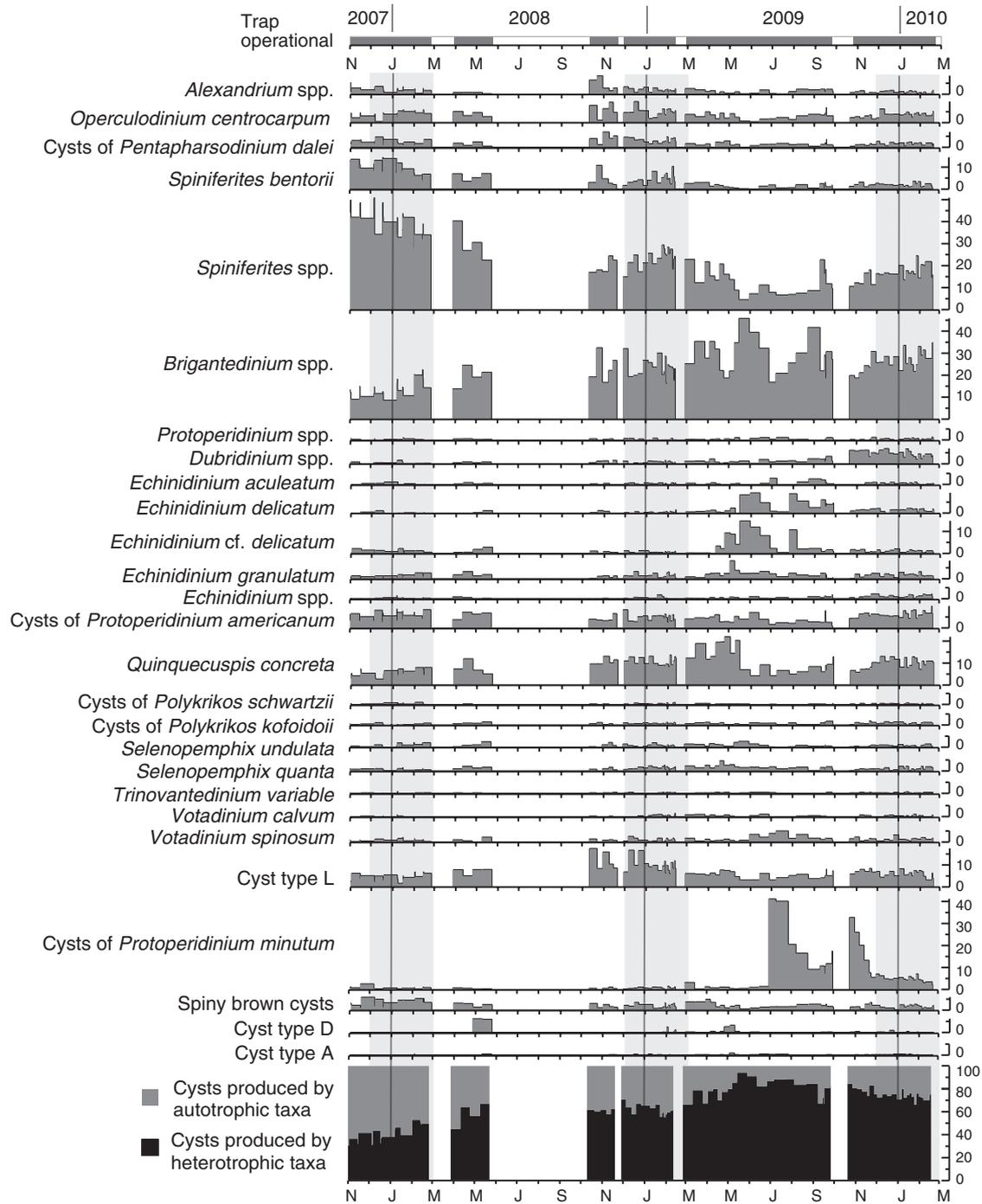


Fig. 3. Time-series of relative abundance of the most dominant cyst taxa observed in the sediment trap samples and total relative abundance of cysts produced by autotrophic and heterotrophic dinoflagellates. The bar located at the top of the figure shows when the sediment trap was not operational (white). Gray bands lengthwise across the figure highlight winter seasons (December–February).

during the early summer. Secondary peaks occurred in late June and early August (Fig. 2). Over the two and a half year study period variation in biogenic silica was recorded for three winter seasons. The average value during winter 2007/08 was $1.8 \text{ g m}^{-2} \text{ day}^{-1}$, whereas the subsequent winters recorded much higher average biogenic silica flux values of $3.1 \text{ g m}^{-2} \text{ day}^{-1}$ and $3.2 \text{ g m}^{-2} \text{ day}^{-1}$, respectively.

4.5. Surface sediment sample

The surface sediment sample contained 32 dinoflagellate taxa, five of which were produced by autotrophic taxa and 27 by heterotrophic taxa. All recorded sediment trap cyst taxa $>0.05\%$ were observed in the surface sediment sample. The assemblage was dominated by *Spiniferites* spp.,

Brigantedinium spp., *Q. concreta*, cyst type L, and *Operculodinium centrocarpum*. Cysts produced by heterotrophic taxa dominated the assemblage comprising 62%, whereas cysts produced by autotrophic taxa comprised 38%. A comparison between the relative abundance of cysts recorded in the sediment trap and in the sediment is shown in Fig. 6.

4.6. Statistical analyses

4.6.1. Relative abundances

The results of RDA show that the first ordination axis, explaining 73% of the variance, is significantly and positively correlated to biogenic silica, SST, and solar insolation (Fig. 7). The ordination of cyst taxa along the first axis shows that cysts produced by autotrophic taxa, particularly *Spiniferites* spp. and *S. bentorii*, are associated with

the negative values, whereas most cysts produced by heterotrophic taxa are associated with the positive values (Fig. 7A). *Brigantedinium* spp. shows a strong positive correlation with biogenic silica. *E. cf. delicatum* and *E. delicatum* are strongly and positively correlated to solar insolation, and cysts of *P. minutum* and *E. delicatum* show a high degree of positive correlation to increased SST (Fig. 7A). The second ordination axis explains an additional 15.8% of the variance and is significantly and positively correlated to SSS and SST. A total of 88.8% of the dinoflagellate species variance can be explained by the first and second ordination axes.

RDA was used to correlate sample scores, which are based on cyst assemblages, to the environmental parameters. Samples were distinguished by seasons and by year (Fig. 7B). Summer samples show a high positive correlation with SST, SSS, solar insolation and

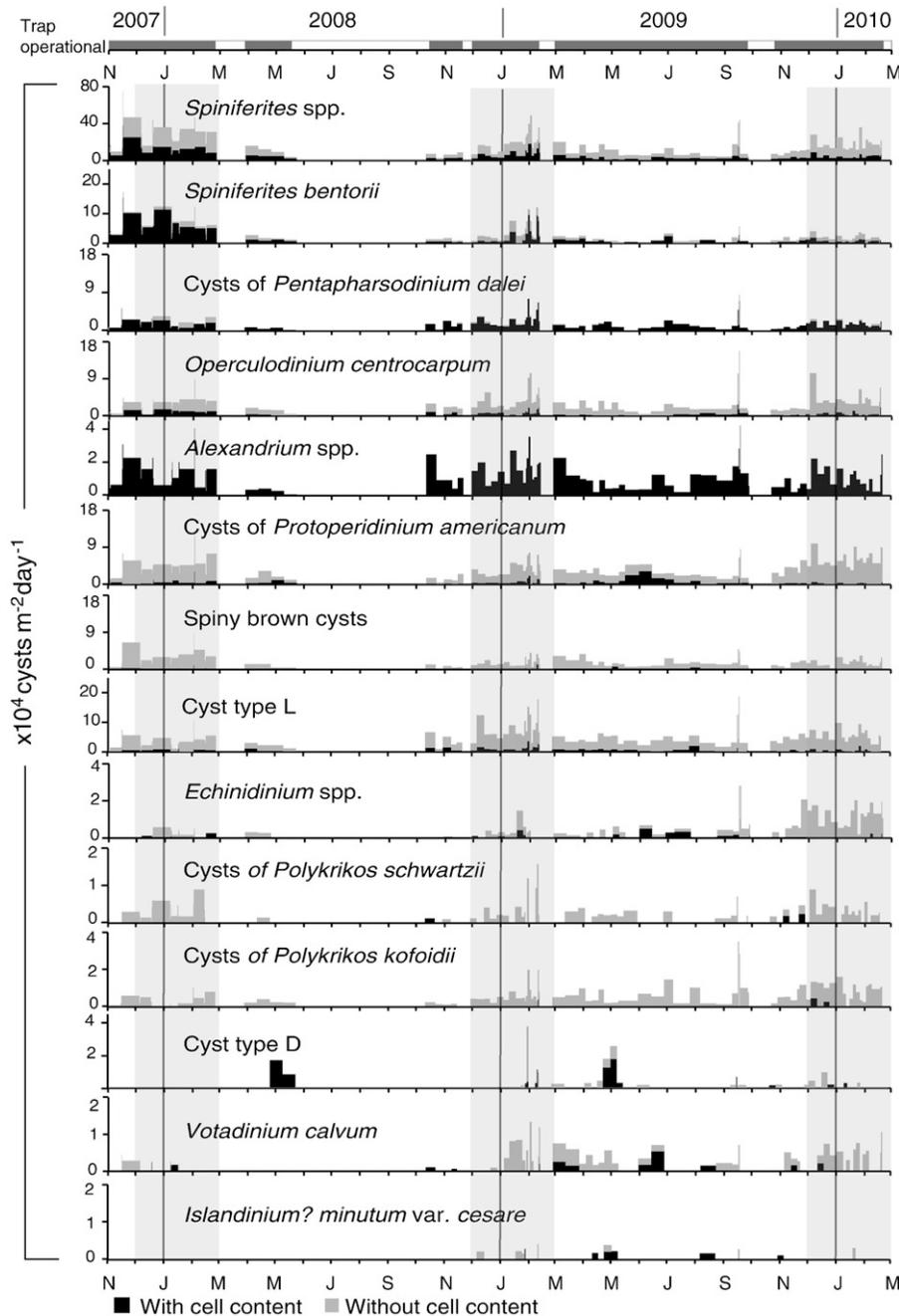


Fig. 4. Time-series of individual dinoflagellate cyst fluxes (cysts $\times 10^5 \text{ m}^{-2} \text{ day}^{-1}$) shown with (black) and without cell content (gray). The bar located at the top of the figure shows when the sediment trap was not operational (white). Gray bands lengthwise across the figure highlight winter seasons (December–February).

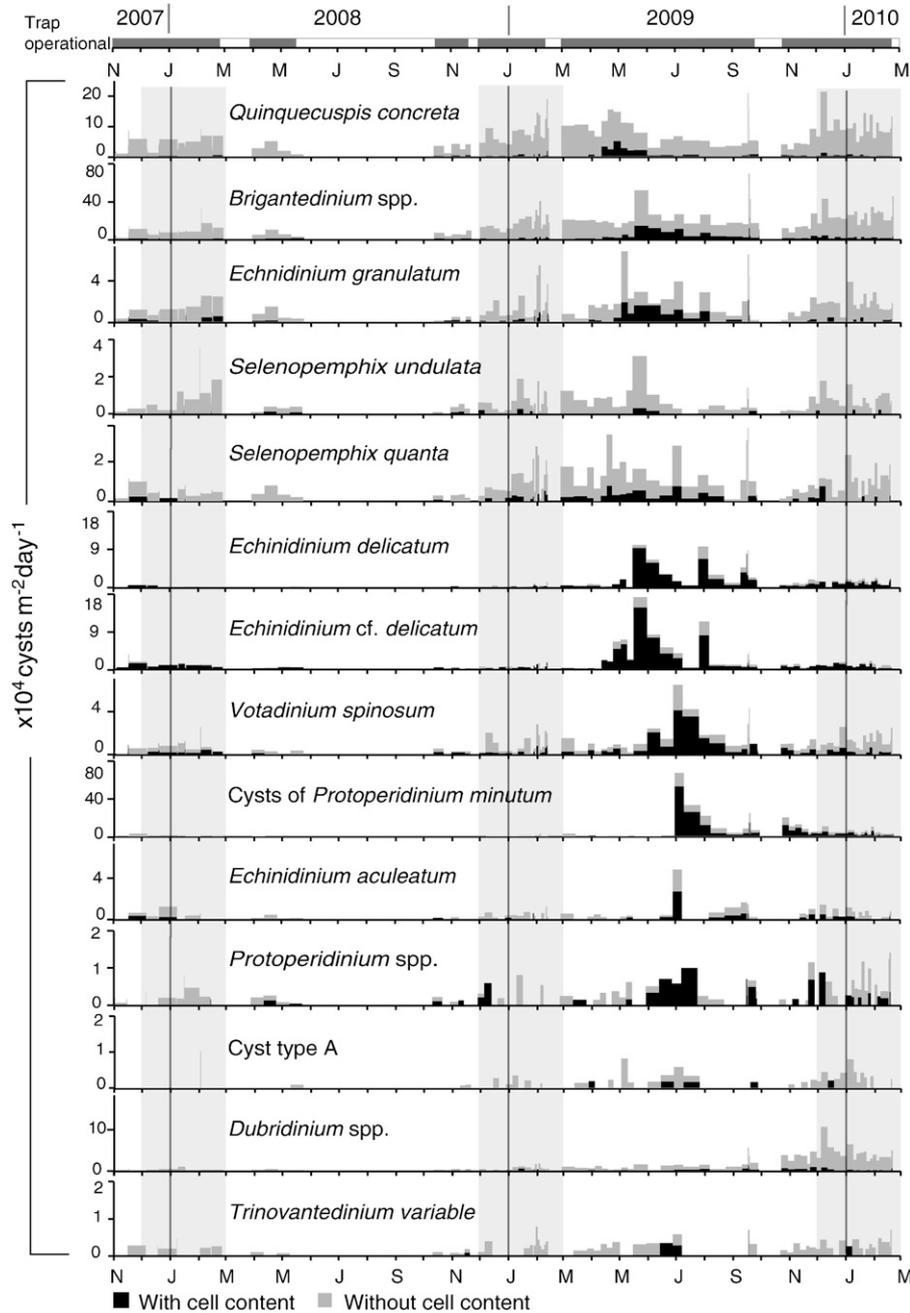


Fig. 4 (continued).

biogenic silica and are ordinated on the positive side of the first ordination axis, whereas winter samples correlate to low SST and are generally located on the negative side of the first and second ordination axes. Spring samples are ordinated on the negative side of the second ordination axis. Fall samples positively correlate to low biogenic silica flux, and are located on the positive side of the second ordination axis (Fig. 7B).

In order to more easily distinguish differences between winters, RDA analysis was performed a second time on relative abundance data using only samples collected during the three winter seasons (Fig. 8). The first ordination axis explains 77.3% of the variance and is significantly and positively correlated to SSS and negatively correlated to biogenic silica. The second axis explains another 12.4% of the variance and is significantly and positively correlated to Cowichan River discharge, and negatively correlated to SSS. Sample scores from Winter 2007/08 show a positive correlation to low biogenic silica flux. Winter 2008/09 correlates to higher

biogenic silica, higher SSS and low Cowichan River discharge. Winter 2009/10 shows a high degree of positive correlation with higher Cowichan River discharge and warmer SST. The sample scores from the three winter seasons are clustered in different locations on the RDA diagram highlighting the year-to-year variability in environmental parameters and cyst assemblages.

4.6.2. Flux data

The results of RDA show that the first ordination axis, explaining 66.9% of the variance, is significantly and positively correlated to biogenic silica (Fig. 9). *Brigantedinium* spp., *E. granulatum*, *S. quanta*, cysts of *P. schwartzii*, and *Q. concreta* show a strong positive correlation to biogenic silica. The second ordination axis, explaining 27.2% of the variance, is significantly and positively correlated to SST, solar insolation, and SSS. Many of the cysts produced by autotrophic taxa, particularly *S. bentonii*, are negatively correlated to the second ordination axis.

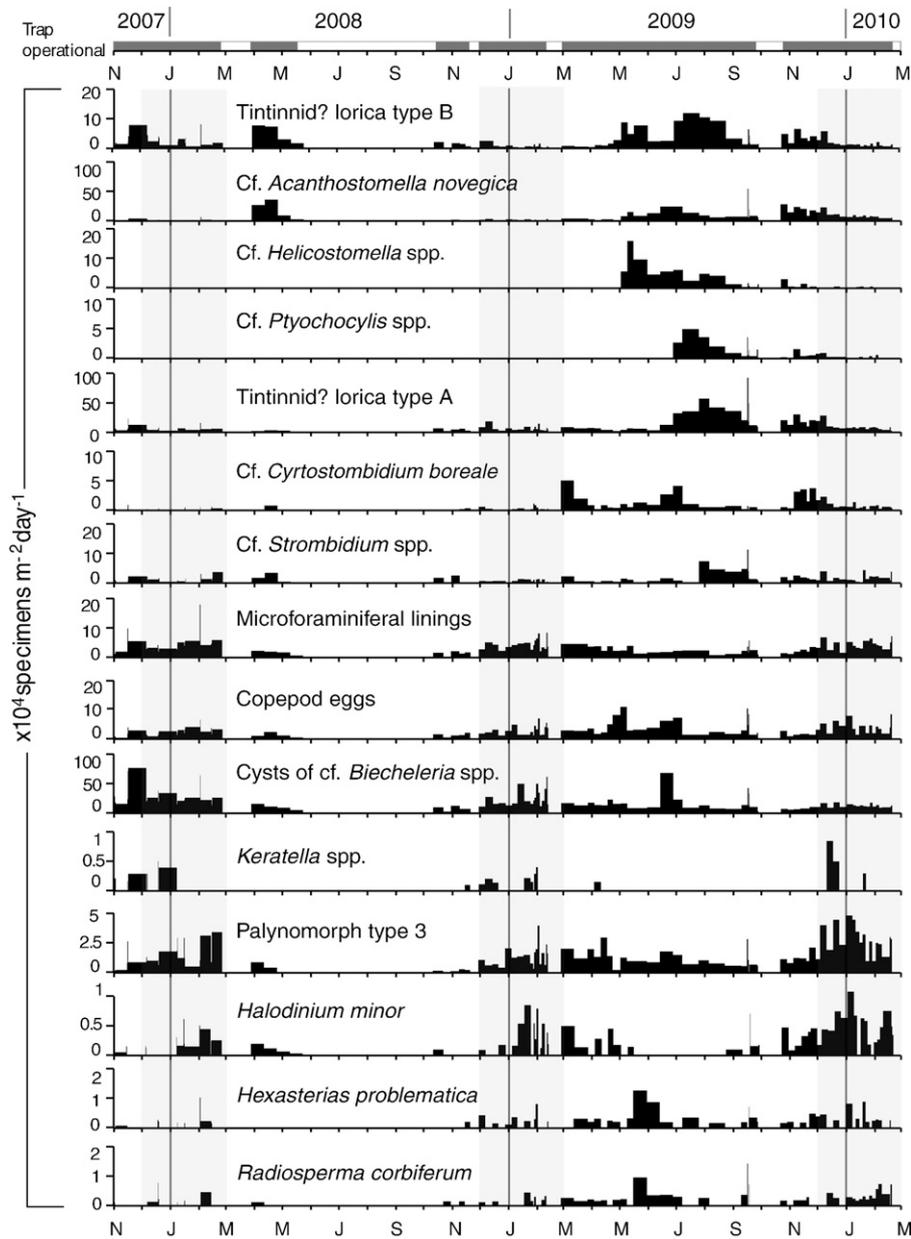


Fig. 5. Palynomorph fluxes (specimens $\times 10^4 \text{ m}^{-2} \text{ day}^{-1}$). The bar located at the top of the figure indicates where the sediment trap was not collecting (white). Gray bands highlight winter seasons (December–February).

Sample scores from cyst flux data highlights the variation in species assemblages that occurs seasonally and from year-to-year (Fig. 9B). Assemblages from summer samples are positively correlated to high SST, SSS, high solar insolation, or high biogenic silica flux. In contrast assemblages from winter samples generally show a negative correlation to these same variables.

5. Discussion

Sediment trap studies of dinoflagellate cyst assemblages provide a valuable tool for comparing cyst production in the water column to cyst assemblages preserved in the sediments, as well as to environmental parameters. This study provides one of the most detailed temporal records of dinoflagellate cyst production in coastal regions. This is the first study where most ($n = 63/96$) of the sampling intervals were one week or less in duration, over a multi-year

deployment period. The short sampling intervals allow for direct correlation between dinoflagellate cyst production and environmental factors on a high-resolution temporal scale. This sediment trap study documents seasonal trends in primary production, as recorded by dinoflagellate cyst production and biogenic silica flux.

Most dinoflagellate cyst taxa recorded in the sediment trap samples from Patricia Bay have been previously documented by Mudie et al. (2002) in Saanich Inlet. Mudie et al. (2002) examined organic-walled dinoflagellate cysts from two sediment cores (cores 93-10, -11; ODP Leg 169S; Hole 1034B) obtained from the central basin of Saanich Inlet, spanning the past 10,650 years. They did not report any cysts of the genera *Echinidinium* or *Votadinium*. Other cyst taxa not previously documented in Saanich Inlet include *Trinovantedinium variable* and cysts of *P. minutum*. *Lingulodinium machaerophorum*, *Pyxidinosia reticulata*, *Gymnodinium catenatum*, *Protoperidinium stellatum*, and *Xandarodinium xanthum* previously reported in Saanich

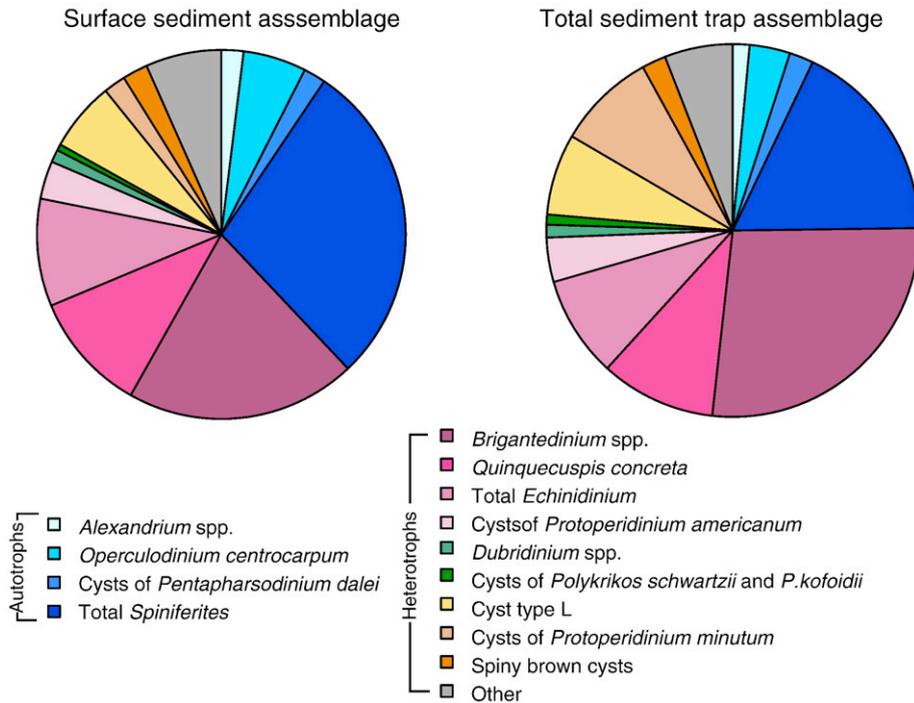


Fig. 6. Relative abundance of dinoflagellate cysts recovered in the surface sediment sample and the sediment trap (October 1, 2008–September 26, 2009).

Inlet by Mudie et al. (2002), have not been observed in our samples or from recent surface samples collected in nearby coastal bays and inlets on southern Vancouver Island (Radi et al., 2007; Krepakevich and Pospelova, 2010). We can only speculate the differences in species composition between this study and that of Mudie et al. (2002) are due to different past and present environmental conditions, different dinoflagellate cyst extraction techniques (i.e. use of acetolysis digestion by Mudie et al., 2002), or differences in cyst identification.

5.1. Sampling interval frequency and flux magnitudes

The length of the sampling interval may be an important consideration in high-resolution sediment trap studies. In this study the greatest variability in flux magnitudes occurred during short sampling intervals of two days or less. There are two possible explanations. Firstly, the volume of material collected during intervals of two days or less may be sufficiently small to cause a greater error during the splitting process, as a small difference in weights between aliquots becomes more significant. Or secondly, there is a high degree of daily variability in cyst production that can only be observed during short sampling intervals. It is likely that both play a role in the flux variation. Previous sediment trap deployments in Saanich Inlet (Sancetta and Calvert, 1988; Sancetta, 1989a,b,c; Timothy et al., 2003) were serviced and redeployed approximately monthly, therefore they cannot provide information on daily flux variation in the study area.

Biological productivity in Saanich Inlet is influenced by the fortnightly spring/neap tidal cycle. Gargett et al. (2003) suggest that macro-nutrient depletion caused by periodic phytoplankton blooms is resupplied on a semi-regular basis due to inlet-scale upwelling, driven by pressure gradient forces set up outside the inlet from spring-tidal mixing. During neap tides a counter clockwise cyclonic eddy is set up at the mouth of the inlet, with water flowing in on the western edge of the inlet and flowing out on the eastern side (Gargett et al., 2003). This brings additional nutrients into the inlet and acts to support higher production at the mouth of the inlet. The time scale on which this process is set up is a matter of a few days. It is therefore plausible,

especially in the spring and summer, to see significant changes in primary productivity on a daily to weekly basis.

5.2. Seasonal variation in dinoflagellate cyst production

In winter, cysts produced by autotrophic taxa became more abundant, especially *Spiniferites* spp., *S. bentorii*, and to a much lesser extent *Alexandrium* spp. Winter 2007/08 recorded the greatest relative abundance and flux of autotrophic taxa during the study period, due to an increase of *Spiniferites* spp. and *S. bentorii*, and was characterized by relatively high Cowichan River discharge rates, high average wind speeds, lower mean SSS, and higher mean SST (Fig. 2 and Table 3). It is notable that this increase in flux of cysts produced by autotrophic dinoflagellates is not accompanied by an increase in biogenic silica flux (Fig. 2) supporting the view that autotrophic dinoflagellates and diatoms have different ecological preferences. High Cowichan River discharge results in the surface water of Patricia Bay becoming less saline and more turbid, which may favor *Spiniferites* spp. cyst production in Saanich Inlet. Higher average wind speeds during this winter may also have played a role.

During spring, SST and the amount of daylight increase, and these are likely to be important contributing factors for the observed increase in diatom production as recorded by an increase in biogenic silica flux. The relative abundance and flux of heterotrophic cyst taxa also increase during spring and may reflect an increase in food availability, mainly diatoms. During mid to late spring cysts with cell content increase for many heterotrophic cyst taxa.

The ratio of cysts with and without cell content in sediment trap samples varies greatly between individual taxa. For instance, *Alexandrium* spp., cysts of *P. dalei*, *E. delicatum*, and *E. cf. delicatum* were consistently found with cell content throughout the entire sampling period, whereas other taxa such as *Q. concreta*, *Brigantedinium* spp., *E. granulosum*, and cysts of *P. americanum* are often found without cell content, except during spring and summer when an increase of cysts with cell content is recorded (Fig. 4). Cysts without cell content found in the sediment trap indicate the cysts may have germinated rapidly within the water column, as archeopyles were

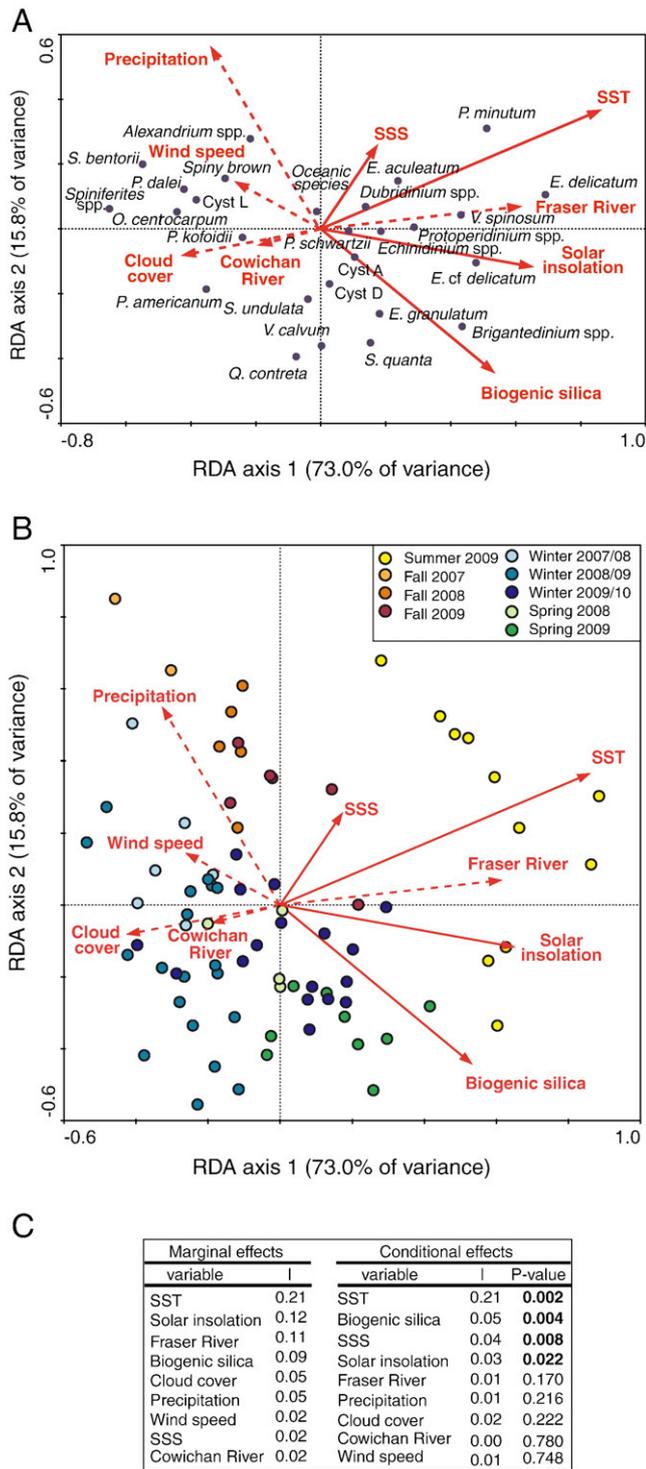


Fig. 7. (A) Redundancy analysis results showing ordination of species (relative abundances) and environmental variables. Statistically significant ($P < 0.05$) environmental variables are shown with solid arrows. (B) Samples scores, where different colors differentiate between different seasons and years. (C) Lambda (l) is the eigenvalue explained by the environmental variable. P-values < 0.05 are statistically significant and are highlighted in bold.

commonly observed. We suggest that those taxa found consistently with cell content may have a longer germination time compared to those taxa that were found consistently without cell content, such as *S. undulata* and cysts of *P. schwartzii/kofoidii*. The sediment trap study

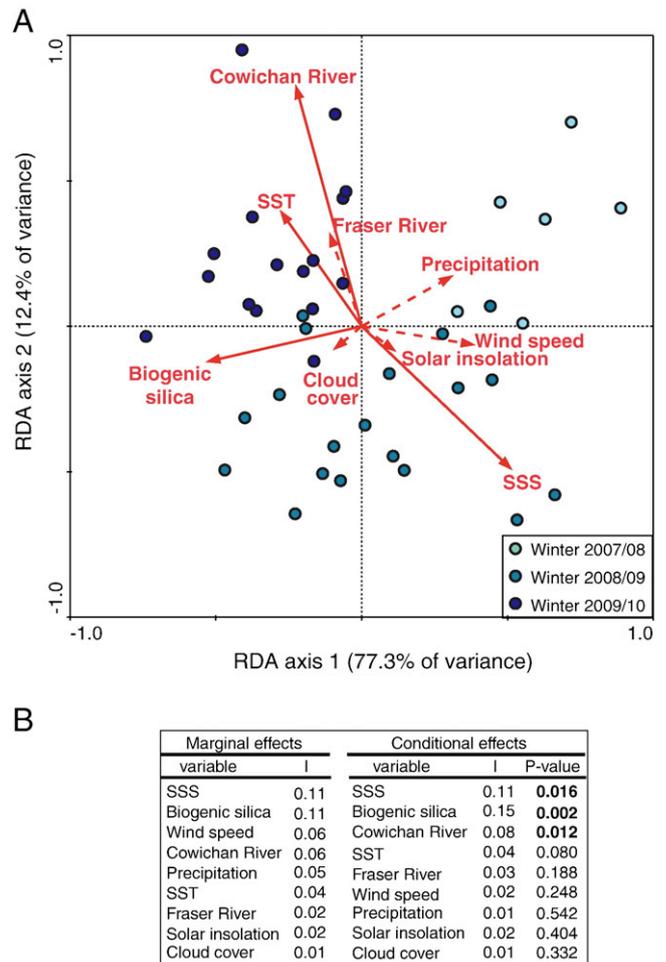


Fig. 8. (A) Ordination diagram generated from RDA, showing sample scores for winter samples, where different shades of blue differentiate between three winter seasons. Statistically significant ($P < 0.05$) environmental variables are shown with solid arrows. (B) Lambda (l) is the eigenvalue explained by the environmental variable. P-values < 0.05 are statistically significant and are highlighted in bold.

from nearby Strait of Georgia shows very similar patterns in the ratio of cysts with/without cell content for the same individual cyst taxa (see Fig. 4 in Pospelova et al., 2010). These observations suggest that there may be a large variability in germination times for different species. Although it is possible that some of the empty cysts recorded in this study may be a result by resuspension, the strong seasonality in cyst fluxes and abundances, as well as similar patterns of cyst taxa with and without cell content to those in the Strait of Georgia, suggests that resuspended sediment into the trap is minor.

In summer, the cyst assemblage is strongly dominated by cysts produced by heterotrophic taxa, particularly cysts of *P. minutum*, *Brigantedinium* spp., *Q. concreta*, *E. delicatum*, *E. cf. delicatum*, *E. granulatum*, *S. undulata* and *S. quanta*. Cysts containing cell content of these taxa show a temporally restricted pattern in production, with a clear succession throughout the late spring to early fall. Fluxes of *Brigantedinium* spp. and *E. granulatum* containing cell content increase in May and remain high until July when their production decreases. Fluxes of *E. delicatum* and *E. cf. delicatum* containing cell content increase sharply in April to May and decrease significantly during June. As these two taxa decrease, reaching low values in July, production of *P. minutum* sharply increases becoming the most dominant cyst taxa during July. *V. spinosum* with cell content also

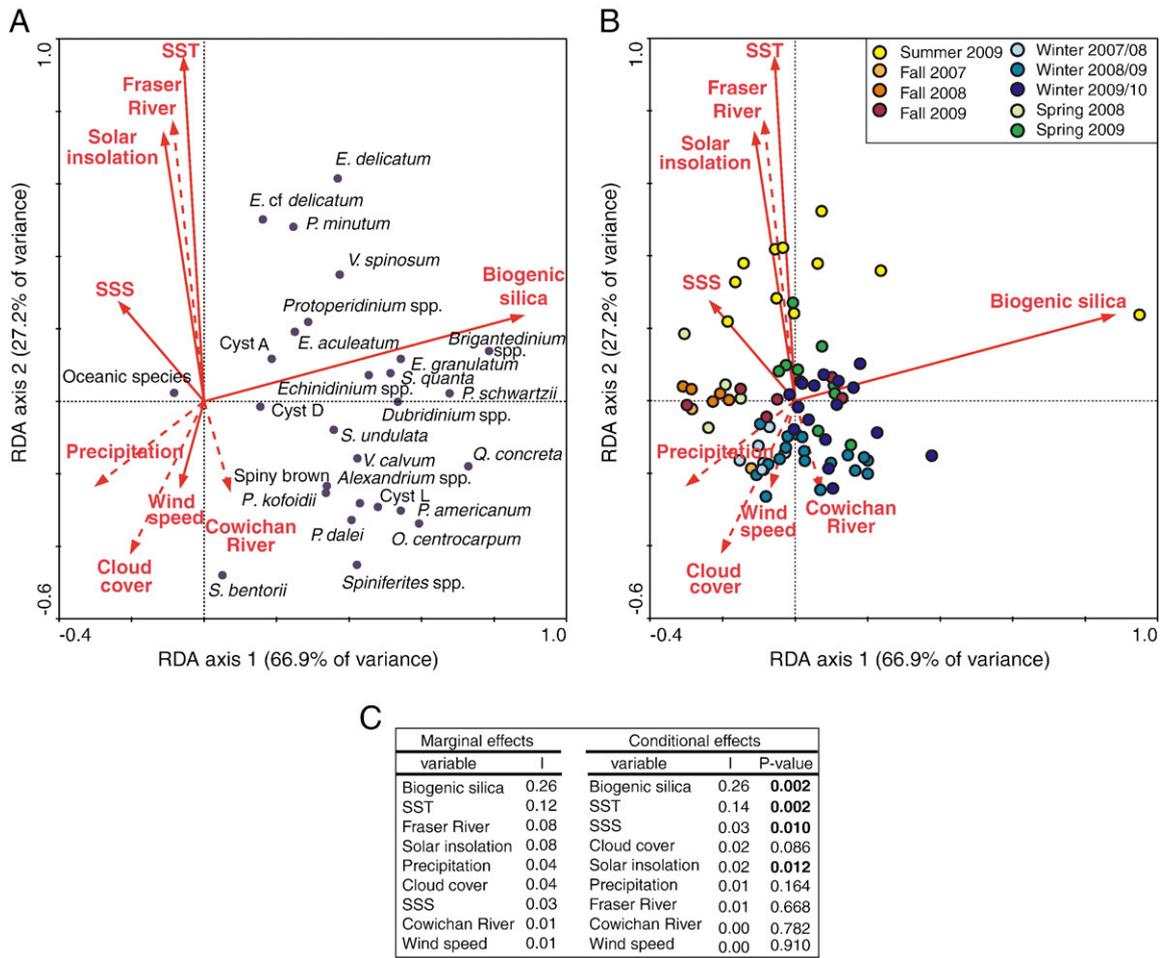


Fig. 9. (A) Redundancy analysis results showing ordination of species (fluxes) and environmental variables. Statistically significant ($P < 0.05$) environmental variables are shown with solid arrows. (B) Samples scores, where different colors differentiate between different seasons and years. (C) Lambda (l) is the eigenvalue explained by the environmental variable. P-values < 0.05 are statistically significant and are highlighted in bold.

shows a significant increase in cyst flux during June, reaching maximum values in July. In early August *E. delicatum* and *E. cf. delicatum* peak a second time. These taxa show a strong positive correlation to SST, solar insolation, and biogenic silica flux, however the reasons for their temporally restricted pattern throughout the late spring and summer is unclear.

Cyst taxa showing distinct seasonal patterns were assigned to the following groups: winter taxa – *Spiniferites* spp. and *S. bentorii*; spring taxa – cyst type D; spring and summer – *E. delicatum*, *E. cf. delicatum*; summer taxa – cysts of *P. minutum* and *V. spinosum*. One complete set of fall samples is not available and no individual cyst taxa were particularly more dominant during fall, therefore no cyst taxa were assigned to this season.

Spiniferites spp. and *S. bentorii* during winters have not been previously recognized. Indeed, in paleoenvironmental studies in the Northeast Pacific (Pospelova et al., 2006, 2008), these taxa in sediment cores and surface samples were associated with warm climatic events and warmer waters. Alternatively, the predominance of *Spiniferites* spp. and *S. bentorii* during winter, may be related to lower salinity surface water. Pospelova et al. (2004) report highest abundances of *Spiniferites* spp. in low salinity lagoons. According to our Saanich Inlet sediment trap results, these taxa may be associated with warm or wet winters.

Previous studies suggest that diatoms are the predominant primary producers in Saanich Inlet during the spring and summer

(e.g. Timothy and Soon, 2001; Grundle et al., 2009). Although this study cannot quantify the dinoflagellate contribution to the total primary production, the recorded high fluxes of autotrophic dinoflagellates suggests that they are important contributors to primary production in the inlet throughout the year, but especially in the fall and winter months when fluxes of cysts produced by autotrophic dinoflagellates are greatest. Given that many cysts in this study are produced by heterotrophic dinoflagellates, the heterotrophic dinoflagellates may also play an important role as grazers in Saanich Inlet.

5.3. Relationship between biogenic silica and cyst flux

Diatoms are the most significant producers of biogenic silica in the inlet, with only a minor contribution from silicoflagellates (Sancetta and Calvert, 1988; Sancetta, 1989a). Previous studies have suggested that heterotrophic dinoflagellates become more abundant when prey (i.e. diatoms, small flagellates, and bacteria) availability increases (e.g. Grattepanche et al., 2011; Hansen, 1991; Landry et al., 2000; Sherr and Sherr, 2007). In this study there is a significant correlation ($R^2 = 0.65$, $p = 0.000$) between biogenic silica flux and flux of cysts produced by heterotrophic taxa, and a poor correlation ($R^2 = 0.07$, $p = 0.008$) between biogenic silica flux and flux of cysts produced by autotrophic taxa (Fig. 10). This observation corroborates earlier observations of Fujii and Matsuoka (2006) who reported a positive correlation

Table 3
UVic sample identification number, start and end of sampling interval, total precipitation, as well as mean values for SST, SSS, cloud cover (1 = clear skies, 3 = mostly cloudy or rainy), wind speed, daily average solar insolation, biogenic silica, and daily averages for Cowichan River and Fraser River discharge.

UVic sample ID	Starting date (hh:mm:ss dd:mm:yyyy) UTC	Closing date (hh:mm:ss dd:mm:yyyy) UTC	Interval (days)	SST (°C)	SSS (psu)	Total Precipitation (mm)	Cloud cover	Wind speed (m s ⁻¹)	Solar insolation (W m ⁻²)	Cowichan River discharge (m ³ s ⁻¹)	Fraser River discharge (m ³ s ⁻¹)	Biogenic silica flux (g m ⁻² day ⁻¹)	
1	09-079	12:50:18 01/11/2007	02:07:31 02/11/2007	0.55	9.1	27.1	0.0	1.1	8.2	N/A	66.7	3090.0	0.9
2	09-080	02:07:31 02/11/2007	00:43:41 03/11/2007	0.94	9.5	27.5	0.0	1.5	8.3	N/A	61.9	3020.0	0.6
3	09-081	00:43:41 03/11/2007	13:44:17 15/11/2007	12.54	9.4	27.7	60.8	2.0	12.6	1195.8	78.3	2726.4	0.5
4	09-082	13:44:17 15/11/2007	01:49:00 16/11/2007	0.50	9.3	27.4	13.8	2.5	8.9	N/A	125.0	2760.0	2.1
5	09-083	01:49:00 16/11/2007	14:02:13 16/11/2007	0.51	7.3	25.1	16.6	2.5	14.5	N/A	141.0	2785.0	3.5
6	09-084	14:02:13 16/11/2007	00:57:57 06/12/2007	19.46	7.1	19.4	168.6	2.0	10.4	964.5	136.8	1970.0	1.9
7	09-085	00:57:57 06/12/2007	13:57:42 06/12/2007	0.54	7.7	22.2	0.0	1.6	8.2	N/A	285.5	1730.0	0.9
8	09-086	13:57:42 06/12/2007	02:12:39 07/12/2007	0.51	6.2	21.3	0.0	1.5	9.6	N/A	265.0	1540.0	1.1
9	09-087	02:12:39 07/12/2007	14:11:07 18/12/2007	11.50	7.3	25.9	34.7	2.1	12.1	719.6	172.7	1360.0	1.6
10	09-088	14:11:07 18/12/2007	02:52:02 19/12/2007	0.53	7.0	25.0	10.5	3.0	13.8	N/A	133.0	1460.0	1.8
11	09-089	02:52:02 19/12/2007	15:36:42 19/12/2007	0.53	6.9	26.6	24.1	2.6	17.3	N/A	135.0	1470.0	1.0
12	09-090	15:36:42 19/12/2007	02:39:38 08/01/2008	19.46	6.7	26.9	75.7	2.0	15.1	760.6	109.0	1225.0	1.6
13	09-091	02:39:38 08/01/2008	15:00:21 08/01/2008	0.51	7.5	28.8	13.2	2.7	29.7	N/A	122.5	974.5	0.7
14	09-092	15:00:21 08/01/2008	00:24:37 09/01/2008	0.39	7.2	26.6	12.6	2.6	25.8	N/A	116.0	980.0	1.2
15	09-093	00:24:37 09/01/2008	02:08:10 16/01/2008	7.07	6.3	26.1	58.9	2.2	15.3	713.9	131.5	969.0	2.5
16	09-094	02:08:10 16/01/2008	15:27:13 16/01/2008	0.55	6.2	26.1	0.0	1.9	5.4	N/A	146.0	955.0	1.9
17	09-095	15:27:13 16/01/2008	01:43:46 17/01/2008	0.43	5.4	25.5	0.0	2.0	6.8	N/A	144.0	950.0	1.3
18	09-096	01:43:46 17/01/2008	02:33:25 02/02/2008	16.03	6.3	27.8	13.5	1.8	10.2	1378.0	88.2	841.2	1.7
19	09-097	02:33:25 02/02/2008	14:25:28 02/02/2008	0.49	6.5	28.4	0.2	2.0	7.2	N/A	52.4	746.0	5.4
20	09-098	14:25:28 02/02/2008	02:44:07 14/02/2008	11.51	N/A	N/A	35.6	2.1	14.3	1219.3	53.0	831.9	2.6
21	09-099	02:44:07 14/02/2008	14:21:49 14/02/2008	0.48	N/A	N/A	0.0	1.3	7.1	N/A	64.7	856.0	1.7
22	09-100	14:21:49 14/02/2008	02:24:04 15/02/2008	0.50	6.5	26.0	0.0	2.0	4.1	N/A	65.5	899.0	1.2
23	09-101	02:24:04 15/02/2008	04:09:00 26/02/2008	11.07	7.7	28.0	4.8	1.6	6.9	2206.7	55.6	870.0	2.2
24	09-102	09:59:26 28/03/2008	09:59:32 11/04/2008	14.00	8.8	28.8	22.2	1.9	9.5	3194.8	45.3	749.5	1.8
25	09-151	09:59:32 11/04/2008	09:59:24 25/04/2008	14.00	9.6	28.6	11.1	1.9	13.5	4413.2	36.6	1247.2	3.0
26	09-152	09:59:24 25/04/2008	10:15:48 09/05/2008	14.01	N/A	N/A	14.7	1.8	10.1	4796.4	25.4	2249.3	2.5
27	09-153	10:15:48 09/05/2008	06:32:59 23/05/2008	13.85	10.7	29.1	10.0	1.9	10.5	4747.1	51.7	5490.7	1.0
28	09-154	16:47:26 10/10/2008	16:02:44 21/10/2008	10.97	N/A	N/A	18.4	2.0	9.8	2058.8	24.1	1476.7	0.8
29	09-155	21:44:21 29/10/2008	23:19:45 07/11/2008	9.07	N/A	N/A	95.0	2.4	9.9	866.6	31.4	1514.0	2.3
30	09-646	23:19:45 07/11/2008	00:20:14 14/11/2008	6.04	N/A	N/A	52.2	2.3	13.3	1064.3	82.2	1865.7	1.0
31	09-647	00:20:14 14/11/2008	21:39:24 19/11/2008	5.89	N/A	N/A	0.8	1.9	5.9	1357.1	98.7	2037.1	0.9
32	09-648	22:35:53 28/11/2008	21:48:25 05/12/2008	6.97	N/A	N/A	9.0	2.1	5.0	654.1	56.0	1495.0	1.9
33	09-157	21:48:25 05/12/2008	22:25:40 13/12/2008	8.03	N/A	N/A	36.2	2.3	9.6	565.0	46.5	1384.4	3.2
34	09-649	22:25:40 13/12/2008	04:04:32 20/12/2008	6.24	N/A	N/A	23.4	2.0	21.2	961.7	41.3	1053.9	1.8
35	09-158	04:04:32 20/12/2008	17:29:25 27/12/2008	7.56	N/A	N/A	70.8	2.2	14.3	492.0	33.2	761.1	2.3
36	09-650	17:29:25 27/12/2008	16:54:13 03/01/2009	6.98	N/A	N/A	32.3	2.1	13.8	911.9	34.2	917.9	2.9
37	09-651	16:54:13 03/01/2009	20:01:35 09/01/2009	6.13	N/A	N/A	45.4	2.4	16.2	573.0	54.6	1001.9	2.7
38	09-159	20:01:35 09/01/2009	21:55:44 16/01/2009	7.08	5.0	23.5	11.9	2.2	9.1	519.0	106.0	1037.1	2.3
39	09-652	21:55:44 16/01/2009	19:40:21 23/01/2009	6.91	4.3	24.5	0.0	1.5	6.9	1450.6	86.1	950.9	3.1
40	09-653	19:40:21 23/01/2009	19:52:32 26/01/2009	3.01	3.4	23.3	0.0	1.4	8.4	1797.5	70.4	885.0	2.4
41	09-160	19:52:32 26/01/2009	22:52:30 27/01/2009	1.12	3.9	22.7	2.4	2.3	13.9	1387.2	63.2	863.0	2.2
42	09-654	22:52:30 27/01/2009	18:35:28 29/01/2009	1.82	5.9	26.0	2.4	2.0	6.6	1249.3	59.4	810.7	4.0
43	09-161	18:35:28 29/01/2009	20:31:08 31/01/2009	2.08	6.8	28.8	0.0	1.7	13.4	1595.0	55.0	766.0	4.2
44	09-655	20:31:08 31/01/2009	17:49:18 02/02/2009	1.89	6.5	28.3	4.5	2.1	7.8	1289.6	51.0	801.0	5.2

45	09-656	17:49:18 02/02/2009	19:41:22 04/02/2009	2.08	6.3	27.5	3.1	1.9	7.2	1699.3	49.1	794.0	2.4
46	09-657	19:41:22 04/02/2009	23:34:31 07/02/2009	3.16	6.3	27.6	3.8	1.9	6.5	1703.9	46.8	802.3	3.3
47	09-162	23:34:31 07/02/2009	21:34:12 09/02/2009	1.92	6.2	27.6	0.0	2.0	8.6	1802.0	44.0	809.7	2.8
48	09-163	21:34:12 09/02/2009	23:00:00 10/02/2009	1.06	6.7	28.9	8.8	1.8	16.9	1311.3	42.4	801.5	3.8
49	09-658	23:00:00 10/02/2009	23:00:00 11/02/2009	1.00	6.7	28.8	10.8	2.5	11.4	1194.4	41.0	795.5	3.9
50	09-387	17:06:13 25/02/2009	17:08:19 11/03/2009	14.00	7.1	28.8	19.4	1.8	13.0	2585.1	34.9	675.5	5.0
51	09-388	17:08:19 11/03/2009	13:53:18 26/03/2009	14.86	7.6	28.2	36.3	2.0	13.2	2930.9	55.2	653.9	5.6
52	09-389	13:53:18 26/03/2009	12:51:55 02/04/2009	6.96	8.8	25.9	21.3	2.1	12.2	2491.2	73.2	697.1	4.6
53	09-390	12:51:55 02/04/2009	23:27:32 09/04/2009	7.44	8.9	27.2	3.4	1.8	8.3	4414.7	54.3	707.8	4.8
54	09-391	23:27:32 09/04/2009	15:53:49 16/04/2009	6.68	10.2	27.8	13.2	1.8	11.4	3801.8	50.8	1030.6	4.8
55	09-392	15:53:49 16/04/2009	15:19:32 22/04/2009	5.98	11.1	27.3	7.6	1.8	9.3	4676.1	69.1	2052.9	4.1
56	09-393	15:19:32 22/04/2009	22:42:10 30/04/2009	8.31	10.6	28.7	3.4	1.5	10.9	5696.6	59.9	3436.7	4.4
57	09-394	22:42:10 30/04/2009	22:50:34 07/05/2009	7.01	10.6	29.1	24.8	2.1	12.9	3332.9	36.2	3407.5	4.0
58	09-395	22:50:34 07/05/2009	16:00:09 14/05/2009	6.71	13.4	28.1	23.6	1.7	12.2	4897.3	57.9	4382.5	3.5
59	09-396	16:00:09 14/05/2009	13:23:36 29/05/2009	14.89	16.3	28.9	14.8	1.5	9.6	6728.8	36.9	4933.1	4.1
60	09-397	13:23:36 29/05/2009	16:07:01 12/06/2009	14.11	15.4	29.4	0.0	1.5	7.8	7183.7	14.5	6502.0	3.6
61	09-398	16:07:01 12/06/2009	17:59:50 26/06/2009	14.08	15.4	28.2	5.6	1.7	11.6	6096.7	8.6	6844.7	6.0
62	09-399	17:59:50 26/06/2009	19:43:10 06/07/2009	10.07	16.6	28.2	0.4	1.3	8.9	7111.3	7.1	5226.9	4.4
63	09-400	19:43:10 06/07/2009	15:12:23 24/07/2009	17.81	18.9	29.1	7.5	1.5	9.6	6066.5	6.3	4597.0	3.6
64	09-401	15:12:23 24/07/2009	18:05:23 04/08/2009	11.12	16.4	29.2	3.6	1.2	8.1	6705.3	6.3	4152.2	4.7
65	09-402	18:05:23 04/08/2009	20:11:38 21/08/2009	17.09	15.7	29.3	16.4	1.8	9.4	4883.0	6.1	3127.1	3.0
66	09-403	20:11:38 21/08/2009	12:22:57 08/09/2009	17.67	15.4	29.4	15.8	1.7	9.7	4547.7	5.8	2156.3	2.7
67	09-404	12:22:57 08/09/2009	20:44:30 14/09/2009	6.35	15.7	29.5	11.2	1.6	7.8	3688.9	8.3	2130.8	3.2
68	09-405	20:44:30 14/09/2009	21:28:38 15/09/2009	1.03	15.8	29.5	0.2	1.6	8.4	N/A	8.3	2026.7	10.8
69	09-406	21:28:38 15/09/2009	14:46:31 16/09/2009	0.72	15.5	29.4	4.6	1.6	7.5	950.2	8.2	1944.9	3.5
70	09-407	14:46:31 16/09/2009	02:38:51 17/09/2009	0.49	14.7	29.5	4.6	2.3	6.5	950.2	8.2	1826.6	8.7
71	09-408	02:38:51 17/09/2009	16:59:13 25/09/2009	8.60	14.7	29.7	11.4	1.3	9.2	4029.9	8.2	1791.5	3.4
72	09-409	16:59:13 25/09/2009	16:43:05 26/09/2009	0.99	11.5	29.4	0.0	1.1	5.5	4370.1	8.1	1860.7	1.4
73	10-006	18:19:37 20/10/2009	01:41:15 28/10/2009	7.31	10.1	27.9	44.5	2.0	8.0	1568.0	28.5	1037.2	3.8
74	10-007	01:41:15 28/10/2009	21:12:51 03/11/2009	6.81	10.2	28.8	27.9	2.0	11.1	1573.9	55.8	1313.6	2.1
75	10-008	21:12:51 03/11/2009	21:09:02 10/11/2009	7.00	9.0	26.5	62.4	2.3	14.9	1001.2	89.9	1727.2	3.4
76	10-009	21:09:02 10/11/2009	00:34:51 18/11/2009	7.14	9.3	26.9	92.5	2.2	15.9	871.5	176.8	1495.3	2.9
77	10-010	00:34:51 18/11/2009	20:15:55 20/11/2009	2.82	8.6	20.3	80.5	2.6	20.1	739.6	307.0	1513.9	1.7
78	10-011	20:15:55 20/11/2009	23:40:50 27/11/2009	7.14	7.9	23.2	71.2	2.4	13.1	737.8	280.3	1521.6	3.9
79	10-012	23:40:50 27/11/2009	16:32:49 02/12/2009	4.70	6.2	25.0	1.4	2.1	15.4	943.4	224.2	1703.3	3.8
80	10-013	16:32:49 02/12/2009	17:02:00 09/12/2009	7.02	3.2	21.0	0.0	1.3	17.1	1314.1	147.3	1321.1	4.9
81	10-014	17:02:00 09/12/2009	16:18:55 16/12/2009	6.97	7.4	26.4	52.7	2.1	8.6	439.1	79.7	922.4	2.9
82	10-015	16:18:55 16/12/2009	03:41:42 23/12/2009	6.47	5.5	25.2	48.2	2.4	9.1	503.9	104.5	1002.9	4.2
83	10-016	03:41:42 23/12/2009	19:22:35 30/12/2009	7.65	7.6	25.1	2.6	1.8	7.5	959.5	89.3	959.0	3.0
84	10-017	19:22:35 30/12/2009	16:21:07 06/01/2010	6.87	6.5	22.1	71.1	2.4	10.2	504.7	68.5	984.1	3.3
85	10-018	16:21:07 06/01/2010	21:45:50 09/01/2010	3.23	7.6	19.2	13.2	2.2	9.6	617.1	89.4	921.1	2.7
86	10-019	21:45:50 09/01/2010	21:23:54 13/01/2010	3.98	7.3	15.0	35.6	2.4	10.4	407.1	167.0	1213.3	2.9
87	10-020	21:23:54 13/01/2010	19:55:37 17/01/2010	3.94	7.3	19.7	43.5	2.2	13.3	593.4	261.7	1350.5	3.3
88	10-021	19:55:37 17/01/2010	20:06:01 20/01/2010	3.01	6.7	20.2	5.1	2.2	14.7	739.4	240.0	1252.3	3.7
89	10-022	20:06:01 20/01/2010	19:56:20 24/01/2010	3.99	7.1	18.2	7.0	1.9	6.7	990.5	183.2	1205.4	3.2
90	10-023	19:56:20 24/01/2010	19:58:27 27/01/2010	3.00	7.3	19.0	7.4	2.1	10.1	N/A	151.7	1105.2	3.1
91	10-024	19:58:27 27/01/2010	18:13:49 31/01/2010	3.93	7.9	22.6	6.8	2.3	6.9	N/A	124.3	945.2	2.5
92	10-025	18:13:49 31/01/2010	16:33:01 03/02/2010	2.93	7.7	19.8	5.6	2.2	6.7	N/A	97.9	871.6	2.8
93	10-026	16:33:01 03/02/2010	01:06:10 07/02/2010	3.36	7.7	23.7	1.8	2.0	8.5	1288.1	79.2	847.8	2.9
94	10-027	01:06:10 07/02/2010	00:47:38 16/02/2010	8.99	N/A	N/A	17.1	2.2	9.9	1016.0	79.6	813.0	2.9
95	10-028	00:47:38 16/02/2010	21:56:39 16/02/2010	0.88	7.8	25.6	8.2	2.1	15.7	1886.1	109.9	835.4	2.8
96	10-029	21:56:39 16/02/2010	01:35:31 18/02/2010	1.15	9.1	27.1	7.4	1.2	11.6	2752.7	104.4	827.8	4.1

between production of cysts produced by heterotrophic taxa and diatom flux, and of Zonneveld et al. (2010) who linked a positive correlation of some taxa of *Protoperdinium* to the flux of total diatom valves.

Given the high degree of correlation between the flux of cysts produced by heterotrophic taxa and biogenic silica flux in Saanich Inlet, and that the majority of heterotrophs in this system are *Protoperdinium*, it suggests a causal relationship between diatom production and heterotrophic dinoflagellate production in this study area. The high degree of correlation may allow cyst fluxes of *Protoperdiniaceae* to be used as a paleoproxy for total diatom production in sedimentary cores. However, given that biogenic silica is subject to dissolution, and *Protoperdiniaceae* to oxygen degradation, such correlations should be made with care. In addition, heterotrophic dinoflagellates have a variety of food sources, complicating this relationship (Naustvoll, 2000).

5.4. Comparison of Saanich Inlet dinoflagellate cyst fluxes to other coastal sediment trap studies

Saanich Inlet is known for high levels of primary production, which is influenced by seasonal changes in light availability, as well as fortnightly variation in nutrient concentrations due to tidally driven water mass advection (Takahashi et al., 1977, 1978; Timothy and Soon, 2001; Timothy et al., 2003; Gargett et al., 2003; Grundle et al., 2009). In comparison to previously studied fjords in the northern hemisphere, Saanich Inlet stands out with one of the greatest estimated values of yearly primary production at $475 \text{ g C m}^{-2} \text{ y}^{-1}$ (Table 4 in Grundle et al., 2009). Estimates near the mouth of Saanich Inlet are even greater at $565 \text{ g C m}^{-2} \text{ y}^{-1}$ ($550 \text{ g C m}^{-2} \text{ y}^{-1}$ at S2, Timothy and Soon, 2001; $580 \text{ g C m}^{-2} \text{ y}^{-1}$ at S2, Grundle et al., 2009).

In Saanich Inlet the cyst flux ranged from $\sim 149,000 \text{ cysts m}^{-2} \text{ day}^{-1}$ to $\sim 2,400,000 \text{ cysts m}^{-2} \text{ day}^{-1}$, with an average of $\sim 777,000 \text{ cysts m}^{-2} \text{ day}^{-1}$. These values are within the range reported by other coastal sediment trap studies (Table 4) (Heiskanen, 1993; Montresor et al., 1998; Godhe et al., 2001; Joyce and Pitcher, 2004; Morquecho and Lechuga-Deveze, 2004; Fujii and Matsuoka, 2006; Pitcher and Joyce, 2009; Pospelova et al., 2010).

Coastal and estuarine systems are often complex and dynamic environments where biotic and abiotic factors can vary substantially even in nearby waters. Although the sampling location of the sediment trap study conducted by Pospelova et al. (2010) was located approximately 60 km north in the Strait of Georgia, cyst fluxes and seasonal patterns were notably different. In the Strait of Georgia cyst fluxes were significantly lower with an average of $\sim 20,000 \text{ cysts m}^{-2} \text{ day}^{-1}$ (Pospelova et al., 2010) compared to Saanich Inlet with an average of $\sim 777,000 \text{ cysts m}^{-2} \text{ day}^{-1}$. Although the studies were conducted over different time periods, the difference in flux magnitudes can at least be partially explained by differences in nutrient inputs, hydrographical conditions, turbidity, stability, and freshwater input. As discussed previously, Saanich Inlet is known to be highly productive due to semi-regular nutrient supply. Whereas the Strait of Georgia may experience moderately limiting nutrient (nitrate) conditions in the summer as the Fraser River plume can act to strongly stratify the water, inhibiting vertical mixing of nutrient rich water to the surface (Mackas and Harrison, 1997).

5.5. Comparison of sediment trap cyst assemblage to surface sediment cyst assemblage

The top $\sim 1.5 \text{ cm}$ of sediment was recovered near the sediment trap location. Sedimentation rates in Saanich Inlet are high, ranging from ~ 5 to 12 mm y^{-1} (Blais-Stevens et al., 1997; Mudie et al., 2002). Thus the sediment sample represents approximately the last few years of sedimentation and is compared to a one year (October 1, 2008–September 26, 2009) average assemblage from the sediment trap. All

taxa comprising greater than 0.05% of the average sediment trap cyst assemblage were recorded in the surface sediment. The overall agreement between the average annual sediment trap cyst assemblage and the surface sediment assemblage is very good (Fig. 6). The Euclidean distance between these two samples was the shortest, at 129, in comparison to 226 other samples from the Northeast Pacific, where the average distance was 435. Thus the average sediment trap assemblage is most similar in its species composition to that of the nearby surface sediment. At the same time, we have noticed that the surface sediment sample contained proportionally more cysts produced by autotrophic taxa (38%) compared to the yearly average of the sediment trap samples (25%), largely due to the higher proportion of *Spiniferites* spp. The other most dominant taxa show a similar relative abundance in both the average sediment trap sample and the surface sediment (Fig. 6).

It is common for surface sediment to contain fewer cysts of heterotrophic taxa compared to sediment trap samples as many heterotrophic taxa have been shown to be more sensitive to degradation via oxidation (Zonneveld and Brummer, 2000; Zonneveld et al., 2007, 2010). For example, Zonneveld et al. (2010) report that the proportion of resistant cysts changes from $\sim 1\%$ in the sediment trap to $\sim 24\%$ in the surface sediment sample, suggesting a factor of ~ 20 depletion of sensitive cysts. In our study, this change is less than a factor of 2, from 24% to 38%. If degradation is a factor, in Saanich Inlet it is a minor one, as a high sediment accumulation rate and relatively low oxygen concentrations, averaging 1.35 ml l^{-1} during the study period (VENUS, 2010), favor good preservation. It should also be recognized that the surface sediment may represent more than one year's worth of deposition and therefore may not precisely reflect the same time period as the average sediment trap assemblage. The fluxes of *Spiniferites* spp. and *S. bentorii* recorded in the trap samples show a large seasonal and year-to-year variation, so that the difference between an average sediment trap assemblage and surface sediment sample assemblage can be easily explained by natural fluctuations in these two taxa.

5.6. Other palynomorphs

In Saanich Inlet primary productivity and sedimentation rates are high, and bottom-water oxygen levels are low throughout the year. The relatively short deployment periods of ~ 6 months and *in situ* preservatives, act to maintain sensitive palynomorphs found in the sediment trap samples.

Tintinnid loricae were abundant throughout many of the sediment trap samples, typically reaching maximum abundances during the spring and summer months (Fig. 5). Chester (1978) collected plankton samples from nearby Strait of Juan de Fuca in 1976–1977 and also found that tintinnids were most abundant during early to late summer, suggesting that there may be a recurring seasonal pattern taking place on a regional scale.

Hexasterias problematica is a species of Prasinophyceae (Parke and Dixon, 1964) that is associated with brackish water and has been observed to increase in abundance near melt-water plumes (Mudie, 1992) and during the Fraser River freshet (Pospelova et al., 2010). In Saanich Inlet the greatest flux of *Radiosperma corbiferum*, an alga suggested to prefer brackish-marine environments (Sorrel et al., 2006) and *H. problematica*, occurs in late May to June when the Fraser River flow is high. This may suggest that these species are associated with the Fraser River freshet. *Keratella* spp. and *Halodinium minor* are most abundant in winter months suggesting a preference for lower SSS or lower SST. Cysts of cf. *Biecheleria* spp. are also most abundant during winter, with the exception of a peak during February 2009 and late May 2009, indicating they may prefer low SSS conditions. Cysts of cf. *Biecheleria* spp. were previously reported as palynomorph type 1 by Pospelova et al. (2010), and found they were most abundant during

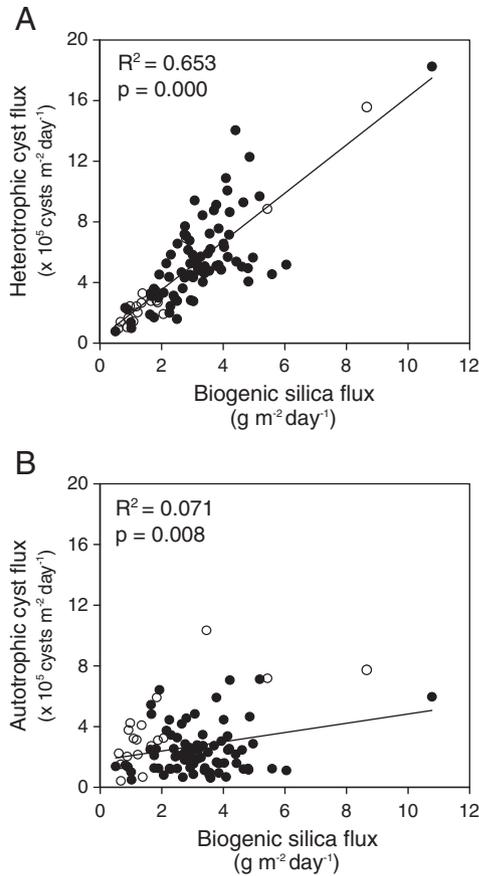


Fig. 10. Relationship between biogenic silica flux and (A) heterotrophic cyst flux and (B) autotrophic cyst flux. Sampling intervals >1 day are shown in solid circles and sampling intervals <1 day are shown in open circles.

summer in the Strait of Georgia when the salinity was low due to the Fraser River freshet.

Copepod eggs and microforaminiferal organic linings did not show clear seasonal trends during the study period. Copepod eggs showed the greatest flux in spring and early summer of 2009 and may be related to increases in primary production or other biological and physicochemical parameters.

Table 4

Coastal organic-walled dinoflagellate cyst sediment trap studies.

Location	Deployment period	Deployment period (years)	Average sampling interval (days)	Water depth (m)	Average cyst flux (cysts m ⁻² day ⁻¹)	Maximum cyst flux (cysts m ⁻² day ⁻¹)	Reference
Gulf of Finland, Baltic Sea	May–Sept 1983	0.4	7	46	N/A	780,000,000 ^a	Heiskanen (1993)
Gulf of Naples, Mediterranean Sea	Aug 1994–Oct 1996	2	15	50	N/A	1,700,000 ^a	Montresor et al. (1998)
Gullmar Fjord, Sweden	May–June 1998	0.06	3	35–55	320,000 ^a	2,700,000 ^a	Godhe et al. (2001)
Benguela upwelling system	Mar–Apr 2001	0.05	~7	50	95,000	176,000	Joyce and Pitcher (2004)
Bahai Concepcion, Gulf of California	Apr 2000–Sept 2001	1.5	14	~25	N/A	1,465,000 ^a	Morquecho and Lechuga-Deveze (2004)
Omura Bay, Japan	July 1998–June 2000	2	14	11	N/A	3,770,000 ^a	Fujii and Matsuoka (2006)
Namaqua shelf, Benguela upwelling system	Jan 2002–July 2005	3.5	26	50	1,400,000 ^a	27,000,000 ^a	Pitcher and Joyce (2009)
Strait of Georgia, BC	Mar 1996–Jan 1999	1.9	11	350	20,000	336,000	Pospelova et al. (2010)
Saanich Inlet, BC	Nov 2007–Feb 2010	2.5	7	97	777,000	2,400,000	This study

^a Includes calcareous cysts.

6. Conclusions

Seasonal and interannual variations in dinoflagellate cyst taxa were recorded from November 2007 to February 2010 in Saanich Inlet. The high-resolution sampling frequency allowed for direct comparison between dinoflagellate cyst production, biogenic silica flux, and environmental parameters. Significant factors affecting cyst production were determined to be SST, SSS, biogenic silica flux and solar insolation.

Cysts produced by autotrophic taxa, in particular *Spiniferites* spp. and *S. bentorii*, were more abundant during winter, whereas cysts produced by heterotrophic taxa dominated during spring, summer and fall. The multi-year deployment period allowed three winter seasons to be compared. The warm, wet and windy winter of 2007/08 had a decreased production of diatoms and increased production of autotrophic dinoflagellates, compared to winters 2008/09 and 2009/10, which had enhanced diatom and heterotrophic dinoflagellate production. Winters showed an increase in *Spiniferites* spp. and *S. bentorii*, and correlated to increased Cowichan River discharge and lower SST. In spring *Q. concreta*, *Brigantedinium* spp., *E. granulatum* and cyst type D increased cyst production. Summer showed a significant increase in *E. delicatum*, *E. cf. delicatum*, *V. spinosum* and cysts of *P. minutum* and demonstrated a high degree of correlation with increased biogenic silica flux, high SST and high solar insolation values. The flux of cysts produced by heterotrophic taxa correlated well with biogenic silica flux, suggesting a strong relationship between diatom production and heterotrophic dinoflagellate production in Saanich Inlet.

The surface sediment cyst assemblage and the average annual cyst assemblage in the sediment trap were similar. The surface sediment had a slightly higher proportion of cysts produced by autotrophic taxa, particularly *Spiniferites* spp. The findings from this study suggest that it would be possible to reconstruct past primary production based on dinoflagellate cysts in Saanich Inlet by analyzing well-laminated sediment cores.

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