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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*, *Islanidium 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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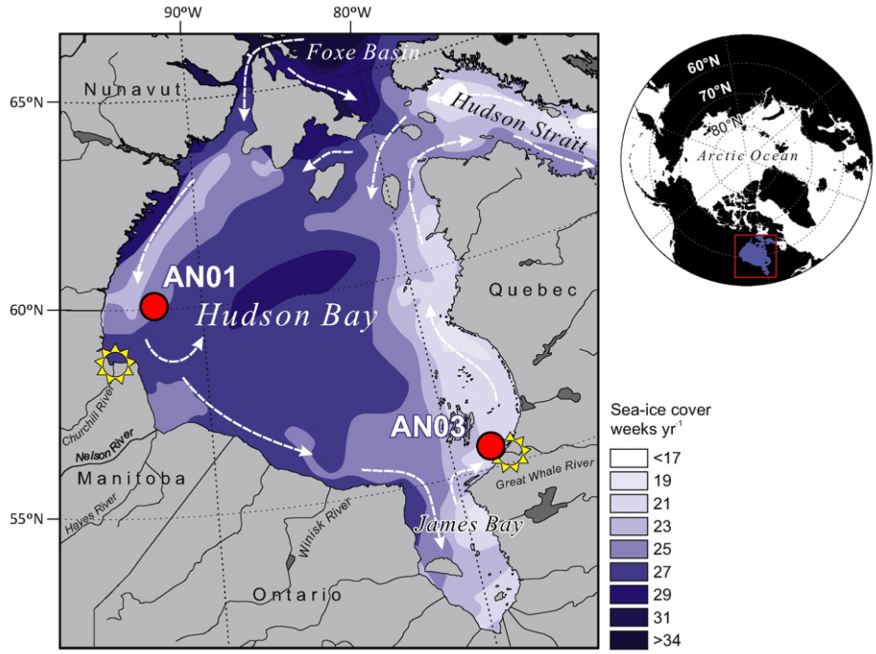

Fig. 1. Locations of the two mooring sites (AN01, AN03) in Hudson Bay, and location of Hudson Bay with respect to the Arctic Ocean. Yellow shapes indicate the two climate stations where solar irradiance data were collected. Annual average (1995–2005) sea-ice cover duration is shown as varying shades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

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; Pfiester 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 subpolar 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

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