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Research paper

Dinoflagellate cyst production over an annual cycle in seasonally ice-covered Hudson Bay

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ABSTRACT

We present continuous bi-weekly to bi-monthly dinoflagellate cyst, tintinnid loricae and tintinnid cyst fluxes at two mooring sites in Hudson Bay (subarctic Canada) from October 2005 to September 2006. The total dinoflagellate cyst fluxes at the site on the western side of the bay ranged from 4600 to 53,600 cysts $m^{-2} day^{-1}$ (average 20,000 cysts $m^{-2} day^{-1}$), while on average three times higher fluxes (average 62,300 cysts $m^{-2} day^{-1}$) were recorded at the site on the eastern side of the bay with a range from 2700 to 394,800 cysts $m^{-2} day^{-1}$. These values are equivalent to the average fluxes calculated from the top 1-cm sediment layer of 210Pb-dated box cores at corresponding locations, and hence lend support to the use of sediment dinoflagellate cysts in palaeoceanography. Tintinnid fluxes ranged from 1200 to 80,000 specimens $m^{-2} day^{-1}$ (average 32,100 tintinnids $m^{-2} day^{-1}$) in the west, and 1600 to 1,240,800 specimens $m^{-2} day^{-1}$ (average 106,800 tintinnids $m^{-2} day^{-1}$) in the east, with the highest *Salpingella* sp. fluxes recorded during the sea-ice cover season.

The dinoflagellate cyst species diversity recorded in the traps was similar at the two environmentally differing locations, with cold-water (e.g., *Echinidinium karaense*, *Islandinium minutum*, *Islandinium? cezare*, *Polykrikos* sp. var. *arctica*, *Spiniferites elongatus*), cosmopolitan (e.g., *Operculodinium centrocarpum*, *Spiniferites ramosus*, *Brigantedinium*) and typical warmer-water (e.g., *Echinidinium aculeatum*, *Islandinium brevispinosum*) species present. Furthermore, the species-specific timing of cyst production behaved similarly relative to the seasonal sea-ice cycle at both locations. Cyst species proportions and species-specific flux quantities, however, differed between the two sites and corresponded to the quantities and species assemblages recorded in the surface sediment, with the exception of cysts of *Polarella glacialis* and cf. *Biecheleria* sp. that seem not to preserve well in sediment but were abundant in both traps. Otherwise, cyst assemblage at the western trap site was dominated by *O. centrocarpum* and *S. elongatus* while at the eastern site very high quantities of cysts of *Pentapharsodinium dalei* were recorded. Our data do not lend support to the hypothesis that trophic status solely determines whether cyst production takes place under-ice or in the open water, since cysts of light-dependent (phototrophic) and light-independent (heterotrophic) dinoflagellates are recorded during both conditions. Most importantly, negligible under-ice cyst production is recorded during the deep arctic winter.

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1. Introduction

Marine phytoplankton and their immediate grazers are excellent tracers of environmental conditions that encumber or enable their growth and reproduction, notably, local and seasonal variability in light availability, nutrient status, temperature, and water-column stability (Margalef, 1978; Falkowski and Oliver, 2007; Cloern and Jassby, 2008; Marinov et al., 2010). Plankton assemblages consist of a large

number of species that exhibit highly species-specific responses to environmental forcing, engendering unique records of multivariate community response to environmental change. Moreover, the turnover rates of phytoplankton biomass are in the order of a week (e.g., Falkowski et al., 1998), enabling virtually immediate reactions to changing habitat conditions in comparison to the response rates of years to centuries for terrestrial higher plants (Walther et al., 2002).

Past phytoplankton communities, and hence, sea-surface conditions in the ocean can be studied using sedimentary remains of common phytoplankton organisms: mainly siliceous frustules of diatoms, organic-walled resting cysts of dinoflagellates, and calcareous plates of coccolithophores. Owing to inherent mixing within the sediment

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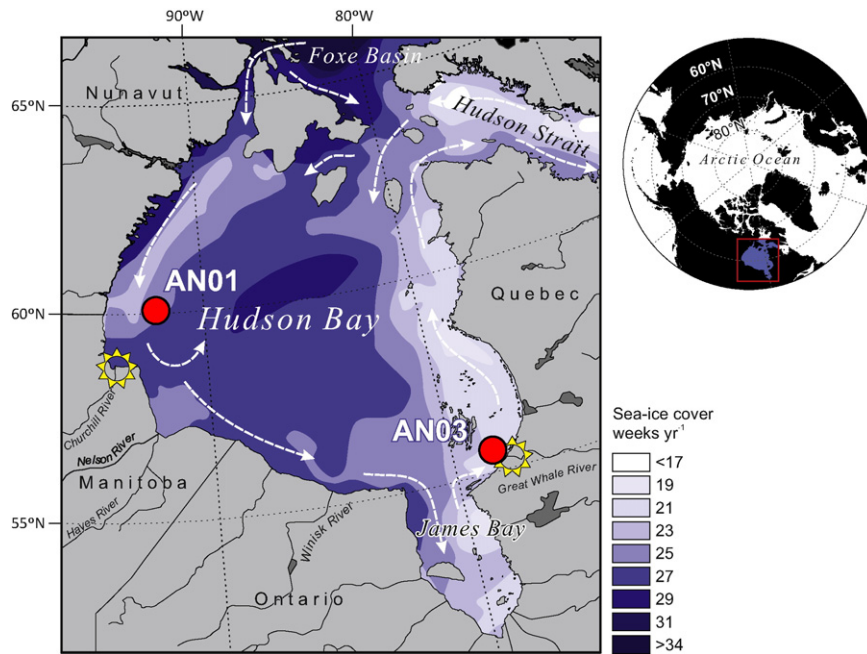


Fig. 1. Locations of the two mooring sites (AN01, AN03) in Hudson Bay, and location of Hudson Bay with respect to the Arctic Ocean. Yellow shapes indicate the two climate stations where solar irradiance data were collected. Annual average (1995–2005) sea-ice cover duration is shown as varying shades of blue, with darker colors corresponding to longer ice-cover times. General surface water circulation is indicated with dashed arrows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

surface layer and generally low marine sediment accumulation rates, the record of phytoplankton dynamics in the upper water column is usually averaged to a temporal resolution from years (coastal sites) to millennia (deep ocean). As a consequence, sedimentary cores or surface samples are not suitable for studying seasonal patterns in the absence of information on seasonal production windows, but they may record long-term changes (decadal or greater) in phytoplankton dynamics including production and dominant species. In certain cases, high quality modern plankton monitoring data, e.g., Continuous Plankton Recorder (Warner and Hays, 1994), may be used to assess the seasonal significance of the species encountered in the sedimentary record. Extensive, long-term biological monitoring data at the species-level are rare, however, and phytoplankton surveys are particularly sparse in remote polar and sub-polar marine regions (Archambault et al., 2010; Wassmann et al., in press; Bluhm et al., 2011). Automated particle-intercepting sediment traps deployed at a depth of interest collect settling particulate matter throughout the year at a selected temporal interval, typically weekly to monthly, and provide crucial information of seasonal plankton dynamics, especially when costly and labor-intensive seagoing monitoring is not feasible year-round. Sediment traps may be retrieved one or more times per year, and the time-slices of settled organic matter analyzed for species composition.

Dinoflagellates comprise autotrophic (light-dependent), heterotrophic (light-independent) and mixotrophic (capable of both photosynthesis and ingestion of prey) microplankton organisms (Taylor, 1987; Jeong et al., 2010). Here we use the term phototrophic for dinoflagellates that are capable of photosynthesis. Life histories of a number of dinoflagellate species alternate between motile planktonic and resting stages, the latter is termed cyst (e.g., Dale, 1983; Pfister and Anderson, 1987; Head, 1996). Production of resting cysts (encystment) is generally indicative of the pelagic bloom (Heiskanen, 1993; Ishikawa and Taniguchi, 1996; Garcés et al., 2004), and in dominantly seasonal marine systems encystment is often an annually recurring event that creates an inoculum for future motile populations. Benthic resting cysts differ from corresponding planktonic dinoflagellates both morphologically and structurally. Motile dinoflagellates are commonly surrounded by cellulosic walls or armour (i.e. theca), whereas most resting cysts are protected by resistant, cell walls composed of carbohydrate-based, structurally variable dinosporin

(e.g. Versteegh et al., 2012; Bogus et al., 2014), enabling excellent preservation in contrast to siliceous and calcareous remains of diatoms and coccolithophores that are subject to dissolution (see however, Zonneveld et al., 1997, 2010b). Consequently, sediment-column dinoflagellate cyst assemblages provide an attractive archive of decadal- to millennial-scale variability in sea-surface conditions (e.g., de Vernal et al., 1997; Rochon et al., 1998; Ellegaard, 2000; Harland et al., 2006; Pospelova et al., 2006; Bouimetarhan et al., 2009; Bonnet et al., 2010; Pieńkowski et al., 2011; Price et al., 2013; Bringué et al., 2014). The striking sea-ice loss in the Arctic seas (–4% per decade of annual average extent and –14% per decade during September sea-ice minimum) (Serreze et al., 2007; Cavalieri and Parkinson, 2012; Stroeve et al., 2012), has a multitude of repercussions, invoking an acute need to understand the natural long-term dynamics of arctic climate and ecosystems beyond the era of satellite observations. Proxy data provide a key element in assessing the resilience of modern-day sea-ice ecosystems to perturbations and defining their pre-anthropogenic variability. Hence, the development and assessment of climate and sea-ice reconstructions in the Arctic is timely and critically needed.

One of the key challenges in the application of sediment dinoflagellate cysts as tracers of past environments, particularly in polar and sub-polar seas, is the limited knowledge of the life-cycle transitions of individual dinoflagellate species (Rochon, 2009; Kremp, 2013): i.e., the seasonal patterns and environmental cues of cyst production and the relationships of sedimentary cysts to their planktonic counterparts are not known. This challenge is not always faced outright since spatial distribution of dinoflagellate cysts in recently deposited surface sediments can be directly linked to modern average surface water conditions via statistical modeling, i.e., “transfer functions”, without the need to consider planktonic motile stages or the transitions in the life cycle. Transfer functions derived from modern data numerically define relations between modern cyst species and environmental variables (Guiot and de Vernal, 2007) and can be applied to sediment-core cyst assemblages to estimate quantitatively past sea-surface conditions, e.g., salinity, temperature, and sea-ice duration (de Vernal et al., 2001, 2005). The transfer function approach can produce high-grade estimates of past environmental variability, but scrutiny and ecological insight are required in the selection of meaningful variable(s) to reconstruct

(Juggins, 2013), and in the design of modern calibration sets (Telford and Birks, 2011). Clearly, the development of transfer functions and the interpretation of qualitative and quantitative reconstructions based on sediment-core assemblages would greatly benefit from the knowledge of the biology and ecology of dinoflagellate life cycle transitions.

There is a handful of studies that portray seasonal sediment trap series of dinoflagellate cyst fluxes, quintessentially located in low- and mid-latitude settings: central (Dale, 1992), southern (Prebble et al., 2013), northwestern (Fujii and Matsuoka, 2006; Shin et al., 2012) and northeastern Pacific (Pospelova et al., 2010; Price and Pospelova, 2011; Bringué et al., 2013), southeastern Atlantic (Susek et al., 2005;

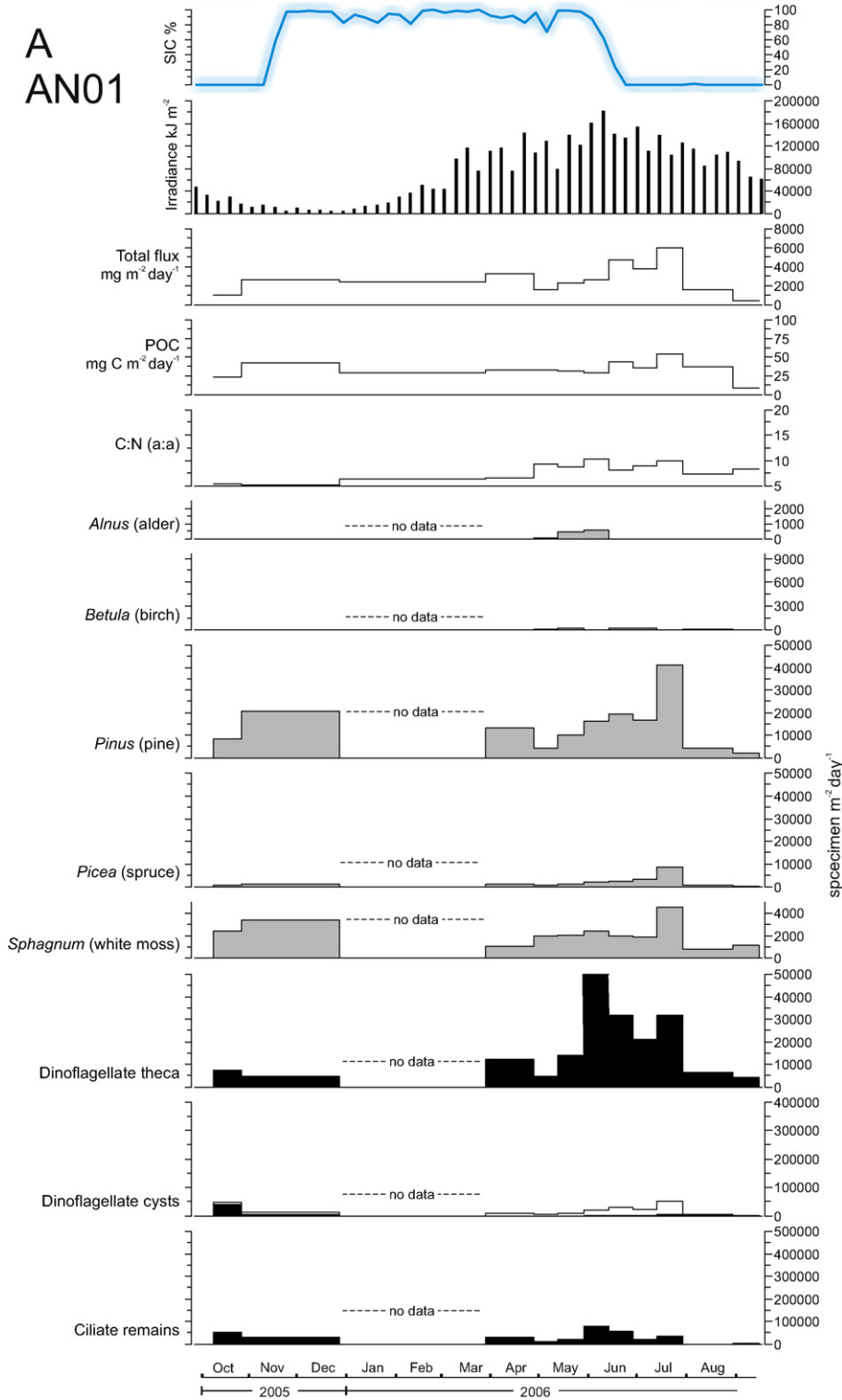


Fig. 2. General annual fluxes at (A) AN01, and (B) AN03, including total fluxes, particulate organic carbon (POC), C:N, pollen fluxes, and overall fluxes of dinoflagellate theca (remains of motile forms), dinoflagellate cysts, and ciliates (tintinnid loricae and cysts). Filled vs. empty silhouettes in dinoflagellate cyst flux panel indicate the proportion of cysts found with vs. without cell content. The two top panels demonstrate the succession of sea-ice cover (concentration in %), and sun light on top of the ice (irradiance in kJ m^{-2}). The X-axis scales are comparable for AN01 (A) and AN03 (B).

Table 1
Dinoflagellate cyst classification, nomenclature and motile stage names attributed to the closest taxonomic unit possible. Where the palaeontological name is not mentioned, the motile stage name is used for the resting cyst stage. 1SAR is a supergroup containing Stramenopiles, Alveolates and Rhizaria (Burki et al., 2007; Adl et al., 2012).

SAR ¹ , Alveolata, Dinoflagellata	
Cyst name (palaeontological)	Dinoflagellate name (biological)
Phototrophic taxa	
Gonyaulacales, Gonyaulacaceae	
<i>Impagidinium</i> Stover & Evitt 1978	<i>Gonyaulax</i> spp.
<i>Impagidinium pallidum</i> Bujak 1984	<i>Gonyaulax</i> sp. indet
<i>Operculodinium centrocarpum</i> sensu Wall and Dale 1966	<i>Protoceratium reticulatum</i> (Claparède & Lachmann) Butschli
<i>Spiniferites elongatus</i> Reid 1974	<i>Gonyaulax elongata</i> (Reid) Ellegaard, Daugbjerg, Rochon, J. Lewis & Harding
<i>Spiniferites ramosus</i> (Ehrenberg 1838) Mantell 1854	<i>Gonyaulax</i> cf. <i>spinifera</i> (Claparède and Lachmann) Diesing
<i>Spiniferites</i> spp. Mantell 1850, emend. Sarjeant 1970	<i>Gonyaulax</i> spp.
Suessiales, Suessiaceae	
–	
cf. <i>Biecheleria</i> sp.	<i>Polarella glacialis</i> Montresor, Procaccini & Stoecker
Peridiniales, Protoperidiniaceae	<i>Biecheleria</i> sp. indet
–	
Heterotrophic taxa	
Gymnodiales, Polykrikaceae	
<i>Polykrikos</i> sp. var. <i>arctica</i> sensu Kunz-Pirrung 1998 (informal description)	<i>Polykrikos</i> sp. indet
–	<i>Polykrikos</i> spp.
Peridiniales, Protoperidiniaceae	
<i>Brigantidium simplex</i> (Wall 1967) ex Lentin & Williams 1993	<i>Protoperidinium conicoides</i> (Paulsen) Balech
<i>Brigantidium</i> Reid 1977 ex Lentin & Williams 1993 spp.	<i>Protoperidinium</i> spp.
<i>Echinidinium aculeatum</i> Zonneveld 1997	Diplopsalid or Protoperidinoid group
cf. <i>Echinidinium delicatum</i> Zonneveld 1997	Diplopsalid or Protoperidinoid group
<i>Echinidinium karaense</i> Head, Harland & Matthiessen 2001	Diplopsalid or Protoperidinoid group
<i>Islandinium brevispinosum</i> Pospelova & Head 2002	<i>Protoperidinium</i> sp. indet
<i>Islandinium minutum</i> (Harland & Reid in Harland & al. 1980) Head, Harland & Matthiessen 2001 emend. Potvin, Rochon and Lovejoy 2013	<i>Protoperidinium</i> sp. indet
<i>Islandinium? cezare</i> (de Vernal & al. 1989 ex de Vernal in Rochon & al. 1999) Head, Harland & Matthiessen 2001	<i>Protoperidinium americanum</i> (Gran & Braarud) Balech
–	<i>Protoperidinium</i> spp.
–	<i>Protoperidinium conicum</i> (Gran) Balech
<i>Selenopemphix quanta</i> (Bradford 1975) Matsuoka 1985	
Indeterminant	
Spiny brown cyst	Unknown
Round brown cyst	Unknown

Pitcher and Joyce, 2009; Zonneveld et al., 2010a), western Indian Ocean (Zonneveld and Brummer, 2000), and Mediterranean Sea (Montresor et al., 1998). As far as we know, there are two studies that probe fluxes

of dinoflagellate cysts underneath sea ice (Harland and Pudsey, 1999; Howe et al., 2010). Harland and Pudsey (1999) placed six sediment traps for 1–2 years in the nepheloid layer of Bellingshausen, Weddell

Table 2
Systematic list of ciliate loricae (choreotrichids), and cysts (oligotrichids) and other palynomorphs found in the samples. Higher level classification follows Adl et al. (2012), ciliate classification Lynn (2008) and incertae sedis World Register of Marine Species. 1SAR is a supergroup containing Stramenopiles, Alveolates and Rhizaria (Burki et al., 2007; Adl et al., 2012).

SAR ¹ , Alveolata, Ciliophora	
Spirotrichea Bütschli, 1889	
Choreotrichia Small & Lynn, 1985, Tintinnida (Kofoid & Cambell, 1929)	Tintinnidae Kofoid & Campbell, 1929
	<i>Salpingella</i> Jörgensen, 1924
	Codonellidae Kent, 1881
	<i>Tintinnopsis</i> Stein, 1867
	Ascampbelliellidae Corliss, 1960
	<i>Acanthostomella</i> Jörgensen, 1927
	Xystonellidae Kofoid & Campbell, 1929
	<i>Parafavella</i> Kofoid & Campbell, 1929
	Ptychocylididae Kofoid & Campbell, 1929
	<i>Ptychocylis</i> Brandt, 1896
Oligotrichia Bütschli, 1887/1889, Strombidiida Fauré-Fremiet, 1970	Strombidiidae Fauré-Fremiet, 1970
	<i>Cyrtostrombidium</i> Lynn & Gilron, 1993
	<i>Strombidium</i> Claparède & Lachmann, 1859
Incertae sedis	
	<i>Radiosperma corbiferum</i> Meunier, 1910
	<i>Halodinium</i> Bujak 1984
	<i>Hexasterias problematica</i> (Cleve) Meunier, 1910
	<i>Palaeostomocystis fritilla</i> Bujak 1984 comb. nov. Roncaglia 2004
	Foraminifera, organic linings
	Invertebrate eggs
	Invertebrate mandibles
	Fungal remains
SAR ¹ , Rhizaria	
Ophistokonta	
Ophistokonta	
Ophistokonta	

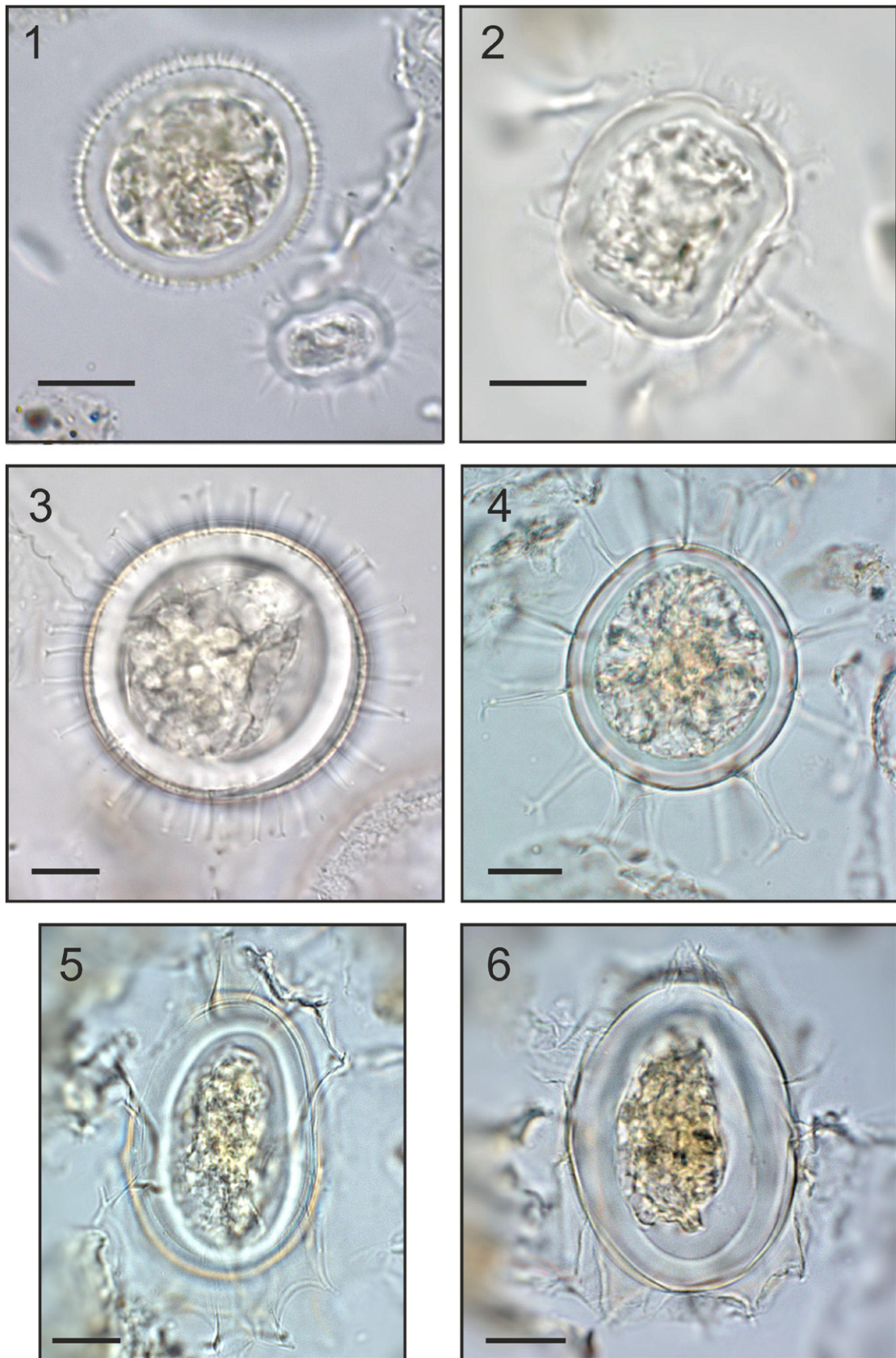


Plate I. Photomicrographs (bright-field images) of dinoflagellate cysts recovered from 2005 to 2006 sediment trap moorings in Hudson Bay, taken with a AxioCamMRC5 microscope camera mounted on a Zeiss Axio10 transmitting light microscope using a EC Plan-Neofluar 100 \times /1.30 oil immersion objective. Black scale bar is 10 μ m. 1. cf. *Biecheleria* sp. (larger round specimen) and *Polarella glacialis* (bottom right corner), optical sections, site AN03, June 1–15 (UVic 11–79). 2. *Pentapharsodinium dalei*, optical section, site AN03, July 16–31 (UVic 11–82). 3. *Operculodinium centrocarpum*, optical section, site AN03, June 16–30 (UVic 11–80). 4. *Spiniferites ramosus*, optical section, AN03, June 16–30 (UVic 11–80). 5–6. *Spiniferites elongatus* s.l., optical sections, site AN01, October 14–31 (UVic 11–61).

and Scotia Seas (Antarctic), and calculated daily cyst fluxes based on the total accumulation over the deployment. They found the highest cyst accumulation outside the sea-ice zone, and dominance of heterotrophic species at all locations, with differing species compositions in relation to sea-ice margin. As the authors note, these data provide average values over the annual or biennial deployment, giving no information about seasonal patterns of cyst production. Howe et al. (2010), on the other hand, analyzed some time slices from a ca. 14-month deployment period in two fjords from Svalbard archipelago, with two samples presenting fluxes under the sea-ice cover and during its breakup. No cysts were recovered from the trap when the sea surface was ice-covered. Interestingly, however, autotroph *Pentapharsodinium dalei* had its peak flux in the summer in the fjord that was ice-covered in the winter, while heterotrophs *Islandinium minutum* and *Selenopemphix quanta* dominated the samples from the other fjord that remained open throughout the year. Globally available surface sediment data demonstrate that the cysts of *I. minutum* and certain other heterotrophic species, particularly *Islandinium? cezare*, the arctic morphotype of the genus *Polykrikos* (*Polykrikos* sp. var. *arctica*), *Echinidinium karaense*, and *Selenopemphix antarctica* (endemic to circum-Antarctic), dominate in marine regions where seasonal ice-cover times are close to a year (Rochon et al., 1999; Mudie and Rochon, 2001; Matthiessen et al., 2005; de Vernal et al., 2013; Zonneveld et al., 2013), and thus their dominance over certain sediment-core intervals has been interpreted as a time period with prolonged seasonal sea-ice cover. It has been assumed that heterotrophic dinoflagellates perhaps dominate over autotrophs in seasonally ice-covered systems because they do not photosynthesize and are better able to cope with reduced periods of light availability. While the above-mentioned “sea-ice indicators” are common in polar seas, it is generally unknown whether the motile life stages producing these cyst types actually thrive in the dark within- or under-ice environments, and whether their encystment occurs inside or under the sea-ice pack, or during the open-water season.

We studied bi-weekly to bi-monthly cyst fluxes using two automated sediment traps deployed close to the seafloor throughout one year (October 2005–September 2006) in western and eastern Hudson Bay, Canadian Subarctic, to document and explain in situ temporal encystment patterns of northern cold-water dinoflagellates. We compare the total annual fluxes and species composition from the traps to the fluxes calculated from modern surface sediments of these two environmentally and biologically distinct locations of the bay (Heikkilä et al., 2014). We then decipher how the seasonal production of different cyst species is linked to sea-ice regime and light availability, and discuss the implications for application of dinoflagellate cyst species for environmental reconstruction.

2. Materials and methods

2.1. Study region

Hudson Bay is a seasonally ice-covered inland sea located in the transition zone of boreal and Arctic Canada. It experiences an annual cycle from fully ice-covered in winter (December–May) to fully ice-free in summer (July–October) (Fig. 1). In western Hudson Bay, where our study site AN01 is located, seasonal sea-ice cover lasts about 4–8 weeks longer than in the eastern part of the Bay, where the study site AN03 lies. The significant freshwater input from ice melt and river discharge in spring is contained in a counter-clockwise circulation gyre along the perimeter of the Bay (Prinsenberg, 1986a, 1986b). On account of the circulation pattern and the substantial input from rivers draining into James Bay, freshwater accumulates in the southeastern and eastern parts of the corridor (Granskog et al., 2011). Hence, even though both of our study sites lie within the freshwater-dominated coastal zone, salinities are higher and summer surface mixed layer depth lower in the west than in the east (Anderson and Roff, 1980; Prinsenberg, 1984; Ferland et al., 2011; Lapoussière et al., 2013). Furthermore, during the open-water season the southeastern region

around trap site AN03 is often the warmest region in Hudson Bay (see Supplementary Table 1) (Galbraith and Larouche, 2011).

Hudson Bay is an oligotrophic system with an estimated annual new primary production of 10–70 g C m⁻² yr⁻¹ (Roff and Legendre, 1986; Sakshaug, 2004; Ferland et al., 2011; Lapoussière et al., 2009). Surface water nutrient availability is limited by strong summertime stratification (Ingram and Prinsenberg, 1998), and the bulk of phytoplankton biomass and marine organic carbon production are concentrated at the polynyas, near-shore and northern regions where coastal currents and upwelling feed the nutrient pool (Kuzyk et al., 2010; Ferland et al., 2011).

Terrigenous organic matter (OM) provides an important contribution to the vertical particle flux in the coastal regions of Hudson Bay, particularly in the east and southeast (Kuzyk et al., 2009, 2010). Furthermore, lateral transport and recycling of sediments play a noteworthy role, manifesting themselves as increasingly oxidized sedimentary OM towards the interior of the Bay (Kuzyk et al., 2011; Hare et al., 2014). The spatial patterns in the quality of sedimentary OM within the Bay indicate that the trap at site AN01 likely records a more marine signature than the trap at site AN03; yet the supply of highly degraded, laterally transported organic sediment is more likely at the former location.

Diatoms are the dominating component in the summer and fall phytoplankton assemblages at the mouth of the Hudson Bay and in Hudson Strait (>80%), while flagellates and dinoflagellates typically represent half of the assemblage and the majority of phytoplankton carbon biomass in Hudson Bay proper (Harvey et al., 1997; Lapoussière et al., 2009; Ferland et al., 2011). Little is known of the phytoplankton composition in spring and winter due to inaccessibility to research vessels, and hence the few studies in the region have concentrated on the near-shore environments, primarily in southeastern Hudson Bay (Michel et al., 1993; Legendre et al., 1996). Average cyst fluxes calculated from surface sediment in the southeast (close to AN03) are over three times higher than in the west (close to AN01), primarily owing to the dominance of the prolific cyst producer *P. dalei* along the eastern shore (Heikkilä et al., 2014). Furthermore, cyst species assemblages on the two sides of the Bay differ distinctly: in the east, *P. dalei* and *Spiniferites ramosus* are the most common autotrophic species, while *Operculodinium centrocarpum* and *Spiniferites elongatus* are typical in the west. Heterotrophs, particularly *Polykrikos* sp. var. *arctica*, are generally more numerous in the west.

2.2. Mooring

Two Technicap PPS 3/3 sediment traps (12 cups; 0.125 m² aperture) were deployed and recovered during ArcticNet annual expeditions on board of the Canadian Coast Guard Ship Amundsen in 2005 and the Canadian Coast Guard Ship Pierre Radisson in 2006, respectively (Lalande and Fortier, 2011). Station AN01 (59°58'N; 91°56'W; water depth = 107 m) was established in western Hudson Bay and station AN03 (55°24'N; 77°55'W; water depth = 136 m) near the mouth of the Great Whale River in southeastern Hudson Bay (Fig. 1). Traps were deployed 20–30 m above the seabed: AN01 at 81 m and AN03 at 100 m depth. The trap sample cups were filled with filtered seawater (Whatman GF/F, nominal pore size of 0.7 μm), poisoned with formalin (5% v/v), buffered with sodium borate, and adjusted to a salinity of 35 with NaCl to preserve samples during deployment and after recovery.

2.3. Light availability

Available light energy was assessed as total solar irradiance (kJ m⁻²) at climate stations in Churchill (58.75°N, 94.07°W, 29.3 m a.s.l) and Kuujuarapik (55.28°N, 77.77°W, 10.4 m a.s.l), corresponding to AN01 and AN03, respectively (Fig. 1). Weekly totals were calculated from modeled hourly global horizontal irradiance amounts derived from Canadian Weather Energy and Engineering Datasets (CWEEDS, 1953–

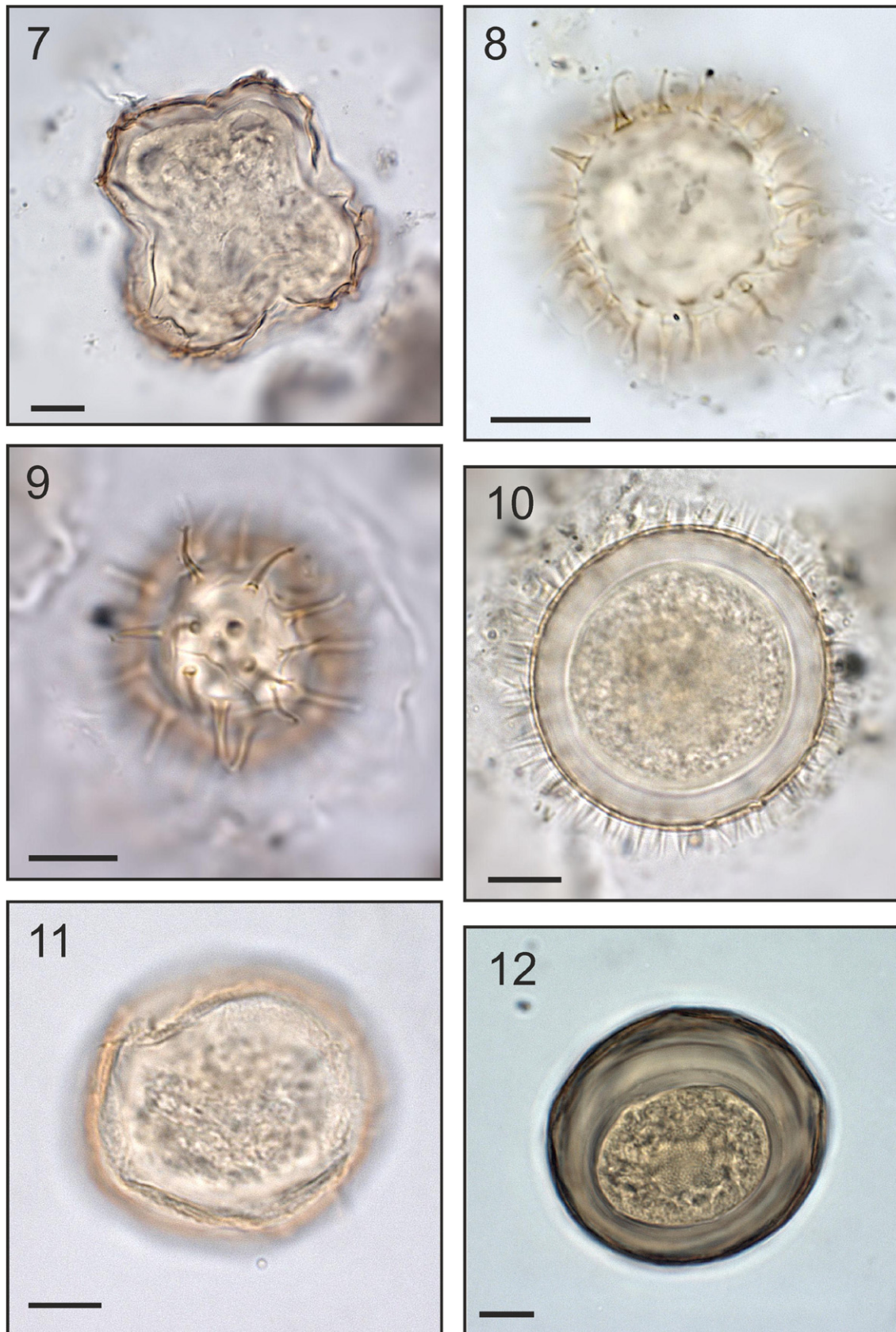


Plate II. Photomicrographs (bright-field images) of dinoflagellate cysts recovered from 2005 to 2006 sediment trap moorings in Hudson Bay, taken with a AxioCamMRC5 microscope camera mounted on a Zeiss Axio10 transmitting light microscope using a EC Plan-Neofluar 100 \times /1.30 oil immersion objective. Black scale bar is 10 μ m. 7. *Polykrikos* sp. var. *arctica*, optical section of a guitar-shaped specimen, AN03 May 16–30 (UVic 11–78). 8. *Echinidinium karaense*, optical section, AN03 June 16–30 (UVic 11–80). 9. *Echinidinium aculeatum*, high focus, AN03 June 1–15 (UVic 11–79). 10. *Islandinium minutum*, optical section, AN03 July 1–15 (UVic 11–81). 11. *Protoperidinium americanum*, mid-focus, AN03 August 1–15 (UVic 11–83). 12. *Brigantedinium* sp., optical section, AN03 June 1–15 (UVic 11–79).

2005), extended by the National Climate Services Canada to the end of year 2006 at the stations concerning this study.

Sea-ice concentrations (%) were derived from remotely-sensed passive microwave sea-ice products of the National Snow and Ice Data Center (NSIDC) (Meier et al., 2013) and are reported as weekly averages for a $0.2^\circ \times 0.2^\circ$ area above the mooring.

2.4. Mass, carbon and nitrogen measurements

Triplicate split samples were filtered with combusted (4 h at 450 °C) GF/F filters, rinsed with distilled water to remove salt, dried for 12 h at 60 °C and weighed. The filters were exposed to concentrated HCl fumes for 12 h to remove carbonates and dried again at 60 °C. Particulate organic carbon (POC) and particulate nitrogen (PN) were analyzed via Perkin Elmer CHNS 2400 Series II elemental analyzer. Mass ($\text{mg m}^{-2} \text{d}^{-2}$) and POC fluxes ($\text{mg C m}^{-2} \text{d}^{-2}$) were averaged for each collection period and should be considered as minimal estimates as they were not corrected for solubilization of organic material.

2.5. Palynomorph extraction and nomenclature

Known proportions of each sediment trap sample were processed in the Paleoenvironmental/Marine Palynology Laboratory at the University of Victoria, Canada, for dinoflagellate cysts according to the preparation protocol by Pospelova et al. (2005). Other organic-walled microfossils, such as pollen grains and spores, zooplankton remains (foraminifer linings, copepod eggs, ciliate loricae and cysts, invertebrate mandibles), as well as remains of dinoflagellate theca were recovered at the same time. Samples were rinsed with deionized water three times to remove salt residue and oven dried at 40 °C. *Lycopodium clavatum* marker grains were added to each sample in order to estimate cyst fluxes (Stockmarr, 1972; Mertens et al., 2009, 2012). Samples were treated with 10% HCl to digest carbonates, sieved with nylon mesh to retain material between 15 and 120 μm , soaked 2–4 days in 48% HF to remove silicates, and treated again with 10% HCl to remove precipitated fluorosilicates. All chemical digestions were made in room temperature acids. Samples were then rinsed, gently sonicated for up to 30 s and collected on a 15- μm nickel mesh. Microscope slides were prepared by mounting ca. 1 ml of homogenized residue in warmed glycerine jelly. Dinoflagellate cysts, pollen, spores and other organic-walled microfossils were identified to species level where possible, using a Zeiss Standard 20 transmitting light microscope with 600 \times and 1000 \times magnifications. On average 410 (min. 102) dinoflagellate cysts and 1387 (min. 340) palynomorphs (total of dinoflagellate cysts, pollen, spores, ciliate loricae and cysts and organic-walled microfossils) were counted per sample.

Higher level taxonomy follows the most recent classification of eukaryotes by Adl et al. (2012), where SAR supergroup containing the groups Stramenopila, Alveolata (including dinoflagellates and ciliates), and Rhizaria was formalized. Dinoflagellate cyst taxonomy follows the palaeontological system according to Fensome et al. (1993), Lentin and Williams (1993), Head et al. (2001), Zonneveld (1997), Pospelova and Head (2002) and Rochon et al. (1999) (Table 1). Tintinnid loricae and ciliate cysts were identified based on Meunier (1910), Bérard-Therriault et al. (1999) and materials derived from World Register of Marine Species (Warren, 2013) and their classification follows Lynn (2008) (Table 2). Some dinoflagellate cyst taxa were grouped for the multivariate statistical analysis. The genus *Brigantedinium* comprises *Brigantedinium simplex* and all unspecified *Brigantedinium* (due to invisible archaeopyle). *O. centrocarpum* consists of *O. centrocarpum* sensu Wall and Dale (1966) that has fully developed processes and other *O. centrocarpum* specimens with short or poorly developed processes (“Type B” or “Arctic morphotype” sensu de Vernal et al. (1989) and Radi et al. (2001)). Undifferentiated *Spiniferites* includes all specimens of the genus except *S. ramosus* and *S. elongatus*. Most of *Polykrikos* specimens in Hudson Bay were assigned to *Polykrikos* sp. var. *arctica* (see also Heikkilä et al., 2014) according to informal descriptions from the Laptev Sea by Kunz-

Pirrung (1998) and in the northern North Atlantic, Arctic and Sub-Arctic dinoflagellate cyst database by de Vernal et al. (2001).

Polarella glacialis and its cysts have been described from sea-ice brine channels in Arctic and Antarctic (Stoecker et al., 1997; Montresor et al., 1999, 2003). However, cyst wall of *P. glacialis* likely is not composed of a structurally resistant type of dinosporin (Montresor et al., 1999), and the long-term preservation in sediment or resistance to chemical sample preparation are unknown. This species is generally not reported in palaeoceanographic studies, but it has been recovered and recorded in surface sediments of Hudson Bay (Heikkilä et al., 2014).

Specimens of cf. *Biecheleria* sp. resemble cysts of *Biecheleria baltica* described from the brackish northern Baltic Sea (Kremp et al., 2005; Moestrup et al., 2009). This taxon has a body diameter ranging from 8 to 22 μm and it is usually observed with cell content. Numerous and evenly distributed processes range from 0.5 and 3 μm . Similar specimens were found in the surface sediments of Hudson Bay (Heikkilä et al., 2014), and have been identified from northeastern Pacific Ocean (Pospelova et al., 2010; Price and Pospelova, 2011; Bringué et al., 2013).

2.6. Multivariate statistical analysis

Constrained ordination was used to summarize species-specific encystment in response to light availability (sea-ice cover and solar irradiance). After data exploration with multiple ordination options, only the data for cysts with cell content were used in an attempt to minimize the influence of resuspended cysts on the analysis. Cyst species data were entered as log-transformed fluxes [$\log(\text{specimen cm}^{-2} \text{a}^{-1})$], to treat log-normal distributions, respectively. First, detrended correspondence analysis (DCA) was performed to decipher the shape of cyst fluxes along the main environmental gradients (Hill and Gauch, 1980). Redundancy analysis (RDA) was selected for constrained ordination, since gradient (DCA Axis 1) lengths 1.8 s.d. for flux data point to mostly linear species responses. Partial RDAs were also run to partition the variance explained by sea ice and irradiance, and their joint contribution (Borcard et al., 1992). Significance of the canonical models was tested with Monte Carlo permutation, and the adjusted coefficients of determination (R^2_{adj}) were calculated according to Peres-Neto et al. (2006) using the formula $R^2_{\text{adj}} = 1 - ((1 - R^2) \times (n - 1)) / (n - m - 1)$, where n is the number of objects (samples) and m is the number of explanatory variables. Traditional R^2 is biased for sample and predictor size, and adjusted values have been corrected for the degrees of freedom in the model. Because R^2_{adj} and adjusted fractions of variation are unbiased estimates, they are generally much lower than unadjusted counterparts (Borcard et al., 2011). In order to assess the predictive power of our model with two predictors (sea ice and irradiance), unconstrained ordination (principal components analysis, PCA) was run on the data. The premise was that since unconstrained ordination attempts to find the underlying gradients in the data (without measured environmental predictors), the first PCA axis represents the best possible environmental variable that theoretically could be found to explain the data structure.

2.7. Comparison with surface sediment data

Dinoflagellate cyst fluxes and assemblages at the two trap sites including cysts with and without cell content were compared with those of the corresponding surface sediment samples (sites 6 and 12 in Heikkilä et al., 2014). Annual total flux data for the traps were calculated over the deployment period and amended with average fluxes for the missing part of the year (ca. 1 month); assemblage data were calculated as average proportions. Annual fluxes for the surface sediment sites were calculated from the top 1-cm samples based on sediment velocities and accumulation rates (Kuzyk et al., 2009); compositional data were raw percentages (Heikkilä et al., 2014). Two dissimilarity measures were used: the chord distance that is more sensitive to cyst assemblage composition (“quality” of the sample) and the Euclidean

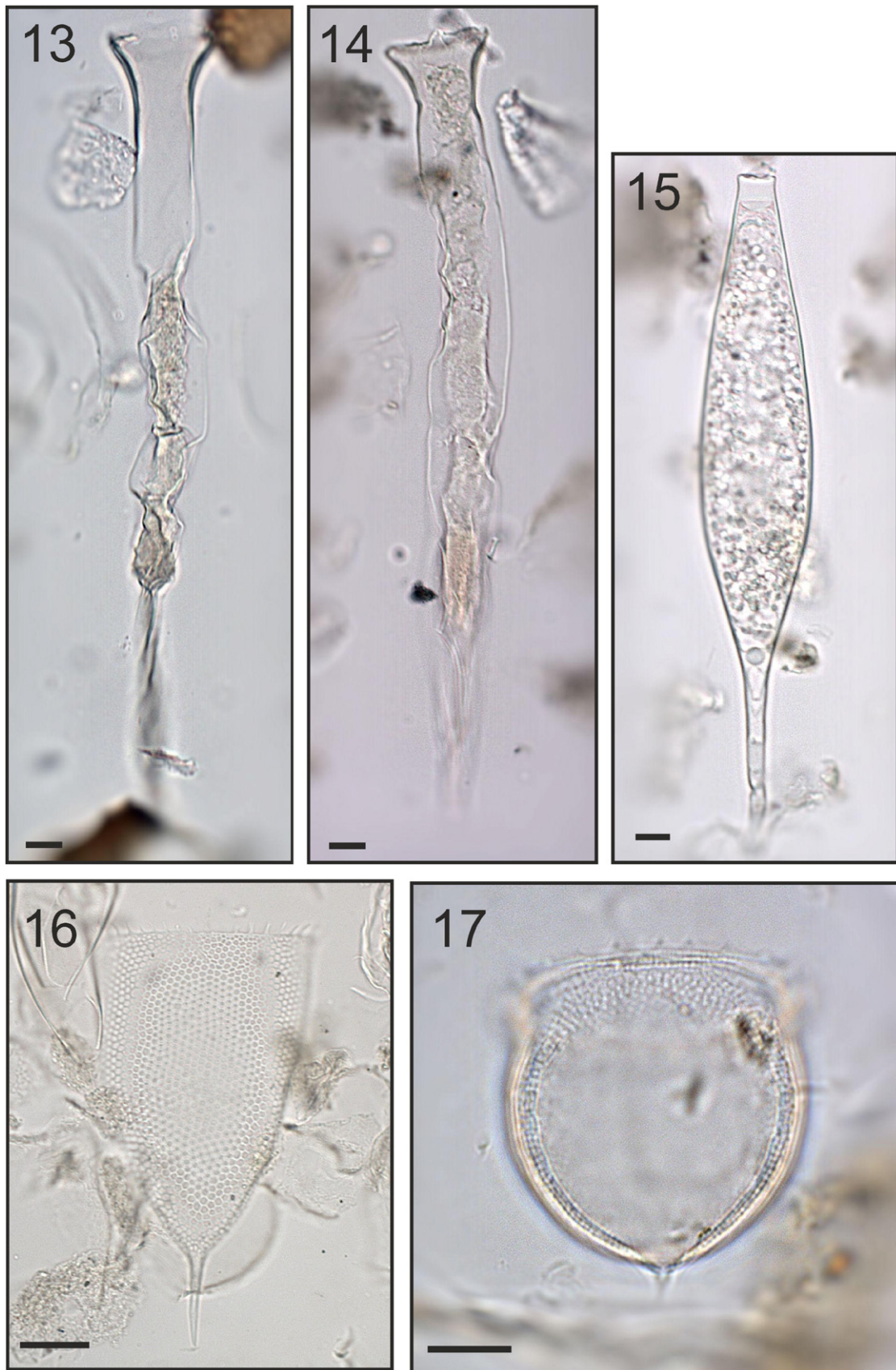


Plate III. Photomicrographs (bright-field images) of tintinnids recovered from 2005 to 2006 sediment trap moorings in Hudson Bay, taken with a AxioCamMRC5 microscope camera mounted on a Zeiss Axio10 transmitting light microscope using a EC Plan-Neofluar 40 \times /0.75 (images 1–3) or EC Plan-Neofluar 100 \times /1.30 oil immersion objective (images 4–5). Black scale bar is 10 μ m. 13–14. *Salpingella* sp. loricae, AN03 January 1–March 31 (UVic 11–75). 15. *Cyrtostrombidium* sp. cyst, AN03 June 1–15 (UVic 11–79). 16. *Parafavella* sp. lorica, AN03 June 16–30 (UVic 11–80). 17. *Acanthostomella* sp. lorica, AN01 (UVic 11–67).

distance that uses untransformed data and hence reflects the scale of the descriptor (here fluxes and percentages). Euclidean distance mirrors the dominant cyst taxa and totals (“quantity” of the sample).

3. Results

3.1. Seasonal cycle of light availability

Consolidated sea ice (sea-ice concentration (SIC) >80%) covered the western trap site (AN01) for approximately seven months from mid-November to mid-June (top panel of Figs. 2A, 3A and 4A). At the eastern site (AN03), freeze-up began about one month later (mid-December) and breakup about one month earlier (mid-May), and duration of sea-ice cover was about five months (top panel of Figs. 2B, 3B and 4B). At both sites the freeze-up was completed in a week, whereas the breakup from consolidated ice to open water took about 1–2 weeks. Solar irradiance at Kuujjuarapik and Churchill stations increased in April, when the trap sites were still ice-covered, and exhibited maxima in May–June (second panel in Figs. 2, 3 and 4).

3.2. Mass, carbon and general fluxes

Seasonal variation in total mass and POC fluxes, C:N (a:a) ratios, and general fluxes of pollen, dinoflagellate theca, cysts and ciliates are presented in Fig. 2 together with SIC and irradiance. Mass and POC fluxes at AN01 were highest (4–6 g m⁻² day⁻¹ and 45–55 mg m⁻² day⁻¹, respectively) after the ice breakup in July, but there was a continuous flux of material to the trap throughout the year (Fig. 2A). C:N ratios vary between 5 and 7 in fall and winter and 7–10 during the breakup and in early summer. At AN03, mass and POC fluxes in spring and summer were lower than at AN01 (1.5–2.5 g m⁻² day⁻¹ and 20–30 mg m⁻² day⁻¹), but C:N ratios were higher (7–18), particularly in under-ice spring samples (13–18, Fig. 2B). Before the freeze-up in November–December a massive particle flux of 38 g m⁻² day⁻¹ (85 mg POC m⁻² day⁻¹) was deposited in the trap, characterized by an elevated C:N ratio (17.6).

Pollen fluxes, particularly at AN03, present a standard phenological spring sequence starting with alder (*Alnus*), followed by birch (*Betula*) and conifers (*Pinus* and *Picea*), but significant quantities of pollen of these trees and spores of *Sphagnum* mosses were also deposited in November–December outside the flowering season. At AN03 this took place concurrently with the anomalously high mass and POC fluxes. Total fluxes of dinoflagellate theca were highest during the open-water season, while copious amounts of theca also settled into the trap underneath spring pack ice. Total dinoflagellate cyst and ciliate fluxes exhibited distinct peaks in the open-water season in June–November, often simultaneously for both groups.

3.3. Dinoflagellate cyst fluxes

Average dinoflagellate cyst flux was ca. 20,000 cysts m⁻² day⁻¹ at site AN01 (min 4600 m⁻² day⁻¹, max 53,600 m⁻² day⁻¹), and approximately threefold higher, ca. 62,300 cysts m⁻² day⁻¹ (min 2700 m⁻² day⁻¹, max 394,800 m⁻² day⁻¹), at site AN03, respectively (Fig. 2, second lowest panel). Overall, dinoflagellate cyst fluxes at the two sites (Fig. 3) portray species-specific patterns of seasonal cyst production, particularly at AN03 (Fig. 3B). At AN01, the majority of the cysts of heterotrophs were found without cell content throughout the year (Fig. 3A). Cysts of ice-dwelling autotroph *P. glacialis* were deposited in a pulsed manner after the ice breakup, concurrently with cysts of cf. *Biecheleria* sp. Cyst fluxes of other autotrophic dinoflagellates (*P. dalei*, *O. centrocarpum*, *S. ramosus*, *S. elongatus*) peaked in October at AN01, and in the end of July and November–December at AN03. Heterotrophic dinoflagellate cysts found during and immediately after the ice breakup were *Polykrikos* sp. var. *arctica*, *E. karaense*, *Echinidinium aculeatum*, *Islandinium brevispinosum* and *I.? cezare*, whereas summertime open-

water cyst producers were *I. minutum*, *Brigantedinium*, cf. *Echinidinium delicatum* and *Protopteridinium americanum*. During the dark winter months cyst fluxes were negligible; no data are available for January–March at site AN01. (See Plates I–II for photomicrographs of typical cyst specimen).

3.4. Dinoflagellate theca and other palynomorph fluxes

Fig. 4 presents fluxes of other microscopic remains of organic-walled organisms: dinoflagellate theca (armours of motile stage), ciliate loricae and cysts, copepod eggs, foraminifer linings, invertebrate mandibles, and arcitarchs (“of unknown origin”) *Halodinium*, *Hexasterias problematica*, and *Radiosperma corbiferum*. Average fluxes of tintinnid loricae and cysts are higher than those of dinoflagellate cysts at both sites: from 1200 to 80,000 specimens m⁻² day⁻¹ (average 32,100 tintinnids m⁻² day⁻¹) at AN01, and from 1600 to 1,240,800 specimens m⁻² day⁻¹ (average 106,800 tintinnids m⁻² day⁻¹) at AN03. (Fig. 2, lowest panel). Again, fluxes of these specimens show clear spring and summer sequences at AN03, but patterns at AN01 are somewhat equivocal. Notably, at both sites *Protopteridinium* theca were deposited in copious amounts under the ice cover in April–May. At AN03, cysts of ciliates *Strombidium* and *Cyrtostrombidium* were deposited during and after ice breakup, whereas other ciliate remains were found in high quantities at the end of July and in November–December concurrently with phototrophic dinoflagellate cysts. These include arctic-boreal genera *Parafavella* and *Ptychocyclus*. Loricae of *Salpingella* were the only specimens found exclusively during the winter months. At AN01, clear peaked patterns are not as obvious, although most dinoflagellate theca and ciliate remains types exhibited highest fluxes during the ice breakup. Remains of zooplankton and other predators were generally found at the same time with high dinoflagellate cyst and ciliate fluxes. (See Plates III for photomicrographs of ciliate remains).

3.5. Relation of cyst species to light availability

Constrained ordination, here RDA, extracts structures in the species data set that are related to predictor variables. Hence, when interpreting the biplot in Fig. 5, one has to keep in mind that our analysis seeks to explain the distribution of the samples and species in relation to sea ice and irradiance, but does not state that those two are the sole factors influencing cyst production.

The two canonical RDA axes explain 20.3% of variation in cyst flux data or 11.9% when accounted for bias (Fig. 5, Table 3). The variation partitioning with unbiased proportions shows that irradiation explains slightly larger part of the variation than sea ice (Fig. 6, Table 3), and only 1.6% of the total variation is explained by their shared effects. A similar conclusion can be drawn from low variation inflation factors in RDA and the low correlation coefficients of SIC and irradiation (diagnostics not shown). The proportion of unexplained variation is notable (88.1%), but not uncharacteristically large for ecological data. A PCA run with the same samples found that the first axis explained 38.4% of total variation in flux data, illustrating the proportion explained by a theoretical environmental variable with highest possible explanatory power. This value can be compared with the variation explained by the RDA model with sea ice and irradiance (20.3%, adjusted estimate 11.9%), showing that the PCA has about three-fold higher explanatory power than RDA model with bias-corrected axes.

The RDA biplot (Fig. 5) demonstrates that, in general, the cyst fluxes are either negatively related to or not related to sea ice concentration. Roughly similar patterns were derived when cysts without cell content were included in the analysis, and when the sites were treated separately. Additionally, fluxes of some cyst species (*Polykrikos* sp. var. *arctica*, *P. glacialis*, *E. karaense*) increase with higher irradiance, whereas cyst fluxes of other species (*S. ramosus*, *S. elongatus*, *P. americanum*, *P. dalei*, *O. centrocarpum*) are higher with lower irradiances.

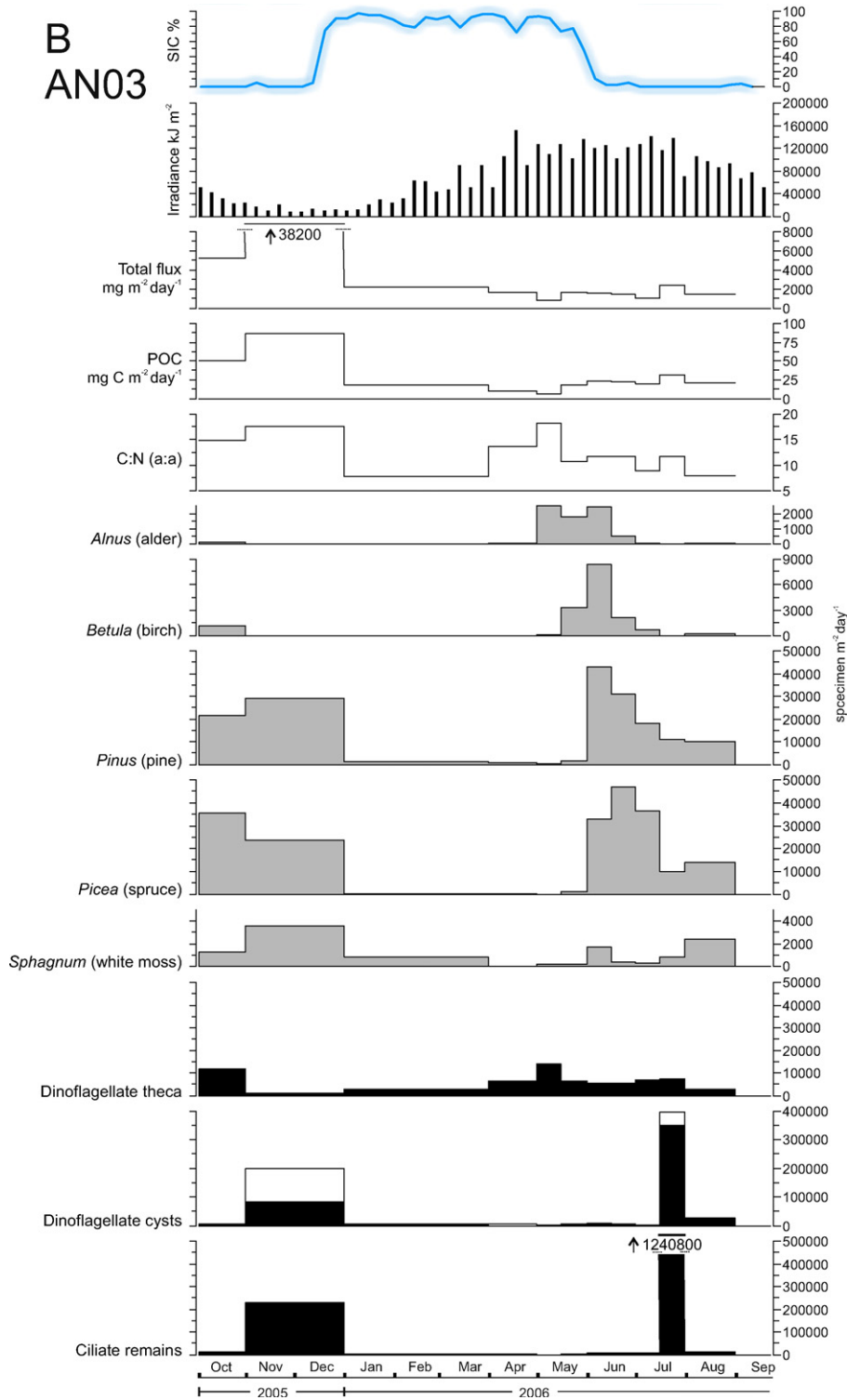
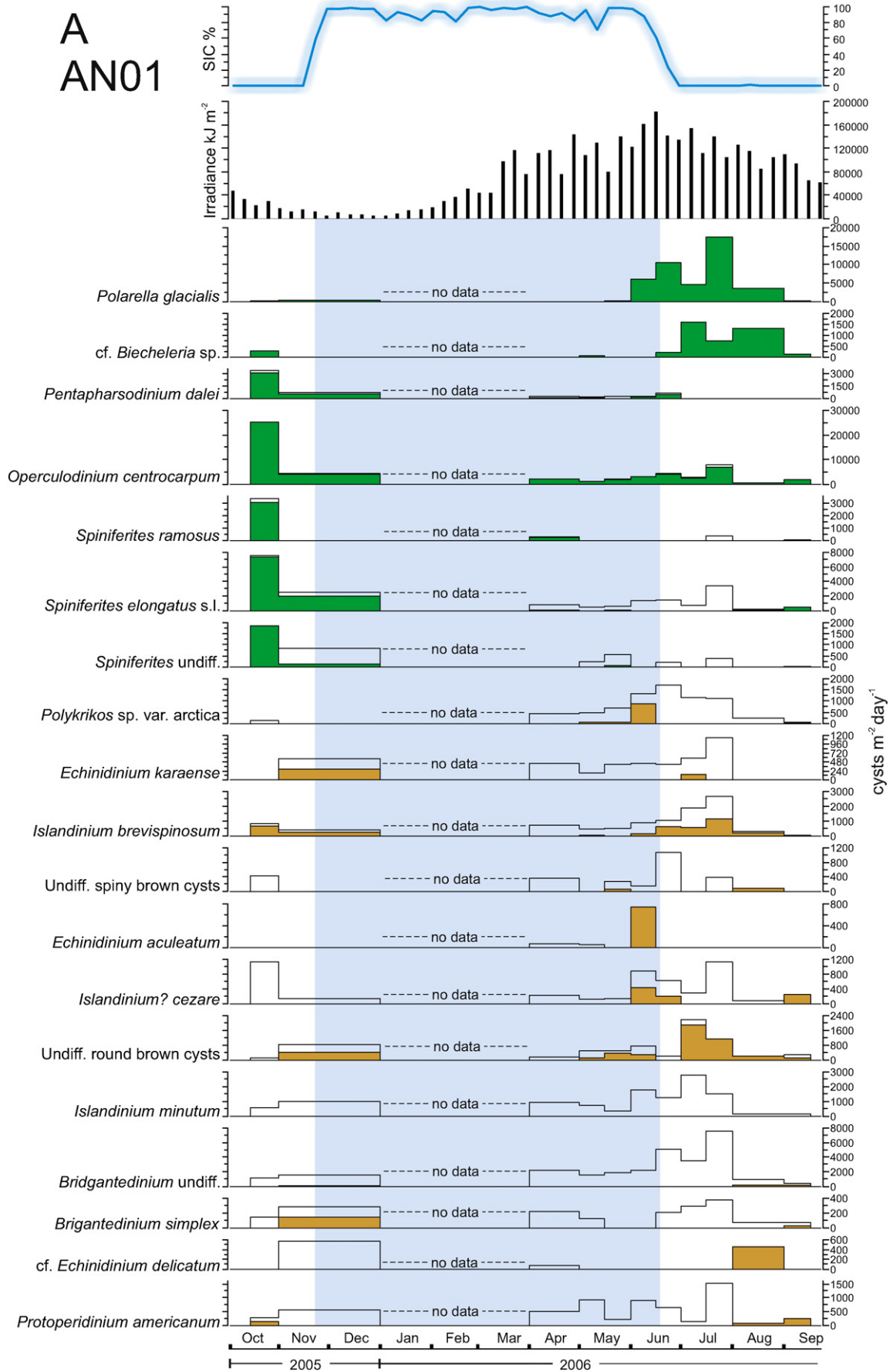


Fig. 2 (continued).

3.6. Comparison with surface sediment data

Dinoflagellate cyst fluxes from October 2005 to September 2006 at the two trap-mooring sites are concordant with average fluxes and composition at corresponding surface sediment sites, with three-fold dinoflagellate cyst fluxes recorded in the eastern location compared

to the western location when assessed by trap data and the surface sediment layer of ²¹⁰Pb-dated box-cores. Furthermore, the estimated average fluxes based on the trap data and the surface sediment data are very close to each other: 62,300 cysts m⁻² day⁻¹ vs. 65,700 cysts m⁻² day⁻¹ for the eastern sites and 20,000 cysts m⁻² day⁻¹ vs. 20,500 cysts m⁻² day⁻¹ for the western sites. Some differences



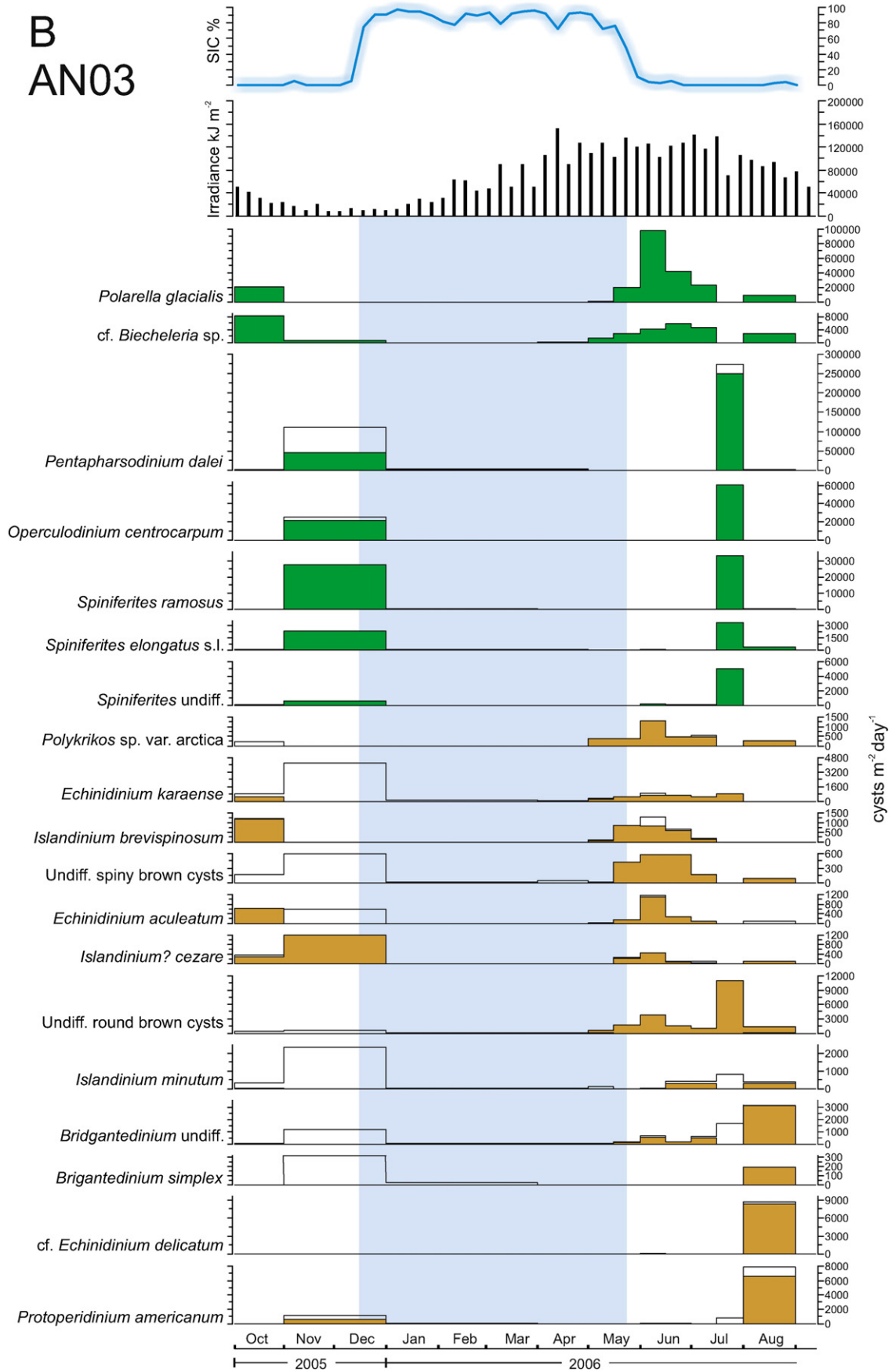


Fig. 3. Dinoflagellate cyst fluxes at (A) AN01, and (B) AN03. Phototrophic taxa are indicated with green and heterotrophic with orange silhouettes, while filled vs. empty silhouettes indicate the proportion of cysts found with vs. without cell content. The two top panels demonstrate the succession of sea-ice cover (concentration in %), and sun light on top of the ice (irradiance in kJ m^{-2}), pale blue shading denotes the ice-covered season ($\text{SIC} > 50\%$). Note that the X-axis scales are different for AN01 (A) and AN03 (B).

were exhibited in the species composition, however: cysts of *P. glacialis* and cf. *Biecheleria* sp. are present in high quantities in the traps but are a minor contributor to surface sediment assemblages (Fig. 7). When

compared with each other and with surface sediment data, the two trap sites exhibit highest similarity to the underlying surface sediment, with respect to both fluxes and compositions (Table 4).

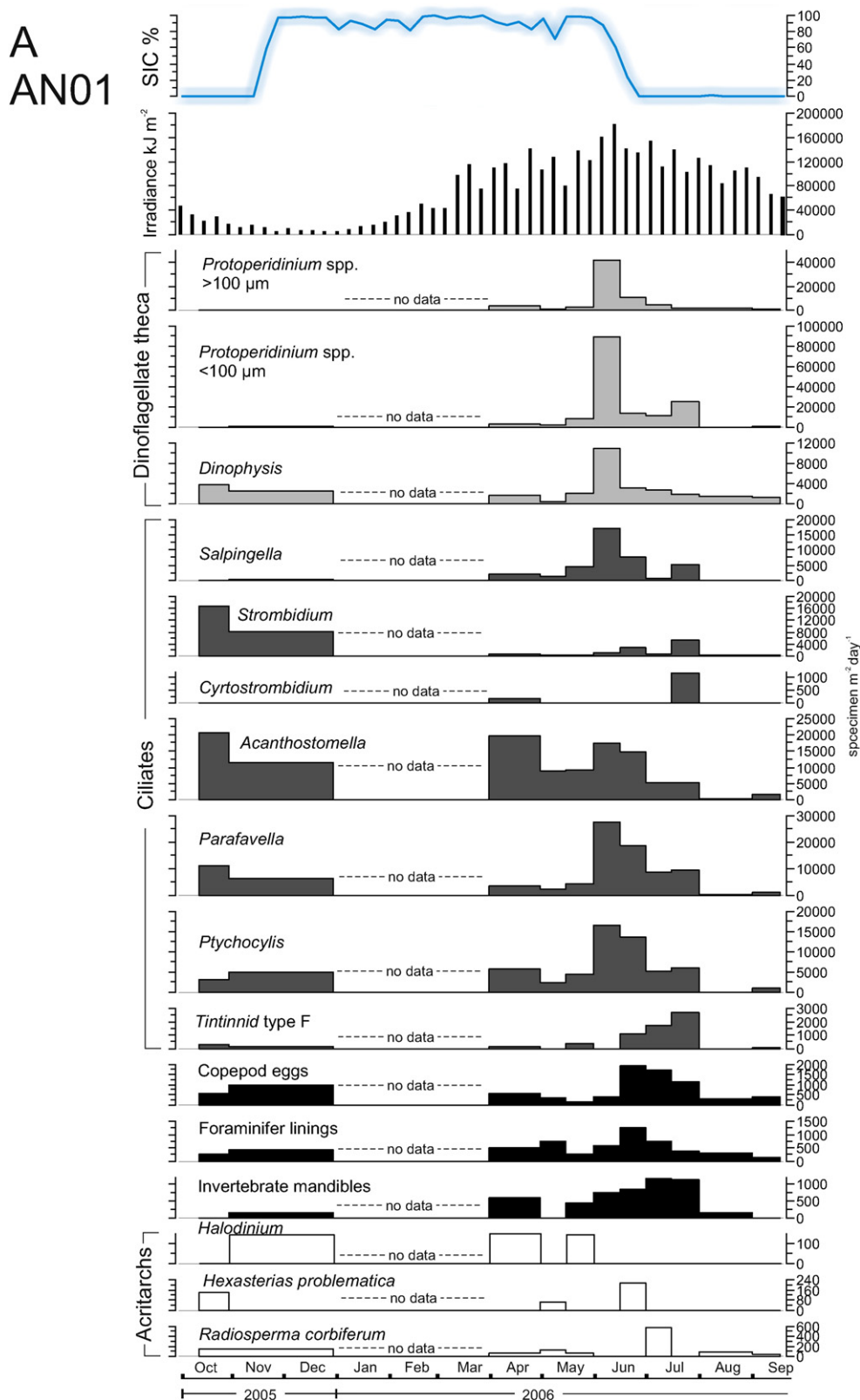


Fig. 4. Species-specific fluxes of observed dinoflagellate theca, ciliate loricae and cysts, microscopic remains of predators, and commonly known marine palynomorphs of unknown origin (acritarchs) at (A) AN01, and (B) AN03. Note that the X-axis scales are different for AN01 (A) and AN03 (B).

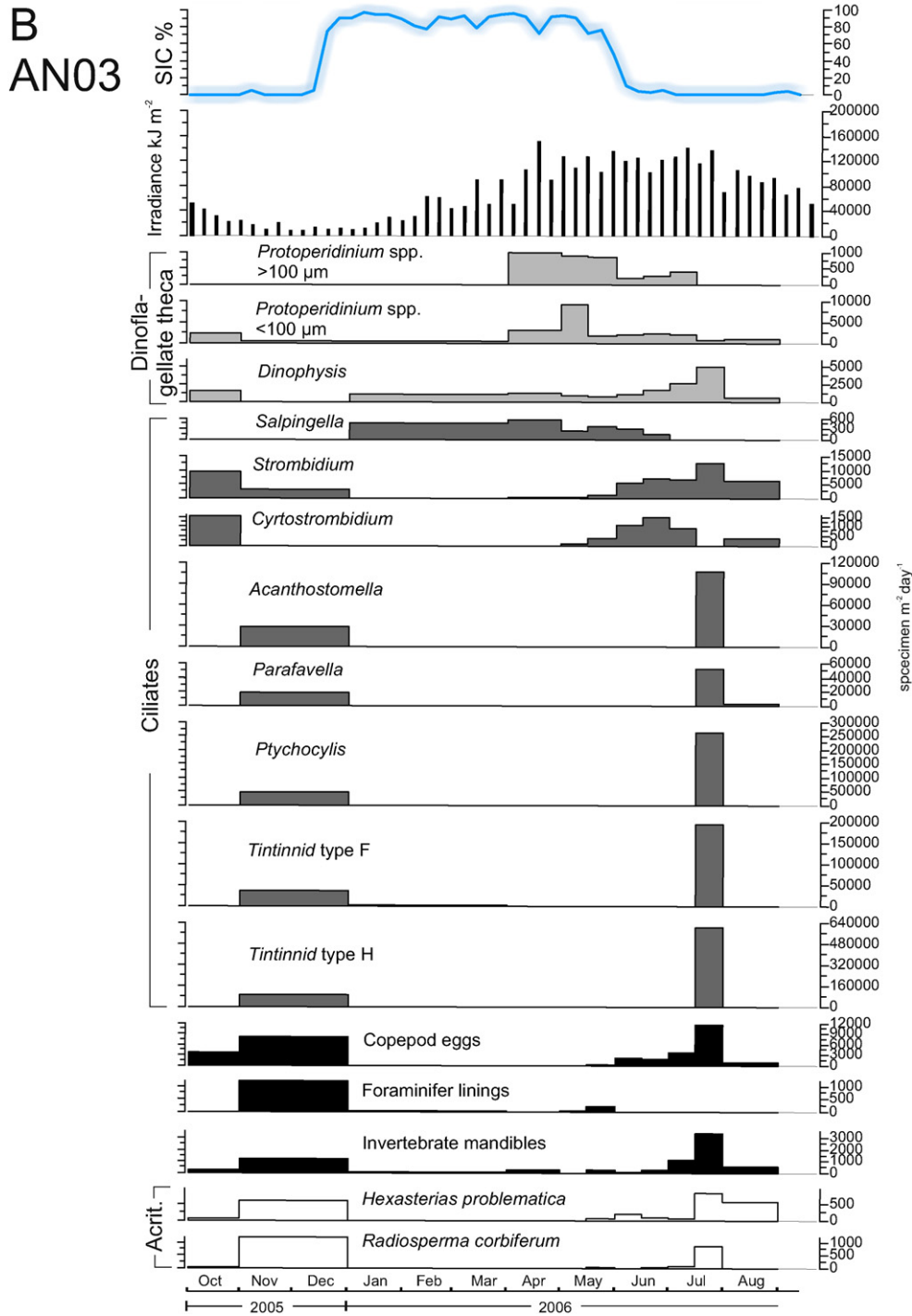


Fig. 4 (continued).

4. Discussion

This study presents continuous sequences of seasonal dinoflagellate cyst production at two environmentally different sites of a seasonally ice-covered marine ecosystem. The data allow two overarching messages: (1) seasonal cyst production of high-latitude dinoflagellates exhibits species-specific patterns where the waxing and waning seasonal ice cover governs the beginning and the end of the succession, while site location has most relevance to species-specific flux quantities, and (2) trophic status does not determine the timing of cyst production relative to seasonal light availability, and there is no evidence for either

autotrophs or heterotrophs producing cysts in the midwinter of Hudson Bay. These two outcomes and their implications will be discussed in detail below. First, however, the presence and role of reworked sediment material in the trap records will be examined to aid further discussion of the results.

4.1. Constraints of sediment trap data

While sediment traps provide a unique method to collect continuous data for seasonal and inter-annual cyst production in situ in an ocean with seasonal ice cover, the assessment of the record may be hampered

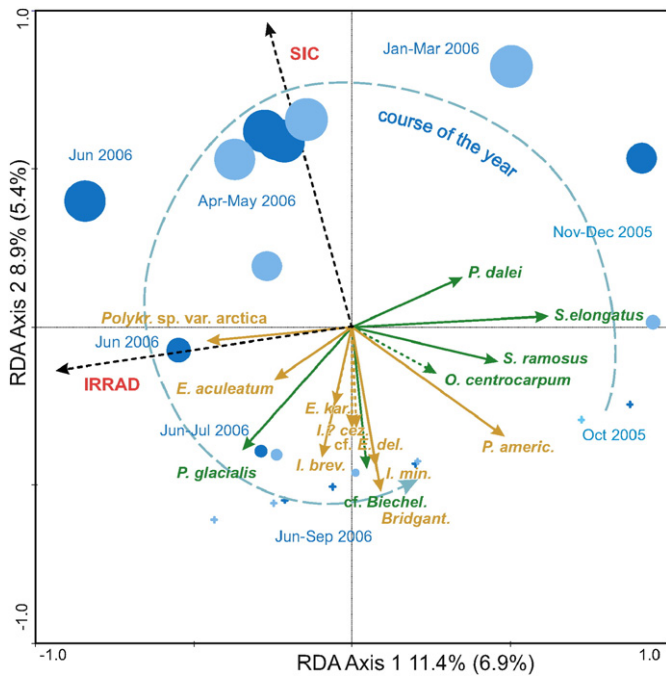


Fig. 5. Correlation biplot of redundancy analysis (RDA) on cyst fluxes (only cysts with cell content) displaying the cyst species responses to sea-ice concentration (SIC) and irradiance (IRRAD). Both sites were included in the analysis: samples from AN01 are marked with darker blue circles/crosses and samples from AN03 with paler blue circles/crosses, respectively. Increasing size of the circle refers to increasing SIC, and samples marked with crosses indicate SIC = 0%. Dashed blue line sketches the approximate course of the year in Hudson Bay from October 2005 to September 2006 (the arch would be slightly larger for AN01 and slightly smaller for AN03). Green and brown arrows are phototrophic and heterotrophic taxa, respectively. Dashed species arrows refer to species with <15% fit in the model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by hydrodynamical interactions between currents and traps (trapping efficiency), and collection of resuspended sediments from the seafloor sediments (Gardner et al., 1983; Buesseler et al., 2007). The latter process is particularly relevant in the offshore areas of Hudson Bay where a major share of OM supply appears to comprise resuspension and lateral transport of sediments deposited in shallow coastal water (Kuzyk et al., 2009). Accordingly, one can assume that the vertical particle flux collected by the western offshore trap AN01 is mixed with seabed-derived OM to a larger extent than that of the eastern coastal trap AN03. An additional point for consideration when interpreting sediment trap data is the potential time lag caused by the transport of organic matter from surface waters to the sea floor. Since marine aggregates and phytodetritus generally have sinking rates in the order of dozens and even hundreds of meters per day (Turner, 2002), and as our traps were installed at ca. 100-m depth, in our case this time lag is probably not relevant.

A few simple features in our data help assess the role of resettled material. First, if cysts are recently produced they are more likely to be found with cell content. Thus, a higher proportion of cysts found with

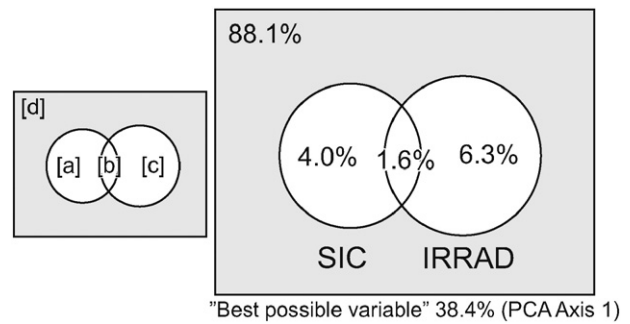


Fig. 6. Partitioning of variance in cyst flux data, explained by sea-ice concentration (SIC) and irradiance (IRRAD). Variation explained by [a] solely SIC, [b] SIC and IRRAD together, [c] IRRAD alone, and [d] unexplained part of variation. Capability of any one theoretical environmental variable to explain the data structure is indicated as the "best possible variable".

cell content indicates a higher probability of the record to be of surface-water origin (Fig. 3, filled vs. empty silhouettes). However, mandatory maturation and hatching times of dinoflagellate cysts vary greatly among species (Pfeister and Anderson, 1987), and even recently produced cysts of species with brief hatching times may be found empty (Price and Pospelova, 2011). These species-specific differences are not always discernible in our data, although phototrophic species are generally found with cell content while heterotrophs are more commonly found empty. At AN01, the cyst fluxes of most heterotrophs and spring-time fluxes of Spiniferites species consist predominantly of empty cells (Fig. 3A). Conversely, the AN03 record comprises mainly cysts with cell content, with the exception of fall fluxes of cysts of some heterotrophs (Fig. 3B). This may indicate that at AN01 partially resuspended and laterally transported bottom sediments are mixed with the vertical particle flux. Second, we measured pollen fluxes of terrestrial tree/shrub species that are known to flower during different seasonal time windows. If pollen was derived aerially or via spring and summer riverine inputs, a phenological sequence starting with alder (*Alnus*), followed by birch (*Betula*), pine (*Pinus*) and spruce (*Picea*), should be discernible (e.g., Nikolov and Helmisaari, 1992; Linkosalo et al., 2009). Corresponding spring sequence is demonstrated distinctly at AN03, while it is vague at AN01 (Fig. 2), further indicating that resuspension of bottom sediments disrupts the AN01 record. However, conifer pollen and Sphagnum spores are also found in the fall (October–December) samples of both sites (Fig. 2), which could be due to either riverine input of pollen stored in soils over the summer, or sediment resuspension. Third, concurrent peaks of all or most of the specimens in the flux record, particularly if simultaneous with high flux totals, points to resuspension. Such occasions are evident at the end of July at AN01 and in November–December at AN03; the latter period takes place in conjunction with very high total matter and POC inputs (Fig. 2B) that could be due to frequent high winds (>50 km h⁻¹) in Kuujuaarapik (Fig. 1) measured at that time (Lalande and Fortier, 2011). For comparison, during the rest of the study period equally high winds were only recorded sporadically. Based on the three measures discussed above it appears that particularly the AN01 record needs to be interpreted carefully,

Table 3
Decomposed variation from partial RDAs on flux data of dinoflagellate cysts with cell content at both sites (AN01, AN03). Fractions of variation [a, b, c, d] refer to the Venn diagram in Fig. 6, where only adjusted values (R^2_{adj}) are used (marked in bold). *P*-values were considered significant at $P \leq 0.05$.

	Proportion (%) of variation (R^2)	Adjusted proportion (%) of variation (R^2_{adj})	% of explained variation (R^2_{adj})	<i>P</i> -value of the model
Sea-ice and irradiance [a + b + c]	20.3	11.9		0.02
Sea-ice [a + b]	10.1	5.6	47%	0.05
Irradiance [b + c]	12.3	7.9	66%	0.02
[a]	8	4.0	34%	
[b]	2.1	1.6	13%	
[c]	10.2	6.3	53%	
[d]	79.7	88.1		

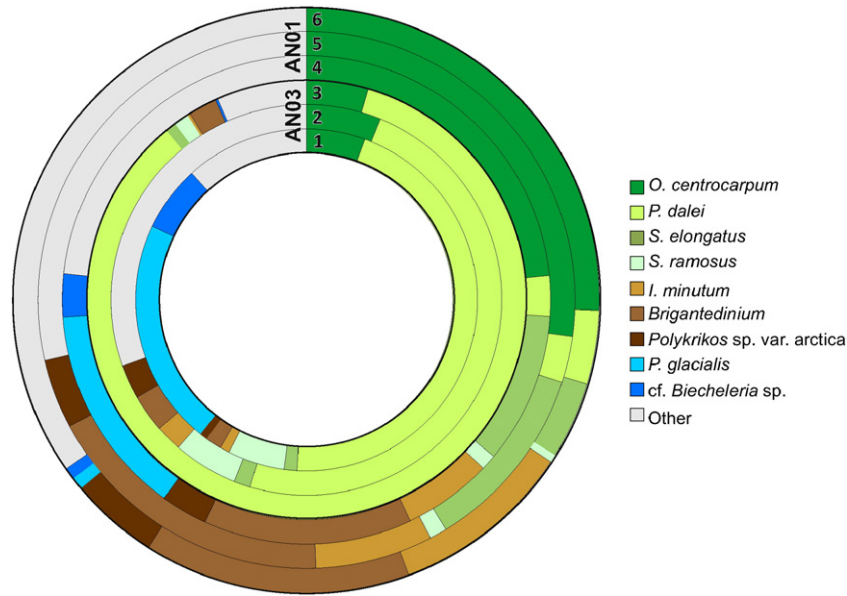


Fig. 7. Comparison of the dinoflagellate cyst assemblages in surface sediment (top 1 cm) and sediment traps (whole year). 1. AN03 trap data, 2. AN03 trap data excluding *Polarella glacialis* and *cf. Biecheleria* sp., 3. Surface sediment close to AN03 (site 6 in Heikkilä et al., 2014), 4. AN01 trap data, 5. AN01 trap data excluding *Polarella glacialis* and *cf. Biecheleria* sp., 6. Surface sediment close to AN01 (site 12 in Heikkilä et al., 2014). Phototrophic species are denoted with shades of green except for *Polarella glacialis* and *cf. Biecheleria* sp. that are denoted with shades of blue; heterotrophic species are colored with shades of brown.

concentrating on the fluxes of cysts with cell content. In addition, the November–December sample at AN03 may contain notable quantities of resuspended material. Overall features of the seasonal cycle in Hudson Bay.

The progression of seasons in Hudson Bay is distinctly delimited by the freeze-up and breakup of sea ice (top panel of Figs. 3, 4, 5, Table 5). As discussed above, the interpretation of our trap records over the fall period 2005 is hampered by potential inclusion of resuspended sediments at both sites. Nevertheless, it is conceivable that some of the key species in the record are late cyst producers, or exhibit multiple cyst production maxima; i.e., one in spring and another in fall (Fig. 3). This behaviour is typical for dinoflagellates in temperate regions, where seasonality is less pronounced and cyst production of phototrophic dinoflagellates, in particular, can take place throughout the year or as multiple seasonal events (Pospelova et al., 2010; Price and Pospelova, 2011). Interestingly, a recent study finds that contemporary lengthening of open-water seasons in the Arctic has led to an appearance of second phytoplankton bloom in the fall, particularly in regions where late season storminess induces vertical mixing, such as the coastal corridor of Hudson Bay (Ardyna et al., 2014). It is hence difficult to discern what proportion of cyst deposition in October–December 2005 (Fig. 3) is due to storm-induced sediment resuspension, and what proportion is due to actual storm-induced nutrient

replenishment in the upper water column leading to successive blooms and cyst production.

The darkest time of the year in Hudson Bay is from November to February when light levels at these latitudes, even at the top of the ice, are extremely low. The only organism in our record that seems to be favoured by this time interval is *Salpingella* (Fig. 4), a cosmopolitan tintinnid that is also found in under-ice plankton assemblages from the Antarctic (Buck et al., 1992). *Salpingella* loricae are abundant in winter at site AN03. Interestingly, theca of phototrophic dinoflagellates from the genus *Dinophysis* are also present during winter, although they are most abundant during the ice breakup and open water season. Most species of *Dinophysis* are kleptoplastidic mixotrophs, i.e., they could derive their chloroplasts from photosynthesizing ciliates (Minnhagen and Janson, 2006). *Dinophysis* can also survive months in starved conditions, perhaps because of its ability to assimilate exogenous nitrogen (Hattenrath-Lehmann and Gobler, 2015). However, current knowledge suggests that *Dinophysis* is obligately mixotrophic and cannot survive long periods without light or prey (Kim et al., 2008). Thus it is somewhat surprising that *Dinophysis* appears under sea ice throughout the polar night. The pattern seen in our data perhaps demonstrates that as yet unknown survival strategies exist at least in some *Dinophysis* species, perhaps because they need to sustain their population throughout the year unlike species with a resting

Table 4

Dissimilarity measures comparing annual dinoflagellate cyst fluxes and compositions at the two trap sites and surface sediment (top 1 cm) samples when adjusted for accumulation during one year. Distances of trap data and corresponding surface sediment are shown in bold.

			Chord distance	Euclidean distance
Flux data	W trap vs. W sediment	AN01 vs. surface site 12	0.41	1,567,650
	E trap vs. E sediment	AN03 vs. surface site 6	0.24	5,628,130
	W trap vs. E trap	AN01 vs. AN03	1.19	14,607,900
	E trap vs. W sediment	AN01 vs. surface site 6	1.30	18,772,700
	W trap vs. E sediment	AN03 vs. surface site 12	1.20	14,443,100
	W trap vs. W sediment	AN01 vs. surface site 12	0.58	21.9
Compositional data	E trap vs. E sediment	AN03 vs. surface site 6	0.47	40.5
	W trap vs. E trap	AN01 vs. AN03	1.12	52.5
	E trap vs. W sediment	AN01 vs. surface site 6	1.32	83.0
	W trap vs. E sediment	AN03 vs. surface site 12	1.25	59.6

Table 5
Seasonal responses of cyst species to sea ice regime in Hudson Bay. Life-cycle modes correspond to those in the conceptual Fig. 9.

Life-cycle mode	Season of "cyst rain"	Season of cyst production/motile population maximum	Example species in Hudson Bay
-	Sea-ice covered	Sea-ice covered	None
1, 2	Sea-ice melt	Sea-ice melt or Sea-ice covered (sea-ice dwellers)	<i>Polarella glacialis</i> , cf. <i>Biecheleria</i> sp., <i>Polykrikos</i> sp. var. <i>arctica</i> , <i>Islandinium brevispinosum</i> , <i>Islandinium? cezare</i> , <i>Echinidinium karaense</i> , <i>Echinidinium aculeatum</i>
3	Open water (summer)	Open water (summer)	<i>Pentapharsodinium dalei</i> , <i>Operculodinium centrocarpum</i> , <i>Spiniferites ramosus</i> , <i>Spiniferites elongatus</i>
4	Open water (fall)	Open water (fall)	<i>Islandinium minutum</i> , <i>Brigantedinium simplex</i> , cf. <i>Echinidinium delicatum</i> , <i>Protoperidinium americanum</i>

stage. When irradiance levels rise in April and some light may be transmitted beneath the ice, heterotrophic dinoflagellates of the genus *Protoperidinium*, including some large (>100 µm) species, start to bloom (Fig. 4). Remains of theca belonging to this group are of special interest because many arctic cyst species of unknown motile affinities are suspected to belong to the genus (Table 1). While it is difficult to identify *Protoperidinium* theca from palynologically treated samples using light microscopy, commonly observed specimens were large and contained pronounced antapical spines, not resembling, e.g., recently described motile stage of *I. minutum* (Potvin et al., 2013). Polar *Protoperidinium* species have been observed feeding on ice and ice-edge blooming diatoms in spring (Archer et al., 1996; Levinson and Nielsen, 2002; Sherr et al., 2013), but there is evidence of *Protoperidinium* populations in ice ecosystems that feed primarily on bacteria and dead OM (Lessard and Rivkin, 1986). Importantly, *Protoperidinium* species use a pseudopodial feeding veil, which enables them to ingest organisms that are much larger than themselves, and they may thus be able to survive through times of starvation using storage products (Menden-Deuer et al., 2005). In our records under-ice *Protoperidinium* species appear concurrently with increasing irradiance levels (Fig. 4), implying that their primary prey consist of early photosynthesizing ice algae, which based on the available data from Hudson Bay comprise mainly pennate diatoms (Tremblay et al., 1989; Michel et al., 1993). Furthermore, *Protoperidinium* theca fluxes begin weeks before the ice melt, indicating that the fluxes are likely of water column origin. Indeed, in many sea-ice governed systems, ice protist communities consist mainly of diatoms whereas under-ice

surface water communities are dominated by flagellates and ciliates (Tremblay et al., 1989; Rintala et al., 2010).

The time around the ice breakup is a very active season in our records with multiple phototrophic (*P. glacialis*, cf. *Biecheleria* sp.) and heterotrophic (*Polykrikos* sp. var. *arctica*, *E. karaense*, *E. aculeatum*, *I. brevispinosum*) dinoflagellate species exhibiting maximum cyst fluxes (Figs. 3, 5 and 8). Fluxes of *Protoperidinium* theca are still significant, tintinnid loricae are abundant particularly at site AN01, and cysts of ciliates (*Strombidium*, *Cyrtostrombidium*) start emerging at site AN03 (Fig. 4). Seasonally retreating ice edge has been identified as a unique stage for space- and time-transgressive ice algal and phytoplankton blooms that support versatile arctic ecosystems (Leu et al., 2011; Perrette et al., 2011). Together with large amounts of runoff, freshwater input from melting ice creates strong stratification and thus favourable conditions for phytoplankton blooms, also providing nutrients and bloom population seeding. Furthermore, solar irradiance at the sea surface increases as the ice cover shrinks. Most studies of plankton composition in Hudson Bay have been conducted during ship-based programs in summer and fall (Bursa, 1961; Anderson et al., 1981; Harvey et al., 1997; Ferland et al., 2011; Lapoussière et al., 2009), and little is known of springtime dynamics. Existing studies were carried out at the mouth of the Great Whale River in southeastern Hudson Bay, near our trap site AN03. These studies identify spring ice melt as a key successional event, preceded by high chlorophyll levels and algal cell counts in ice, and followed by under-ice phytoplankton blooms and copepod grazing of released ice algae in the water-column (Tremblay et al., 1989; Runge et al., 1991; Michel et al., 1993). The earlier studies did not analyze sympagic and under-ice

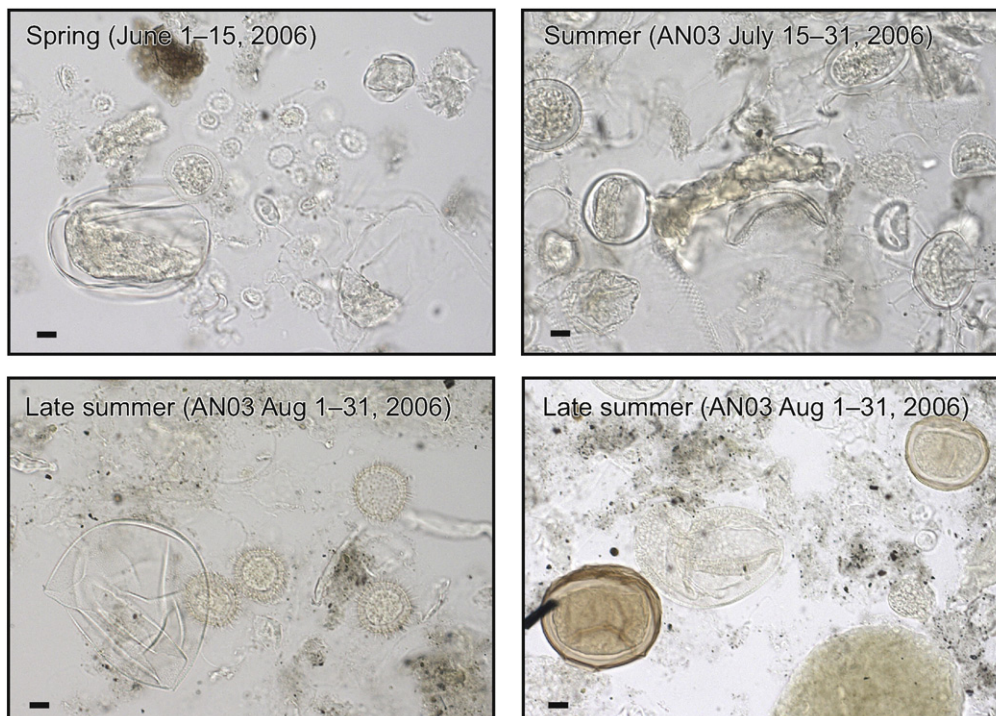


Fig. 8. Examples of seasonal palynomorph assemblages from trap site AN03.

microzooplankton (i.e., heterotrophic dinoflagellates and tintinnids), but our data suggest that they constitute an important group in the spring-time production cycle of Hudson Bay (Figs. 3 and 4).

Our data indicate that none of the dinoflagellate species in our record produce cysts in winter, at least not in the water column, but many do so in spring along with increasing irradiance and ice breakup, while the remainder prefer the successive open-water season (Figs. 3, 5 and 8). It is, however, not possible to distinguish the cyst production events of sea-ice dinoflagellates, since cysts are released to the water column following the sea-ice melt, and may hence appear in the trap records coincidentally with under-ice or ice-edge bloomers (Fig. 9).

4.2. The role of sea-ice cover and light availability

Subsequent to determining the fundamental role of life cycle transitions in dinoflagellate bloom dynamics (Dale, 1983; Anderson and Rengefors, 2006), biologists have made substantial efforts to understand the regulation mechanisms of cyst germination following dormancy (excystment) and cyst formation following blooms (encystment). While the processes leading to the formation of resting cysts have only been deciphered for a limited number of species, it seems unequivocal that species-specific controls are at play. For example, encystment is related to nutrient depletion in *Gonyaulax tamarensis*, *Alexandrium catenella* and *Gymnodinium corollarium* (Anderson and Lindquist, 1985; Figueroa et al., 2005; Kremp et al., 2009), suboptimal temperature in *Scrippsiella hangoei*, *B. baltica*, *Gyrodinium uncatenum* and *Gymnodinium nolleri* (Anderson et al., 1985; Ellegaard et al., 1998; Kremp and Parrow, 2006; Kremp et al., 2009), and day length in *Scrippsiella rotunda* (Sgrosso et al., 2001). Resting stage is generally considered as a means of population continuum over stressful or suboptimal environmental windows, although there is some evidence for population dynamics, such as cell density, playing a role (Uchida, 2001).

As outlined above, neither light-dependent phototrophs nor light-independent heterotrophs produce cysts in the deep arctic winter of Hudson Bay (Figs. 3 and 5), suggesting bloom quiescence in the dark winter months for all of the species in our records. On the contrary, certain taxa exhibit significant under-ice fluxes along with higher irradiances in the spring (April–June). Such fluxes can result either from surface-water cyst production following under-ice blooms or from the melt-mediated release of sea-ice-dweller cysts to the water column (Fig. 9, Table 5). Furthermore, many species in our record are explicit

open-water producers, exhibiting cyst fluxes in June–October. Seasonal light availability thus plays an unquestionable role in dinoflagellate life cycle dynamics in Hudson Bay, but exactly how much irradiance is transmitted through spring sea ice? What conditions select for different life cycle modes of spring and summer cyst producers if not the trophic level?

Recent research has elucidated the significance of ice thickness, surface structure and snow cover for light transmittance and dynamics of seasonal sea ice (Stroeve et al., 2014; Wang et al., 2014). Observations of dense under-ice phytoplankton blooms have been made, e.g., in the Chukchi Sea where ice cover is thinning and the frequency of melt ponds has increased (Arrigo et al., 2012), and under land-fast ice of Canadian Arctic Archipelago through a complete sequence from snow melt and melt-pond formation to ice-cover collapse (Mundy et al., 2014). In Hudson Bay, very close to the trap site AN03, Michel et al. (1993) recorded bottom ice, ice–water interface and under-ice algal blooms during a melt season, demonstrating how spring succession was initiated at the same time as the disappearance of light-limiting snow cover. The ice-algal bloom in early spring was replaced by ice–water interface bloomers simultaneously with decreasing snow depth and by under-ice bloomers concurrently with accelerated sea-ice melt (Michel et al., 1988, 1993). Furthermore, there was evidence of seeding from ice to the water column. While most of the ice algal biomass studied by Michel et al. (1993) comprised diatoms, microflagellates exhibited a similar successional pattern. Assuming microflagellates entail dinoflagellates belonging to the size class (clarification is not made in the paper) there is an indication that spring cyst producers in our flux data (Fig. 3) may originate from different compartments of the ice-water continuum and hence exploit different ecological strategies.

P. glacialis is the only spring species in the Hudson Bay record whose ecology is reasonably well-known. In the Antarctic it grows in sea-ice-brine channels in early austral spring and produces cysts in response to nitrate depletion (Montresor et al., 1999; Stoecker et al., 2000), it is extremely halotolerant (Stoecker et al., 2000), and survives temperature extremes (Zheng et al., 2012). Cysts of *P. glacialis*, however, do not consist of resistant dinosporin and likely degrade in sediment (Montresor et al., 1999), as evidently happens in Hudson Bay (Fig. 7). Hence, the application of *P. glacialis* as a sedimentary tracer of past sea-ice environments can be hampered by poor preservation. The motile affiliation of the other phototrophic spring cyst producer, cf.

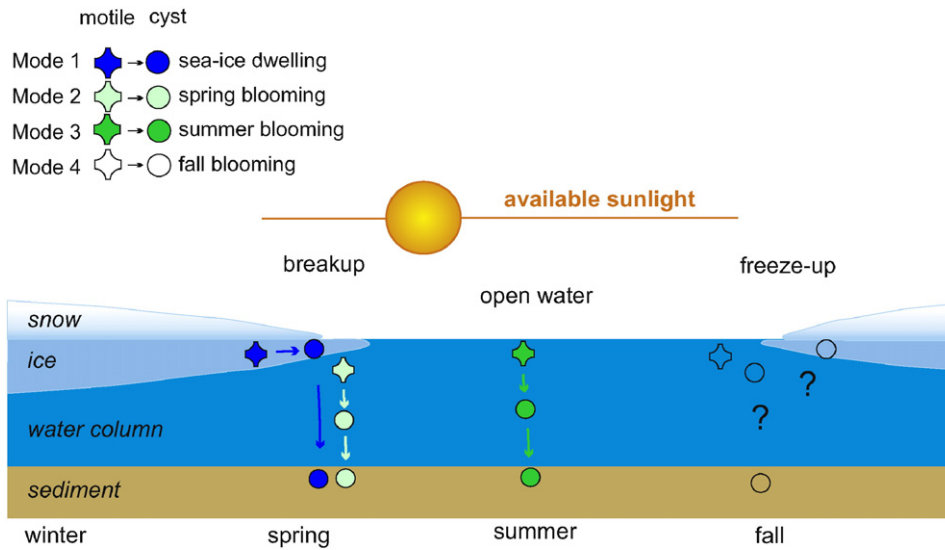


Fig. 9. Conceptual diagram of dinoflagellate encystment and cyst fate in the course of the subarctic year. The figure illustrates the four seasonally distinct life-cycle modes separated by this study: sea-ice dwelling (1), spring blooming (2), summer blooming (3), and (late) fall blooming (4). Challenges in sediment trap data interpretation occur during breakup and freeze-up, the former because of the difficulty in separating the origin of settling cysts (melting ice or water column), the latter because of the unknown “seed bank” for the produced cysts (ice, sediment, or both).

Biecheleria sp., is uncertain, but it closely resembles *B. baltica*, an abundant spring bloomer of the seasonally ice-covered northern Baltic Sea (Kremp et al., 2005). Dense under-ice blooms of *B. baltica* have been observed in salt-stratified cold surface waters of the Baltic Sea (Spilling, 2007), where massive cyst sedimentation events follow the bloom maximum (Heiskanen, 1993). A comparable seasonal encystment pattern is evident in our data from Hudson Bay, where salt-stratification can be similarly created by river plumes penetrating under the sea-ice cover (Legendre et al., 1996). Based on the available ecological data it is likely that the habitat and life cycle strategies of *P. glacialis* and cf. *Biecheleria* sp. are divergent, so that in ice-covered ecosystems the former is an ice-dweller and the latter an under-ice bloomer (modes 1 and 2 in Fig. 9), even though the species exhibit roughly comparable seasonal cyst flux patterns (Fig. 3). The other recorded phototrophic species (*P. dalei*, *O. centrocarpum*, *S. elongatus*, *S. ramosus*) are abundantly found in arctic sediment cores, and exhibit clear signatures of open-water cyst production in our records (modes 3 and 4 in Fig. 9).

Heterotrophic spring cyst producers comprise a peculiar species assemblage with co-occurring fluxes of high-latitude “sea-ice indicators” (*Polykrikos* sp. var. *arctica*, *E. karaense*, *I.? cesare*) and common low- to mid-latitude cyst species (*E. aculeatum*, *I. brevispinosum*) (Fig. 3). The motile stage has not been described for any of these five species despite their common occurrence in marine sediments, and ecological information is thus based on the global distribution of cysts in surface sediment (Zonneveld et al., 2013). Moreover, the classic “sea-ice indicator” *I. minutum* seems to be, rather surprisingly, a summertime cyst producer in Hudson Bay (corresponding to mode 3 in Fig. 9), indicating that the motile population blooms in surface waters at the peak of the northern summer. This species is most abundantly found in surface sediments from Hudson Strait (Heikkilä et al., 2014), however, and the fluxes in our trap records within Hudson Bay are not very high. Other heterotrophic summertime cyst producers include *P. americanum* and cosmopolitan species of the genus *Brigantedinium* (cysts of *Protoperidinium* species), as well as the spiny brown species cf. *E. delicatum*. Our trap data thus manifest that cold-water heterotrophs exhibit a variety of life-cycle strategies, and highlight the fact that light conditions are not a common control of their cyst production in Hudson Bay.

It is known from productive marine systems (e.g., upwelling coasts, eutrophic estuaries) that heterotrophic dinoflagellates, particularly those belonging to Protoperidiniaceae, are abundant where and when their predominant prey, diatoms, bloom (Lessard, 1991). Recent comparisons of cyst fluxes with diatom abundance indicate a similar dependency of heterotrophic dinoflagellates on their prey (Pospelova et al., 2010; Zonneveld et al., 2010a; Price and Pospelova, 2011; Bringué et al., 2013). The general preference of heterotrophs for nutrient- and diatom-rich areas within the Hudson Bay system is also reflected by areal distributions of cysts in surface sediments (Heikkilä et al., 2014). An exception to this pattern was exhibited by *Polykrikos* sp. var. *arctica* whose cysts were found most abundantly in areas where ice-cover persisted longest (Figs. 3–5 and Panel F in Appendix A, Heikkilä et al., 2014). The possible affiliation with sea ice, or with niche conditions shaped by sea ice, is also indicated by the common occurrence of *Polykrikos* cysts in surface sediments of arctic regions where seasonal ice-cover duration is close to a year and annual salinity range is pronounced (de Vernal et al., 2001; Kunz-Pirrung, 2001; Zonneveld et al., 2013). Indeed, *Polykrikos* is one of the common dinoflagellate genera found in sea ice along with *Gymnodinium*, *Gyrodinium*, *Scrippsiella* and *Polarella* (Stoecker et al., 1993; Garrison et al., 2005; Thomson et al., 2006; Comeau et al., 2013), although to our knowledge, ice-affiliated *Polykrikos* has only been reported from the Antarctic (Stoecker et al., 1993). It is important to focus on the ecology, habitat and biological affinity of the arctic *Polykrikos*-type, as the taxon could potentially be an ice dweller. It has to be pointed out that even though the abundance of *Polykrikos* sp. var. *arctica* is not related to the amount of nutrients and biogenic silica in the Hudson Bay system (Heikkilä et al., 2014), the species may still be dependent on certain diatom species as prey.

While it is evident that light availability and seasonal sea ice shape the patterns of dinoflagellate blooms and cyst production in Hudson Bay the multivariate analyses presented above suggest that other moderators could be important as well: 12% of seasonal cyst flux patterns were explained by sea-ice and irradiance (Table 3, Fig. 6). The proportion of unexplained variation is large despite the generally low theoretical probability for a parameter to explain the biological data structure as reflected by the 38% variance accounted for by PCA (Fig. 6). Sediment trap data can be noisy, and depending on the trap location and weather patterns, laterally transported or resuspended material may enter the sample jars and get mixed with vertically transported particles (see discussion in Section 4.1). At the same time, the moderate explanatory power of SIC and irradiance in explaining the seasonal data structure may indicate that environmental factors other than light availability are important in triggering dinoflagellate blooms and cyst production. As discussed above, such factors entail nutrient and prey availability, both of which are largely controlled by vertical stratification in the Hudson Bay system (Kuzyk et al., 2010). Moreover, diatoms are by far the most dominant and most diverse sympagic protist group, particularly in spring, with over 700 sea-ice dwelling species recorded in the Arctic (Poulin et al., 2011), and diatom blooms thus provide an ample food source for under-ice blooming heterotrophic dinoflagellates recorded in our traps during ice breakup (Fig. 3).

Water temperature and salinity also vary drastically in the course of the subarctic year, and particularly the former has been found an important regulator of encystment for certain dinoflagellates (e.g., von Stosch, 1973; Anderson et al., 1985; Kremp et al., 2009; Figueroa et al., 2011). Surface temperatures of Hudson Bay have been rising since mid-1990s (Galbraith and Larouche, 2011; Hochheim and Barber, 2014), against that trend the years 2005 and 2006 were not anomalously high (Galbraith and Larouche, 2011; Table 3; Supplementary Fig. 1). The available sea surface temperature, salinity and nutrient measurements from Hudson Bay that co-occur with the time frame of this study were taken in late summers 2005 and 2006 (Supplementary Table 1), and hence represent snapshots in time that are not comparable with our bi-weekly to bi-monthly trap data series. However, since southeastern Hudson Bay generally experiences lower salinities, stronger stratification and higher peak season surface temperatures (Barber, 1967; Prinsenberg, 1986a, 1986b; Ferland et al., 2011; Galbraith and Larouche, 2011; Granskog et al., 2011), the differences in general species abundances between the sites (Fig. 7) could be explained by these oceanographic features (see further discussion in Heikkilä et al., 2014).

Importantly, none of the above-mentioned environmental factors operate separately, and sea-ice has a noteworthy role in controlling seasonal sea-surface temperatures, nutrient levels, salinity and water column structure through melt-water mediated salt-stratification in spring, and conversely, through upper water column mixing via ice-formation and brine-rejection in fall (Ferland et al., 2011; Granskog et al., 2011).

4.3. Comparison of the trap signal with surface sediment

The comparison of trap fluxes with those of the surface sediment demonstrate that both the species diversity and the quantified cyst fluxes in sediment are generally equivalent to the vertical fluxes recorded in the bottom of the water column, lending support to reconstruction of past conditions based on sedimentary dinoflagellate cysts (Fig. 7, Table 4). However, cysts of *P. glacialis* and cf. *Biecheleria* sp. that are not commonly recorded in sedimentary archives, seem to quickly mineralize after sedimentation. Another deviance is the abundance of *P. dalei* at the sediment surface relative to the trap record in eastern Hudson Bay. *P. dalei* is a prolific cyst producer in stratified high-latitude waters, such as fjords (Dale, 1976, 1977; Godhe et al., 2001; Howe et al., 2010; Milzer et al., 2013), and it can dominate assemblages in relatively productive high-latitude seas such as Hudson Bay (Radi

et al., 2001; Marret et al., 2004; Heikkilä et al., 2014). The calculation of annual averages for the traps is based on the record from October 2005 to September 2006, while the 1-cm surface sediment record represents ca. 20 years of accumulation prior to core collection in September 2005 (Kuzyk et al., 2009). Since inter-annual differences in cyst production are often significant (see e.g., Pospelova et al., 2010; Zonneveld et al., 2010a), discrepancies such as the differing abundances of *P. dalei* in the trap and surface signals may be explained by the temporal mismatch. Furthermore, while it looks likely that *P. glacialis* and cf. *Biecheleria* sp. do not preserve in downcore records, these species should be surveyed more carefully in any future palynological studies from sea-ice environments.

4.4. Lessons for palaeo application

Dinoflagellate cysts are currently one of the most widely applied proxies for late Quaternary sea-ice reconstruction in the Northern Hemisphere along with newly developed biomarker tools (Belt et al., 2007; Belt and Müller, 2013). An extensive modern reference database incorporating over 1400 surface sediment sites has been developed (de Vernal et al., 1997, 2001, 2013) and applied to reconstruct sub-millennial-scale sea-ice conditions in the Arctic (e.g., Levac et al., 2001; de Vernal and Hillaire-Marcel, 2005; Bonnet et al., 2010; Ledu et al., 2010). Since the reconstructions give quantitative estimates of sea-ice cover (ice-cover in months yr^{-1} , or mean annual concentration 1:10–10:10), they provide much needed estimates for comparison with modern and predicted sea-ice trends, and for climate model evaluation. Nonetheless, sea-ice reconstructions based on dinoflagellate cysts do not always corroborate commonly observed large-scale temperature trends inferred from other proxies. Validation of reconstruction results and assessment of the causalities in the reconstruction procedure will benefit from the understanding of the ecology and biology of dinoflagellate life cycles.

Our seasonal cyst flux data demonstrate that some of the traditional “sea-ice indicator” species, namely *Polykrikos* sp. var. *arctica*, *I. ? cezare*, and *E. karaense*, exhibit cyst fluxes during ice breakup along with other heterotrophs that are known as temperate species (*I. brevispinosum*, *E. aculeatum*) (Table 5). The most abundant and commonly applied “sea-ice indicator” *I. minutum*, on the other hand, appears unexpectedly as an open-water cyst producer in Hudson Bay together with heterotrophs *P. americanum*, *Brigantedinium* spp. and cf. *E. delicatum*, which indicates a population maximum during the polar summer rather than a direct affiliation with sea ice. Since proxy-based reconstructions are often derived from individual sites (sediment cores) set against a global or hemispheric reference database, the assumption is made that predominant environmental drivers of species distributions and controls of life-cycle transitions are uniform across regions. In consequence, in locations where sea-ice is not a primary control, “sea-ice reconstructions” may reflect other, regionally pivotal environmental controls, such as nutrient and prey availability in the Hudson Bay system.

Interestingly, there is lack of evidence for a uniform seasonal time windows or life-cycle behaviour of commonly applied “sea-ice proxy” species in our data. We do not know, however, whether the seasonal fingerprints of the species in our dataset persist from year to year, or whether the phenological pattern demonstrated in Hudson Bay is repeated in other arctic marine regions. Moreover, distinguishing cysts derived from melting ice from those produced concurrently in the upper water column is a challenge (Fig. 9) and requires on-ice sampling before and during ice breakup to complement the results from sequential trap data. Furthermore, it is not apparent in the trap data if cysts are incorporated into sea-ice during freeze-up (Fig. 9), another question which can only be answered by direct on-ice field work. Establishing species-specific time windows and cues of cyst production for arctic dinoflagellates and exploring their geographic resilience can advance and tune proxy-based reconstruction by redefining appropriate spatial

coverages for reference data sets and by providing detailed knowledge of ecological characteristics of cyst production in relation to environmental variables.

5. Conclusions

Here we have presented two continuous, annual sequences of dinoflagellate cyst production based on sediment trap data from Hudson Bay to elucidate the seasonal patterns of arctic dinoflagellate encystment and thus enhance the ecological understanding of the proxy. Our data show that overall cyst production is controlled by the sea-ice regime and that sediment cyst assemblages closely resemble those caught by the vertical flux measured in the traps, thus lending support to the use of dinoflagellate cysts as environmental proxies in arctic seas. Furthermore, seasonal time windows of cyst production are species-specific, and broadly similar, at the two oceanographically differing sites. Nevertheless, the relation of trophic status to seasonal darkness, i.e., preferential cyst production of heterotrophs over the dark season, was not demonstrated, and the most common sea-ice indicator species *I. minutum* did not appear as a sea-ice dweller in our dataset. The data here present the first continuous records of cyst production throughout the year in an ice-covered system. Nevertheless, these records should be considered preliminary. A longer period of record, incorporating several years, a wider selection of arctic regions and environmental parameters, would be a key requisite for ecologically robust proxy reconstructions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.marmicro.2016.02.005>.

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