

**Mid-to Late Holocene changes in the hydrographic conditions in the Baltic
Sea, as inferred from dinoflagellate cysts assemblages**

by

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Abstract

Dinocyst assemblages from marine sediments in the south-central Baltic Sea provide a record of changes in the Holocene Baltic Sea hydrographic system for the last 6000 years. A low diversity assemblage of four genera of autotrophic dinocysts is observed throughout, dominated by the species *Operculodinium centrocarpum*. Dinocyst assemblages, especially process length variation in *O.centrocarpum* are used to interpret qualitative paleosalinity. The Littorina Transgression, a period of increasing salinity was already underway in the eastern Gotland Deep by 6000 years BP, and continued until 4750 years BP. The highest dinocyst concentrations were observed during Mid Holocene Warming 6000 – 4000 years BP. Littorina Sea A Phase (6000 – 4750 years BP) is defined by an inferred major increase in salinity.

From 4750 – 1000 years BP, only minor changes in salinity are reflected in the dinocyst assemblage. From 4000 – 1000 years BP, stable, low concentrations of dinocysts are interpreted as a result of shorter blooming seasons during Neoglacial summers. Littorina Sea B Phase (4750 – 1000 years BP) is defined by inferred minor fluctuations in salinity and stable concentrations of dinocysts throughout.

Increased dinocyst abundance is observed from 1000 – 800 years BP before declining from 800 – 100 years BP to low concentrations (25 000 dinocysts/g sediment). This is interpreted as caused in part by longer, warmer summers during the Medieval Warm Period (MWP) and shorter, cooler summers during the Little Ice Age as well as increased nutrient runoff into the Baltic Sea from increased anthropogenic land use during the MWP. Dinocyst assemblages indicate gradually decreasing salinity from 1000 – 100 years BP. Late Littorina Sea B Phase (1000 – 100 years BP) is defined by an inferred minor decrease salinity and elevated concentrations of dinocysts during the MWP.

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LTS-A = Littorina Sea A LTS-B = Littorina Sea B LLTS-B = Late Littorina Sea B

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1. Introduction

The Baltic Sea is a semi-enclosed brackish body of water in Northern Europe. Covering 377 400 km² with a water body of 21 200 km³, the Baltic Sea is the largest brackish basin in the world by volume and surface area (Miettinen et al., 2007). The Sea is composed of saline North Sea waters mixing with fresh precipitation and runoff from over 200 basins draining 1.74 million km² of Scandinavia and Europe (Miettinen et al., 2007; BACC II Author Team, 2015). The evolution of the Baltic Sea during the last glaciation is poorly understood. Conversely, the sedimentary record since the glaciation is relatively complete, abundant and microfossil-rich (Brenner, 2004; Yu and Berglund, 2007; Andrén et al., 2011; Ning et al., 2017).

However, issues with the dating methods for post-glacial sediment cores have complicated the task of accurately documenting the environmental conditions of the Holocene Baltic Sea. It has been shown by Hedenström and Possnert (2001) that bulk sediment C-14 dating in the Baltic Sea may overestimate dates by 700-1500 years when compared to *in situ* terrestrial macrofossils due to the reworking of older reservoir sediment into younger sea bottom sediment. In addition, the reservoir effect of the Baltic Sea is not well understood (Hedenström and Possnert, 2001; Andrén et al., 2011). Kortekaas et al. (2007) employed optically stimulated luminescence (OSL) to date quartz crystals in a Baltic sediment core for the last 15000 years and found differences between bulk sediment C-14 dates up to 3000 years. While such methods provide useful age-depth estimates, a reliable, accurate dating method for Holocene Baltic sediments has not been found. While Holocene Baltic Sea dating methods are not ideal, parallel sediment core analyses such as microfossil assemblages have the potential to provide valuable data on paleoenvironmental conditions, perhaps leading to future inferences that will help determine an accurate Holocene geologic and hydrographic history.

Previous work relevant to this study includes paleosalinity reconstructions by Gustafsson and Westman (2002) and Emeis et al. (2003), as well as numerous studies examining the relationships between microfossil assemblages and paleoenvironmental conditions. Ning et al. (2017) examine multiple salinity proxies in the Mid Holocene Baltic Sea, including dinocysts, sedimentary fabric, benthic foraminifera and mollusk shells. Brenner (2004) also uses a multi-proxy approach of dinocysts, pollen grains, cladoceran eggs and various algae to analyze climatic and hydrographic variations in the Baltic Sea in the interval covering the entire Holocene. Yu and Berglund (2007) plotted dinocyst assemblage along with physical properties of the sediment such as magnetic susceptibility, density and porosity to analyze hydrographic changes in the Early to Mid Holocene Baltic Sea. Diatom assemblages in Baltic Sea sediments are studied extensively, and include studies that discuss the same climatic and hydrographic changes analyzed in this study (Andrén, 1999; Westman and Sohlenius, 1999). In general, the Holocene Baltic Sea is well understood, but accurate dates remain a challenge and the details of each period are still valuable paleoenvironmental information, as we a species deal with and attempt to predict the behaviour of a warming climate.

This study presents a dinoflagellate cyst record from a 2 m section of Gotland Basin sediment core, with inferences on the salinity and dinoflagellate component of primary production, as well as discussion of the timing of significant regional events such as the Littorina Transgression and Medieval Warm Period.

Virtasalo et al. (2011) detail the stratigraphy, chemistry, ichnofauna, sedimentary fabric and Accelerator Mass Spectrometry (AMS) C-14 dates for the entire 10.55 m sediment core, as well as another similar core also retrieved in the Gotland Basin.

2. Regional Setting

2.1 The Holocene Baltic Sea

Although this study deals with a Mid-to late-Holocene sedimentary record, a discussion of the previous 15000 years BP is required to fully understand the Holocene Baltic depositional environments.

During the last 15000 years BP, the Baltic Sea region has undergone significant environmental changes, transforming the geological, hydrological and biological components of the Sea. These environmental changes define four hydrologically distinct phases, commonly referenced in academic discussion of the Holocene Baltic (Table 1). The present Baltic Sea is shown in Figure 1.

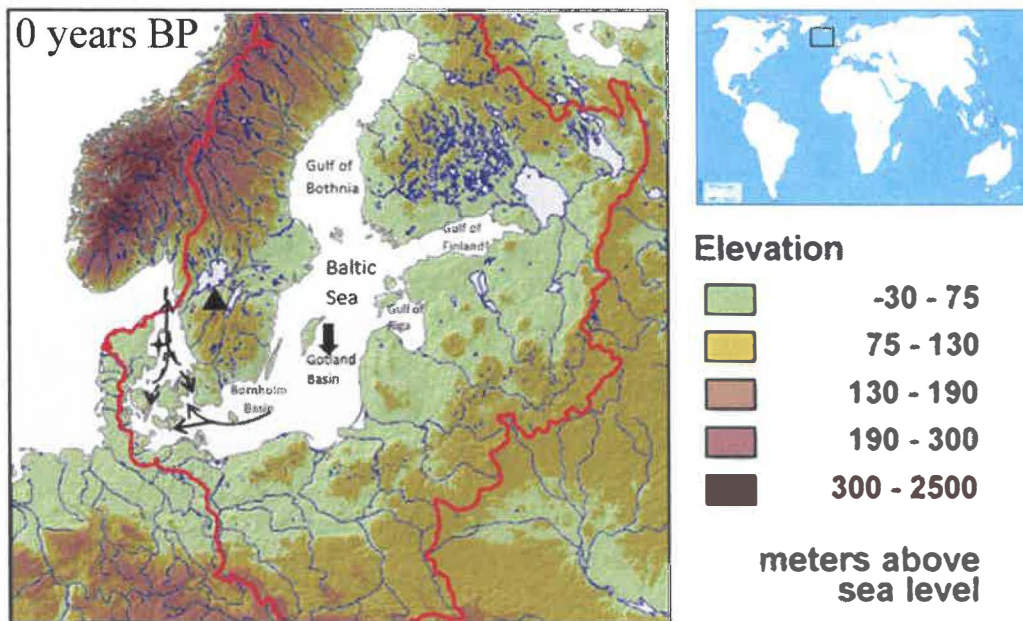


Figure 1: The Baltic Sea and surrounding landmass, showing the Sea's drainage basin (—), sediment core #303600-3 (↓) at 56°55.01'N 19°19.99'E, Billingen, Sweden (▲) inflowing (--->) and outflowing (—>) dominant currents (redrawn from Kothoff et al., [In Prep]), Kattegat (✚) and major tributaries. Baltic hydrographic data by Ahlenius (2005).

The Holocene sedimentary record is composed of brackish to freshwater sediments, reflecting the sum of sedimentary inputs from the North Sea and terrestrial runoff (Miettinen et al., 2007). The glacial ice covering the entirety of the Baltic Sea during the last glacial period began to melt and recede North and

Northwest around 16000 years BP, leaving less than half of the Baltic ice-covered by 11700 years BP (Panel A Fig 2, Fig. 4.4 Andrén et al., 2011). Post-glacial

Table 1: The major phases of the Holocene Baltic Sea, each characterized by a major change in hydrographic conditions. Descriptions combined from (Brenner, 2004; Andrén et al., 2000; Andrén et al., 2011 Ning et al., 2017).

Time (years BP)	Baltic Sea Phase	Namesake	Description
14000	Baltic Ice Lake	Ice	Glacial and glaciolacustrine sediments deposited as the glaciers receded North
11800			Melting ice opens a marine channel via Billingen, Sweden
11800	Yoldia Sea	Marine bivalve <i>Yoldia artica</i>	Some marine mixing with fresh Baltic deposited brackish lake sediments
10700			Isostatic uplift closed the Baltic-North Sea connection
10700	Ancylus Lake	Freshwater snail <i>Ancylus fluviatis</i>	Marine-isolated fresh Baltic deposited continental runoff freshwater lake sediments
8000			Eustatic rise established new marine connection
8000	Littorina Sea A	Marine snail <i>Littorina littorea</i>	Slow transition from freshwater to brackish sea sediments as marine connection increases
4000			
4000	Littorina Sea B	Marine snail <i>Littorina littorea</i>	Stable brackish water sedimentation
Recent			Anthropogenic inputs

isostatic rebound in the region separating the Kattegat strait and Baltic Ice Lake precluded the formation of a Baltic-marine connection, creating a giant ponded ice lake up to 25 m above sea level (Andrén et al., 2011, Ning et al., 2017). This phase is the Baltic Ice Lake (BIL). Sedimentation in the BIL was typical of retreating glaciers, with glaciolacustrine sediments deposited as varved clays proximal to the retreating glacial margin and homogeneous clays throughout the rest of the lake (Andrén et al., 2011).

Further glacial retreat just before the beginning of the Holocene opened a marine connection between the BIL and the North Sea via Billingen, Sweden (Brenner,

2004; Andrén et al., 2011; Ning et al., 2017). This connection was the mechanism for the massive draining of the BIL, lowering the water level from 25 m above sea level to approximately equal (Andrén et al., 2011). This event occurred over 1-2 years (Andrén et al., 2011), at 11800 years BP (Brenner, 2004) to 11700 years BP (Jakobsson et al. 2007, Ning et al., 2017) and defines the end of the BIL and the beginning of the Yoldia Sea (YLS) phase (Panel B Fig 2, Fig 4.6 Andrén et al., 2011). Conditions in the Baltic during the YLS were fresh to brackish, although the most significant influx of marine water occurred from 11300 -11100 years BP (Andrén et al., 2011). Sedimentation during the YLS phase consisted of varved clays proximal to retreating glaciers in the Northern Baltic and the Gulf of Bothnia, and post-glacial lacustrine sediments throughout the rest of the sea. Continuing isostatic rebound closed the Baltic-marine connections approximately 10700 years BP (Andrén et al., 2011).

Another freshwater phase, the Ancylus Lake (ACL) is defined by the closure of the marine-Baltic connection at 10700 years BP and an increase in freshwater input (Panel C Fig. 2, Fig. 4.7 Andrén et al., 2011). Low volume outflowing currents and increased meltwater runoff from the Scandinavian ice sheet into the Baltic Sea caused a freshwater surplus in the ACL, allowing water levels to rise above sea level once again (Andrén et al., 2011). Sedimentation in the ACL was dominated by low-organic lacustrine freshwater sediments, indicating a low-productivity environment (Andrén et al., 2011). Further eustatic rise, influenced partially by the final melting of the Scandinavian ice sheet led to new marine-Baltic interaction beginning in low volume at 9800 but intensifying into a major marine connection by 8500 - 6500 years BP (Andrén et al., 2000; Kortekaas et al., 2007; Andrén et al., 2011). The intermediate period of low salinity brackish water preceding the major marine influence known as the Littorina Transgression is sometimes referred to as the Initial Littorina Sea or the Mastogloia Sea (Andrén et al, 2000; Brenner,

2004). The occurrence of a major marine connection between the Baltic Sea and the Kattegat defines the beginning of the Littorina Sea (LTS) phase (Panel D, Fig. 2, Fig. 4.8 Andrén et al., 2011).

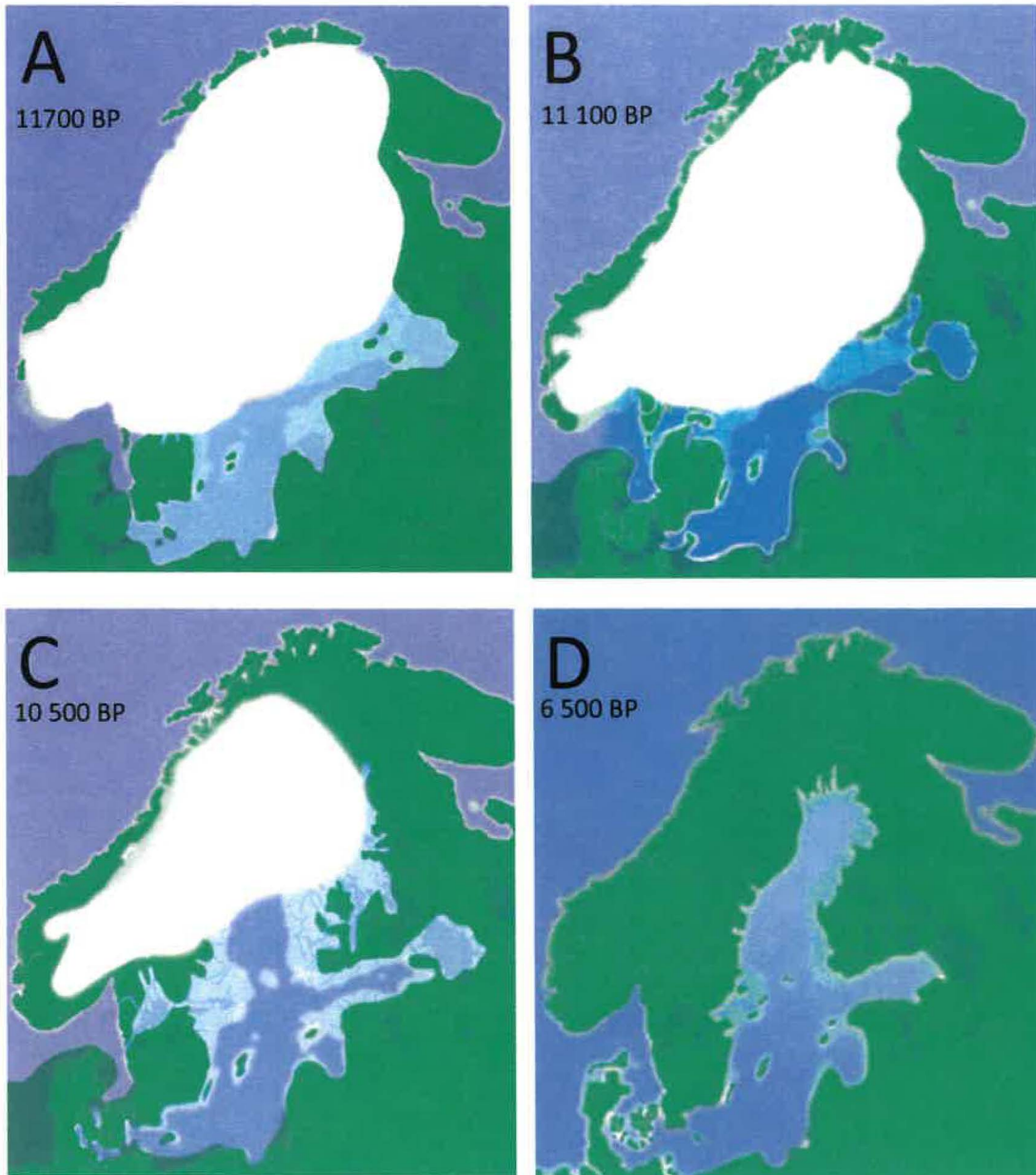


Figure 2: The four major phases of the Holocene Baltic Sea (after Figures 4.4, 4.6, 4.7, 4.8, Andrén et al., 2011). A = Baltic Ice Lake (BIL) B = Yoldia Sea (YLS)
C = Ancylus Lake (ACL) D = Littorina Sea (LTS)

The exact date of the transgression is a subject of ongoing debate, with several dating methods yet to show a consensus. For example, Kortekaas et al., (2007)

used OSL to date quartz crystals alongside C-14 AMS dates for bivalves from a Baltic sediment core and dated the Littorina Transgression to 6500 years BP and 8500 years BP, respectively. Bulk sediment C-14 AMS dates range from 8500 – 74000 years BP (Sohlenius et al., 1996; Andrén et al., 2000; Brenner, 2004; Andrén et al., 2011).

This lack of consensus between published dates is typical of the geochronology of the entire Holocene Baltic Sea sedimentary sequence. The Baltic Sea-Kattegat connection reached a maximum at 6000 years BP, before declining in volume but remaining a constant source of marine input until recently (Andrén et al., 2011). The LTS phase can be further divided into sub-phases based on inferred changes in salinity. The timing of these sub-phases varies from author to author and are described for this study in the *Results* and *Discussion*.

Sedimentation during the LTS consisted of clay to clay gyttja, notable for their relative enrichment in organic carbon, abundant brackish water microfossils and common stratification.

2.2 Hydrographic setting

The current hydrographic circulation of the Baltic Sea is driven by two major factors: i) a positive barotropic gradient between the Baltic Sea and the Kattegat and ii) episodic seasonal inputs of marine North Sea water.

The positive barotropic gradient between the Baltic and the Kattegat is derived from freshwater input into the Baltic Sea in the form of terrestrial runoff and precipitation flowing from all over the Baltic into the Kattegat at a lower rate than the freshwater inputs accumulate (Kotthoff et al. 2017). This barotropic gradient drives the surficial outflowing currents shown in Figure 1.

Decadal scale episodic marine inputs flow into the Baltic Sea from the North Sea via the Kattegat into narrow, shallow (<18 m water depth) straits before entering

the Baltic Sea proper (Reissmann et al., 2007; Yu and Berglund, 2007). There are two distinct types of episodic marine inputs; winter-springtime episodes driven by the aforementioned barotropic gradient along with persistent southwesterly prevailing winds, and summer-autumn episodes driven by lateral variations in salinity and persistent calm conditions (Reissmann et al., 2007; Yu and Berglund, 2007). These episodic marine inputs are the dominant inflowing currents shown in Figure 1.

After passing through the straits into deeper water, the higher salinity inflowing water sinks to the bottom, resulting in a stratified water column throughout the entire Baltic Sea. Saline bottom water is separated from fresher surface waters by a permanent halocline at 20-80 m depth (Kotthoff et al. 2017). Episodic marine inputs are the only mechanism for ventilating bottom water in the Baltic Sea (Reissmann et al., 2007), the weakness of which allows the creation of anoxic bottom waters in the deeper sub-basins such as the Gotland Basin. These anoxic bottom waters are reflected in the sedimentary record as dark clay laminae. In the Gotland Basin, the permanent halocline rests at 70-80 m water depth, separating 11-14% saline bottom water from 7% saline surface water (Matthäus, 1995). Throughout the Mid-to late-Holocene study timeframe, similar hydrographic circulation occurred, dependent on inter-related changes in sea level, glaciation, isostatic rebound and climate.

The water volume of the Baltic Sea is approximately at equilibrium, with annual terrestrial runoff (+436 km³/year), precipitation (+224 km³/year), evaporation (-184 km³/year), surface outflow (-947 km³/year) and North Sea inflow (~500 km³/year) showing a negligible net volumetric difference (HELCOM, 1993; Reissmann et al., 2007).

2.3 Dinoflagellates in the Baltic Sea

Dinoflagellates are a diverse group of aquatic eukaryotic protists with a complex life cycle (Figure 3; Figure 2, Bravo and Figueroa, 2014). Over 2000 species of dinoflagellates have been described, inhabiting a wide range of hydrological conditions (Bravo and Figueroa, 2014). Dinoflagellates can be autotrophic, mixotrophic or heterotrophic (Brenner, 2004; Bravo and Figueroa, 2014). These include dozens of genera that occur in the Holocene Baltic Sea (Brenner, 2004; Yu and Berglund, 2007; Mertens et al., 2012; Ning et al., 2017).

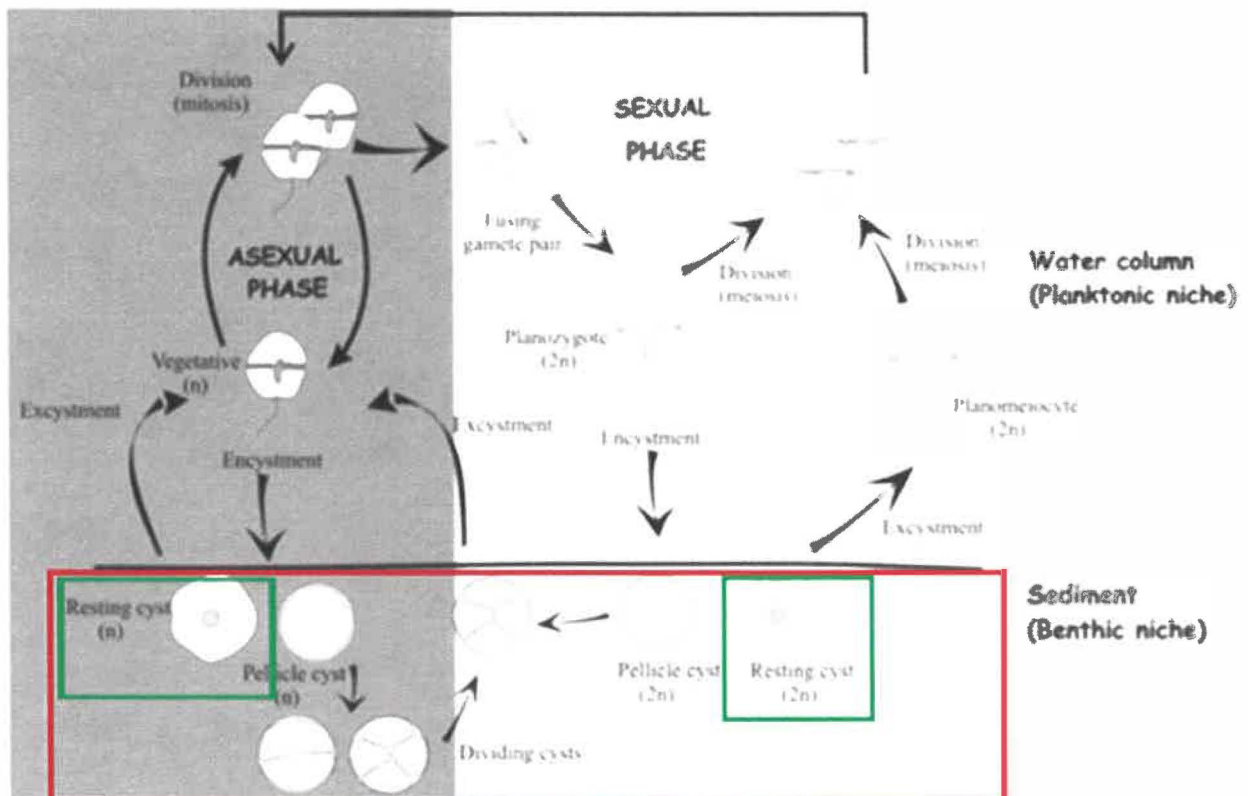


Figure 3: Life-cycle of dinoflagellates, showing the process of encystment and burial (□). Dinocysts analyzed in this study are preserved resting cysts (□) (Figure 2. Bravo and Figueroa, 2014)

As part of their life cycle, many dinoflagellates form a resting cyst in response to environmental conditions. Although some conditions are known to force encystment such as nutrient stress and harmful UV exposure, the mechanisms behind changes in the dinoflagellate life cycle are not well understood (Bravo and Figueroa, 2014). Resting cysts are composed of carbohydrate-based refractory

organic matter also referred to as dinosporin, making them exceptionally chemically and physically tough (Bravo and Figueroa, 2014). In regions such as the Baltic Sea where dinoflagellates thrived and sedimentation was sufficient, dinocysts are well preserved in high abundance in the Holocene sedimentary record.

Dinoflagellate cyst assemblage composition and intra-specific morphological variations reflect environmental conditions in which they lived. In the Baltic Sea, dinocysts preserved in the sediment are likely produced in spring and summer, when the dinoflagellates generally bloom in the surface waters (Brenner 2004).

3. Materials and Methods

3.1 Sediment Core

The source material for this study is sediment core #303600-3 or 303600N, recovered in 2011 from 170 m water depth at (56°55.01N - 19°19.99E) in the Gotland Deep, Baltic Sea (Virtasalo et al., 2011). The core was recovered using a gravity corer by the crew of the *R/V Poseidon* and immediately sealed on board. This study deals with the Mid-to late-Holocene (96-6040 years BP) sedimentary sequence, or the top 201 cm of the core, composed of organic rich clay (Figure 4 modified from Fig. 3 Virtasalo et al., 2011). Intervals of deep water hypoxia interpreted by Zillén et al. (2008) and Andrén et al. (2011) from 6000 – 4000 years BP and 2000 – 800 years BP correlate with intervals of dark clay laminae in the core.

3.2 Palynological Slide Preparations

Prior to analysis, palynological microscope slides were prepared at Geotop research center, Montréal, QC. After the core was sub-sampled at every 10 cm, the sediment samples were processed chemically and physically, as shown in Figure 5. A standard procedure for palynological preparation is generally followed for all

dinocyst analyses worldwide, with small methodological variations adapted to the local sediments. This allows for better data comparison between the different laboratories and study areas. For example, Price et al., (2016) used 15 and 120 μm sieves to filter residue from their samples collected in diverse marine sediments, while Geotop used 10 and 106 μm sieves. The addition of a known quantity of *Lycopodium clavatum* spores are used to calculate the absolute abundance of dinocysts in the sediment, as well as a useful, nearly omnipresent scale. To avoid false comparisons with other pollen grains, the *Lycopodium clavatum* are

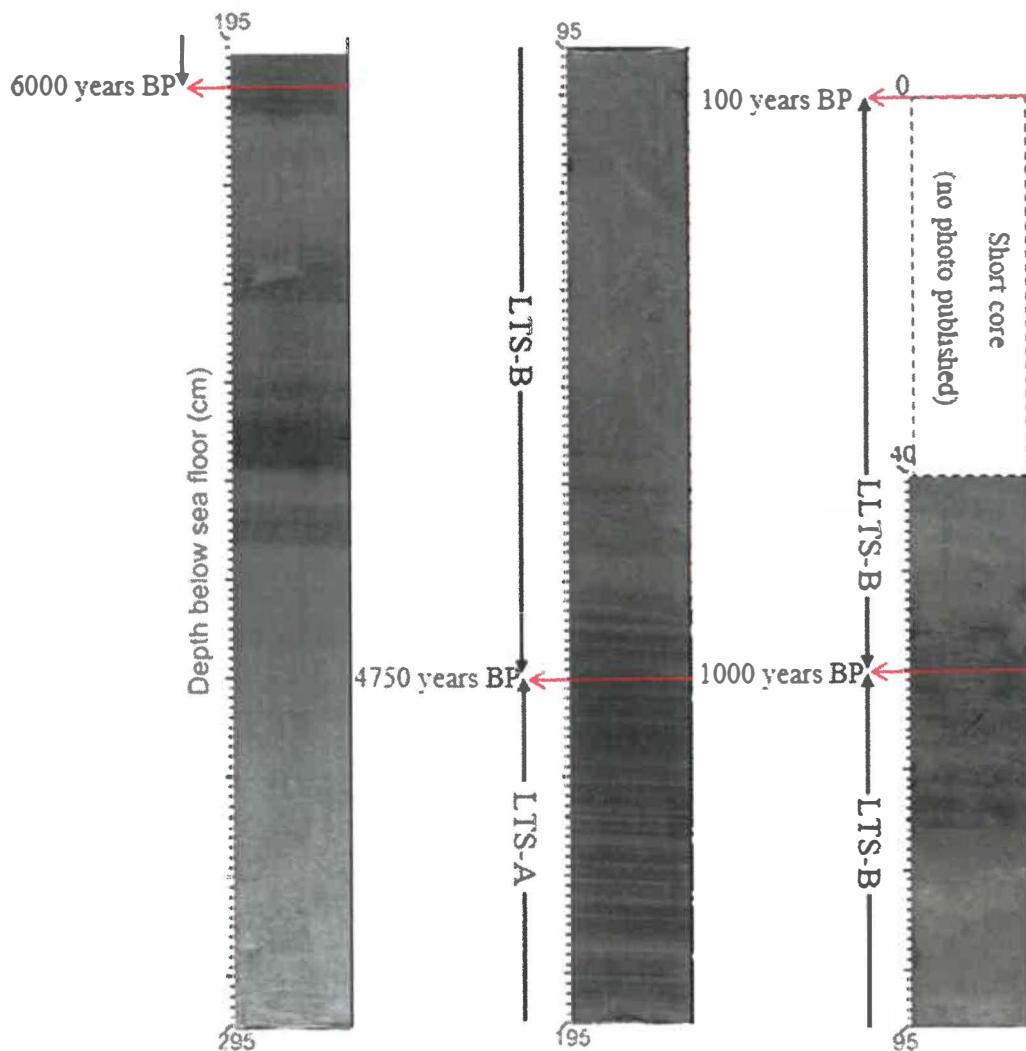


Figure 4: Sediment core 303600-3, showing the 201 cm section analyzed and interpreted hydrographic phases inferred from dinocyst assemblages (modified from Fig. 3 Virtasalo et al., 2011).

LTS-A = Littorina Sea A LTS-B = Littorina Sea B LLTS-B = Late Littorina Sea B

chemically marked before being used (Price et al., 2016). The pollen marker grains are in the form of tablets produced by the Department of Quaternary Geology, University of Lund, Lund, Sweden.

Diverse microfossils composed of similar organic material, such as pollen and planktonic crustacean eggs (Mertens et al., 2009) may also resist the palynological slide preparation.

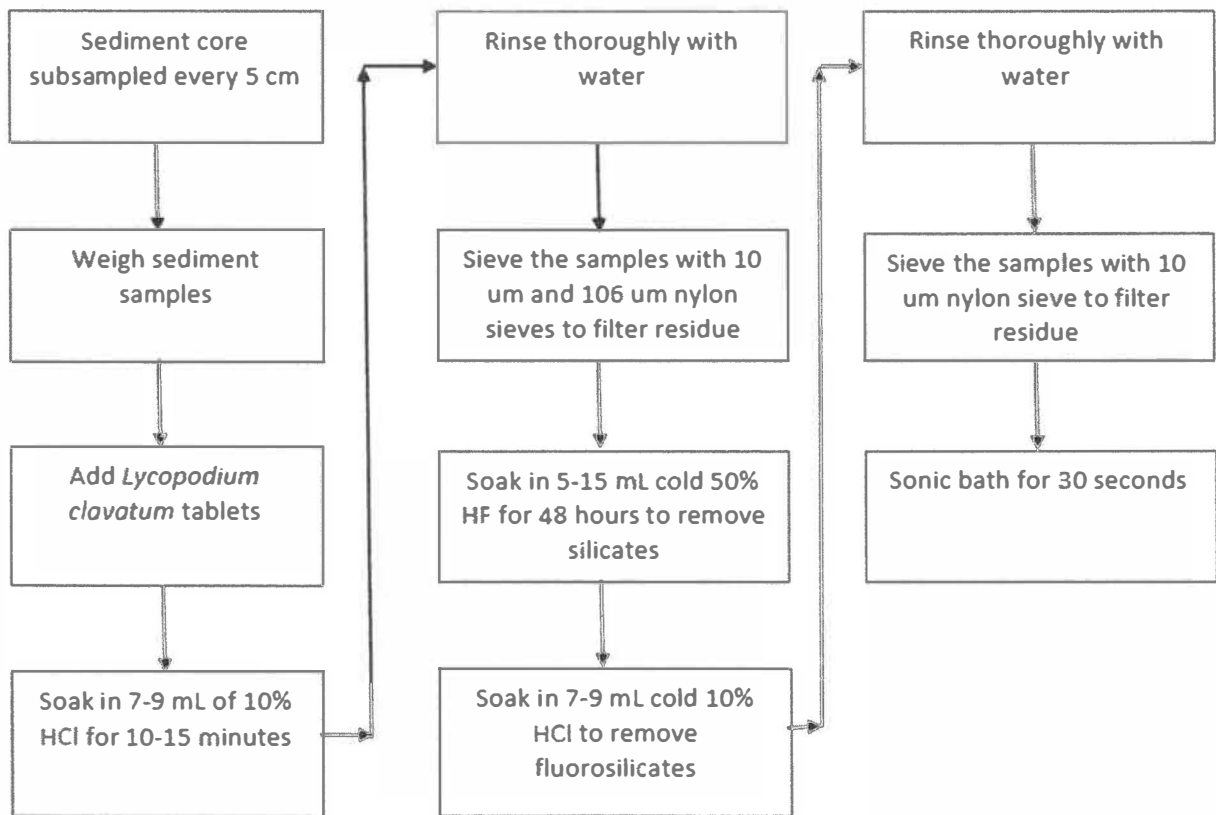


Figure 5: Palynological slide preparation process undertaken at GeoTop lab in Montreal, allowing for easy observation of diverse organics, including dinoflagellate

3.3 C-14 Dating and Sedimentation Rate

As part of the drilling and recovery process, Virtasalo et al. (2011) also published AMS C-14 dates for sediment core 303600-3, from the Poznan Radiocarbon Laboratory, Poland (Figure 6). The reservoir effect was corrected using a Baltic Sea average $\Delta R = -107 \pm 24$ and the international standard MARINE04 data set (Hughen et al., 2004). The age data is given in years before present (BP), with

1950 = 0 years BP. From this chronology the trend of constant, nearly linear sedimentation can be observed. The sedimentation rate varies between ~1-5 cm/100 years, with an average of 3.5 cm/100 years.

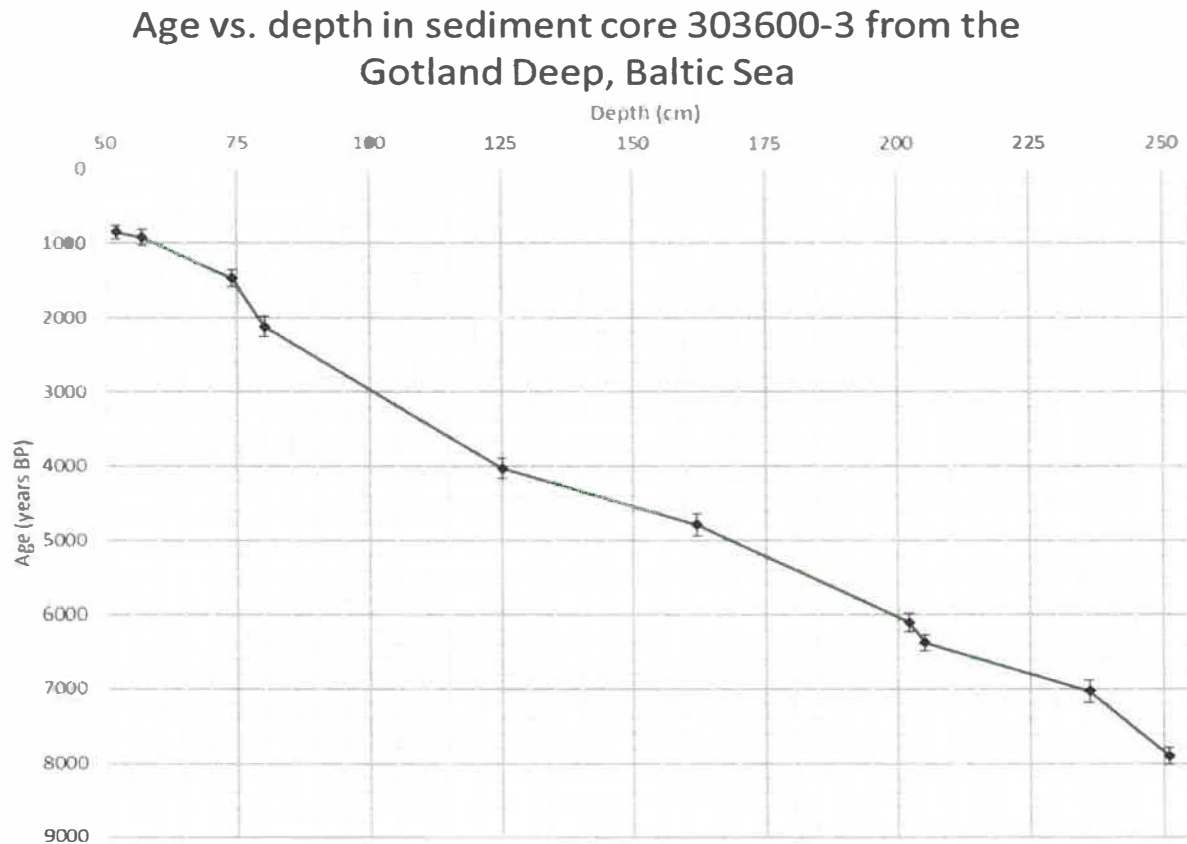


Figure 6: The age of the sediments in core 303600-3 versus depth below the seafloor, as determined by AMS-C14 dates of bulk sediments resolved by the Poznan Radiocarbon Laboratory, Poland, from Fig. 4 Virtasalo et al., (2011).

3.4 Dinocyst counts

Dinocysts were counted from the palynological slides on a Henry Louis SCISCOPE biological microscope at 40X magnification (Figure 7). Counting methods are simple; dinocysts and *Lycopodium clavatum* were observed in a side-to-side, grid observation pattern until a total of 300 dinocysts were counted for each sample. Specimens were identified to the highest level of taxonomic precision possible, using the determination key by Rochon et al. (1999). However, preservational ambiguities in the marine-brackish dinocyst genus *Spiniferites* such

as the lack of an exposed, open archeopyle required all dinocysts of genus *Spiniferites* to be counted together as *Spiniferites* spp.

3.5 Dinocyst abundance

Total populations of dinocysts in Baltic Sea sediments can be greater than 300 000 cysts/g sediment (Fig. 2, Brenner, 2004). Because of these vast populations, accurately extrapolating a sample size of counted dinocysts is essential.

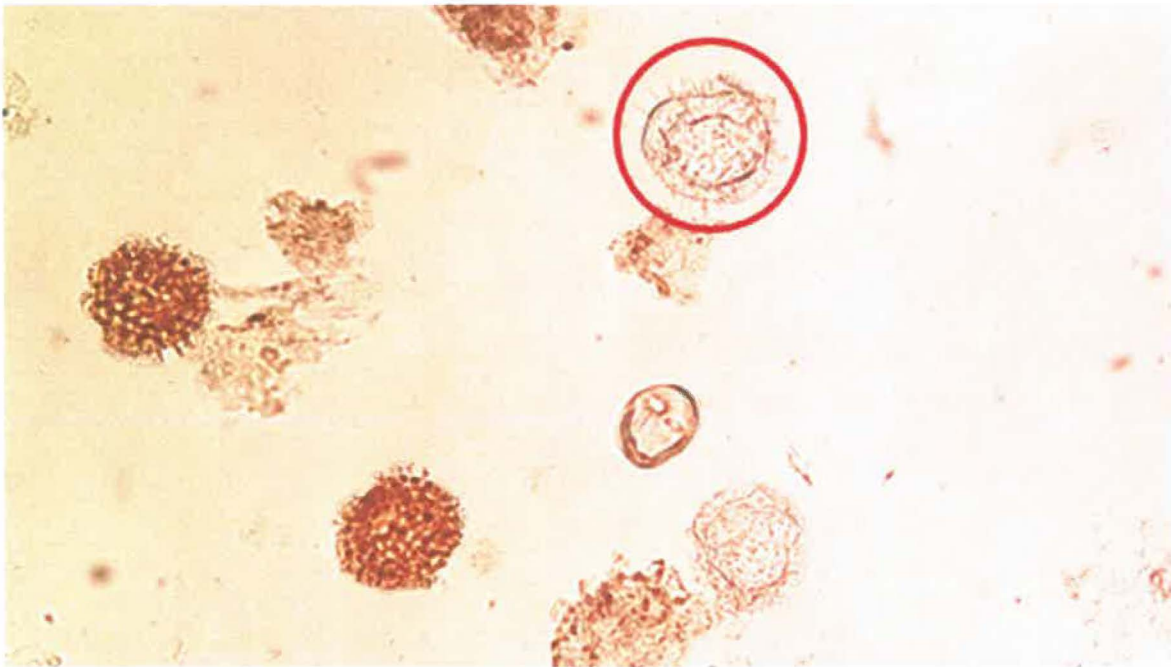


Figure 7: Dinoflagellate cyst *Operculodinium centrocarpum* (○) and *Lycopodium clavatum* spores, absolute abundance marker with a diameter of 25 μm .

A standardized method (Figure 8) by Benninghoff (1962) was used to relate *Lycopodium clavatum* and sediment weight to absolute dinocyst abundance.

4. Results

4.1 Dinocysts

During this study, 4800 dinoflagellate cysts were counted, comprising seven distinct morphological and taxonomical groups. Dinocysts were counted by taxonomical division to the species level where possible; *Ataxodinium*

zevenboomii, *Spiniferites* spp., *Lingulodinium machaerophorum* and *Operculodinium centrocarpum* were identified. *O. centrocarpum* was further divided into four groups based on process length: long (>3µm) processes, cf. Arctic morphotype with both long and short processes, truncated processes and short processes. Dinocyst counts were conducted from depths of 1-201 cm on 10 cm intervals. During this time, dinocyst abundances varied significantly from 16000 to 205000 dinocysts/g sediment.

Absolute abundances of dinoflagellate cysts were calculated following the equation by Benninghoff (1962):

$$c = \frac{d_c \times L_t \times f}{L_s \times w}$$

where

c concentration = number of dinoflagellate cysts / gram dried sediment.

d_c number of counted dinoflagellate cysts
 L_t number of *Lycopodium* spores/tablet
 f number of tablets added to the sample
 L_s number of counted *Lycopodium* spores
 w weight of dried sediment (g)

Figure 8: Description of the formula used to calculate the absolute abundance of dinocysts in sediment core 303600-3 (Benninghoff, 1962).

4.1.1 Littorina Sea Transgression/A

6000 – 4750 years BP

Beginning at the bottom of the sedimentary sequence analyzed (6000 years BP/ 201 cm), dinoflagellate assemblages are dominated by *O. centrocarpum*, 80% with short processes. During the entire 6000 – 4750 years BP range, there is a constant increase in the relative abundance of *O. centrocarpum* with long processes and concurrent decrease in *O. centrocarpum* short processes. This trend is strongest from 6000 – 5400 years BP, but continues until 4750 years BP. The relative

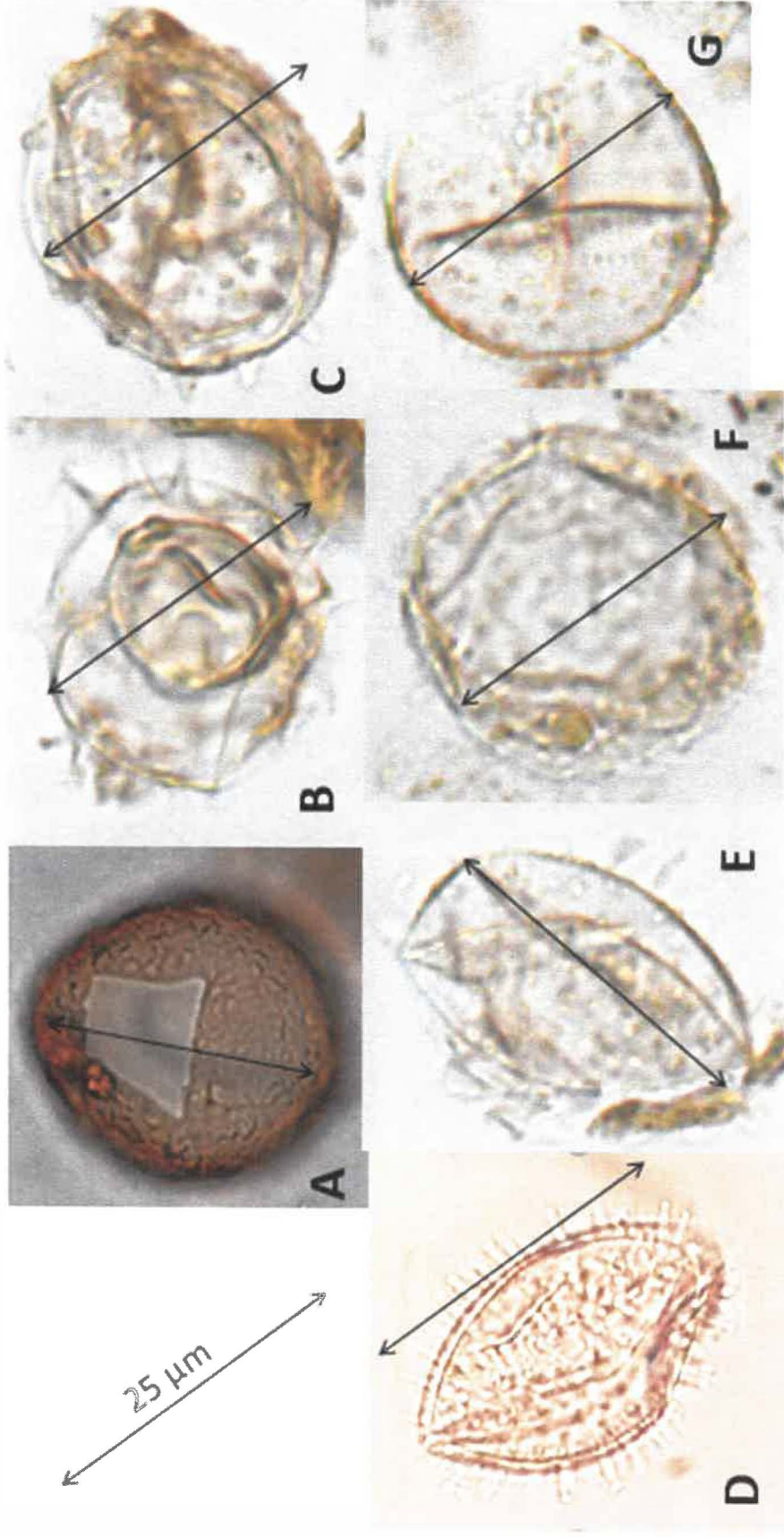


Figure 9: Dinoflagellate cysts observed in the Gotland Basin sediment core 303600-3.

A = *Ataxodinium zevenboomii*

B = *Spiniiferites* spp.

C = *Lingulodinium machaerophorum*

DEFG = *Operculodinium centrocarpum*, morphotypes long (>3µm) processes (D), cf. Arctic (E), truncated processes (F) and short processes (G)

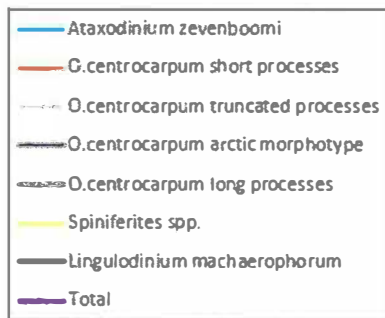
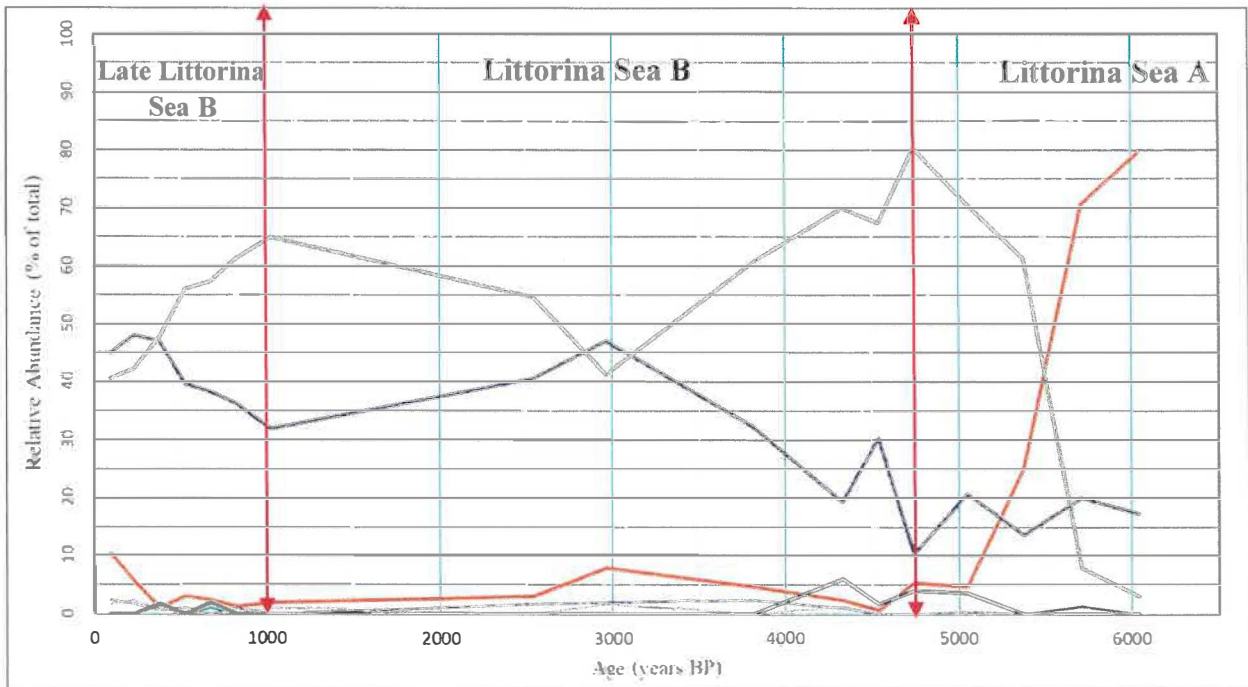
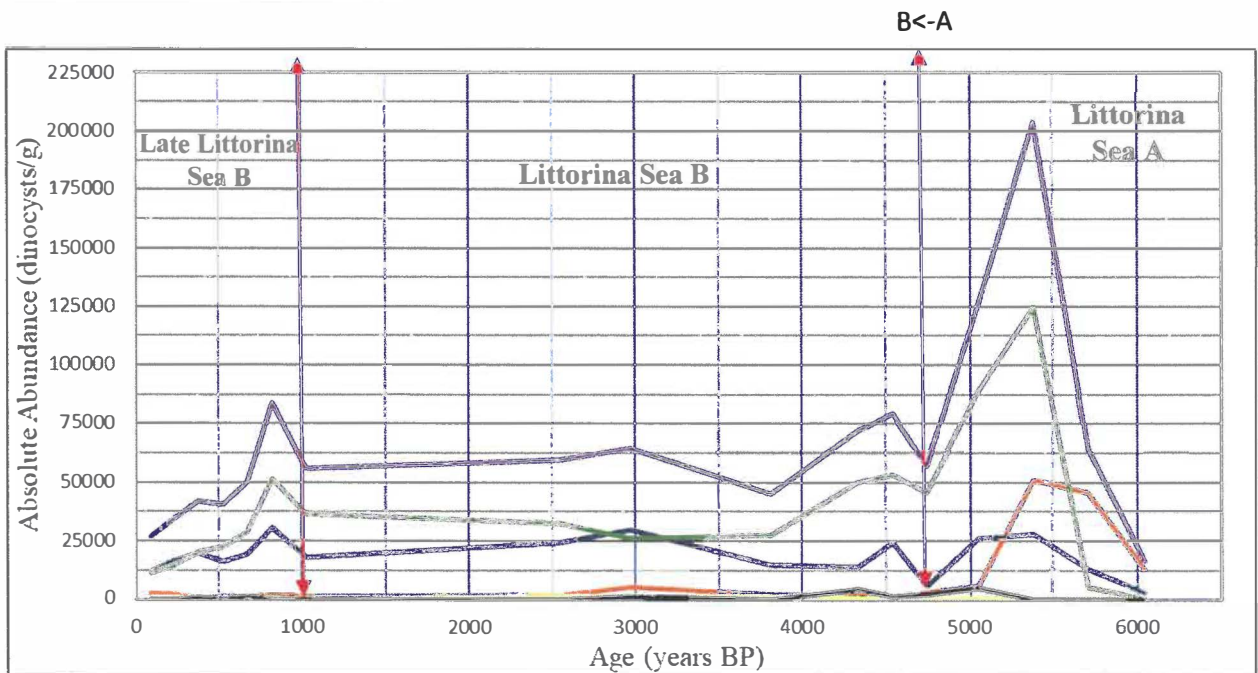


Figure 10: Relative abundance (% of taxa) versus age in sediment core 303600-3, showing the interpreted division between the Littorina Sea A/B and the Late Littorina Sea.

Figure 11: Absolute abundance of dinocyst taxa observed in dinocysts/g versus age in sediment core 303600-3, showing the interpreted division between the Littorina Sea A/B and the Late Littorina Sea.



abundances of short and long process *O.centrocarpum* switch from <5% to 80% during this time. *L. machaerophorum* first appears at 5400 years BP and remains in low concentrations (1 – 6%, <5000 dinocysts/g sediment) for the rest of the phase. Low concentrations (<3%) of *Spiniferites* spp. are present at 6000 and 5000 years BP.

Total dinocyst abundance is at a minimum of 16000 dinocysts/g sediment at 6000 years BP, then increases quickly to a study maximum of 205000 dinocysts/g sediment at 5400 years BP before decreasing to 57000 dinocysts/g sediment at 4750 years BP. *O.centrocarpum* long processes, cf. Arctic morphotype and short processes all reach an absolute abundance maximum at 5400 years BP, with 125000, 50000 and 28000 dinocysts/g sediment before declining to 45000, 6000 and 3000 dinocysts/g sediment, respectively. *O.centrocarpum* short processes reach low concentrations (5%, <5000 dinocysts/g sediment) by 5000 years BP.

4.1.2 Littorina Sea A→B

4750 – 1000 years BP

The assemblage at 4750 years BP is 80% dominated by *O.centrocarpum* long processes, with Arctic morphotype, short processes and *L.machaerophorum* making up the rest. From 4750 – 3000 years BP there is a gradual decrease in the relative abundance of *O.centrocarpum* long processes and a concurrent increase in *O.centrocarpum* cf. Arctic morphotype and short processes. This trend is caused by a decrease in absolute abundance of *O.centrocarpum* long processes from 47000 – 27500 dinocysts/ g sediment from 4750 – 3800 years BP followed by a constant absolute abundance from 3800 – 3000 years BP. During this time, *O.centrocarpum* cf. Arctic morphotype absolute abundance increase from 6000 – 30000 dinocysts/g sediment. There is a sharp maximum (31%) in the *O.centrocarpum* cf. Arctic morphotype relative abundance and associated

minimum in *O.centrocarpum* long processes (41%) at 4500, interrupting the trend. This is caused by a minor increase in *O.centrocarpum* Arctic morphotype absolute abundance and a concurrent, but less pronounced increase in *O.centrocarpum* long processes absolute abundance. *L.machaerophorum* is present in low concentrations (<5000 dinocysts/g sediment, <6%) from 4750 – 3800 years BP. From 3000-1000 the *O.centrocarpum* assemblage trend reverses, with a gradual increase in *O.centrocarpum* long processes relative abundance and associated decrease in *O.centrocarpum* cf. Arctic morphotype and short processes. By 1000 years BP, *O.centrocarpum* relative abundances had returned to 65% long processes and 32% cf. Arctic morphotype. This is caused by a decrease in *O.centrocarpum* cf. Arctic morphotype (27 000 – 18 000 dinocysts/g sediment) and short processes (3 000 – 1000 dinocysts/g sediment) absolute abundance and increase in *O.centrocarpum* long processes absolute abundance (26 000 – 37 000 dinocysts/g sediment). Relative abundances of *O.centrocarpum* short processes are low in this phase, peaking at 8% at 3000 years BP. *Spiniferites* spp. is present in low concentrations (<1500 dinocysts/g sediment, <3 %) from 4300 – 2500 years BP. *O.centrocarpum* truncated processes are present in low concentrations (<3%, <1500 dinocysts/g sediment) at 4300, 3000 and 1000 years BP. Total dinocyst abundance during this phase ranges from 45000 – 80 000 dinocysts/g sediment. Beginning at 4750 years BP, the absolute abundance increases to a phase maximum of 80 000 dinocysts/g sediment at 4500 years BP, then fluctuates to a phase minimum of 45000 dinocysts/g sediment at 3800 years BP and a minor maximum of 64000 dinocysts/g sediment at 3000 years BP. From 3000 – 1000 years BP the total absolute abundance remains relatively stagnant at 56 000 dinocysts/g sediment. Notably absent from the entire assemblage are dinocysts *Pyxidinopsis psilata* and *Ataxodinium choane*, observed in similar studies by Brenner (2004), Yu and Berglund (2007) and Ning et al., (2017).

Figure 12: Relative abundance of dinocysts (%) identified in sediment core 303600-3 versus time (years BP).

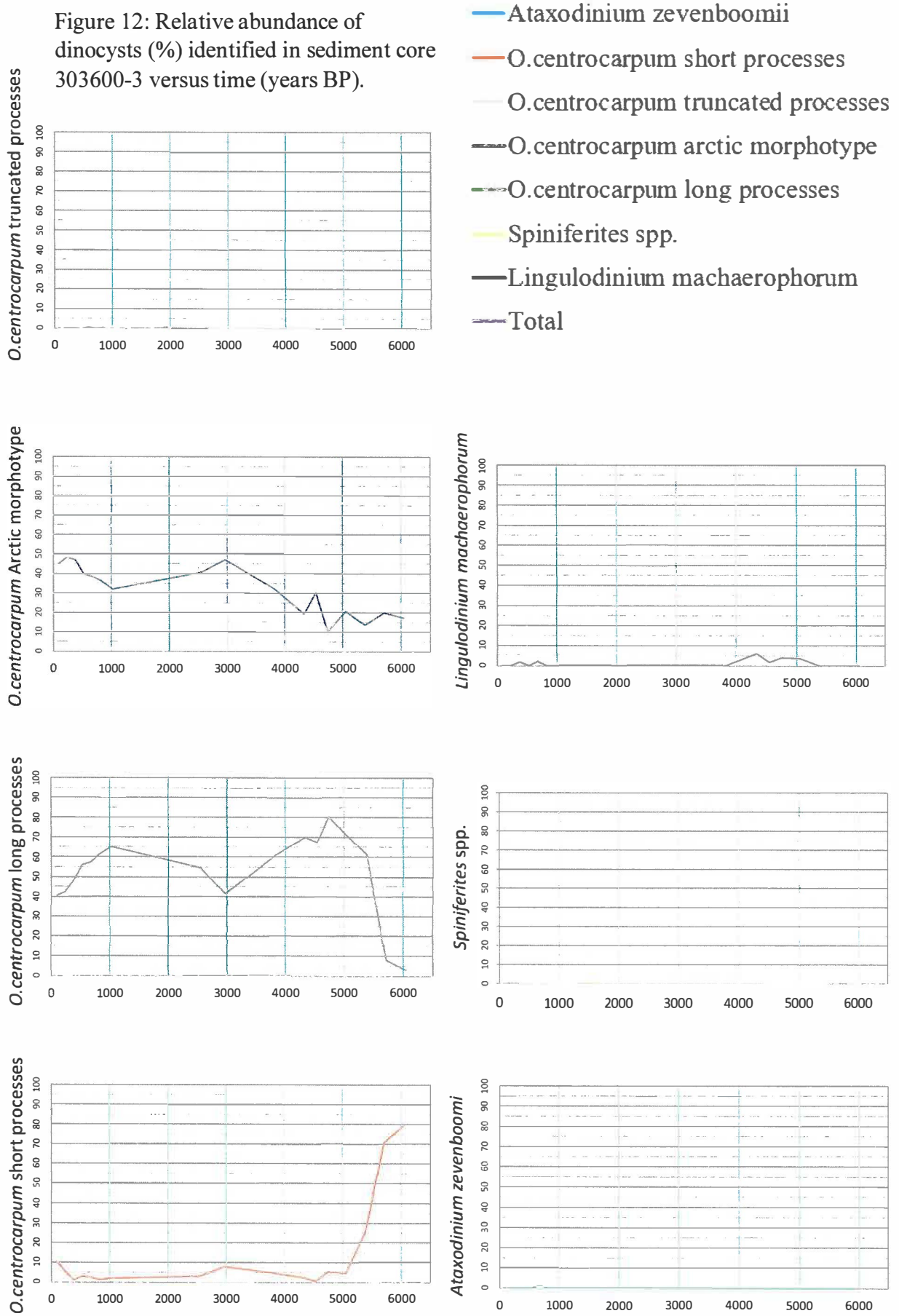
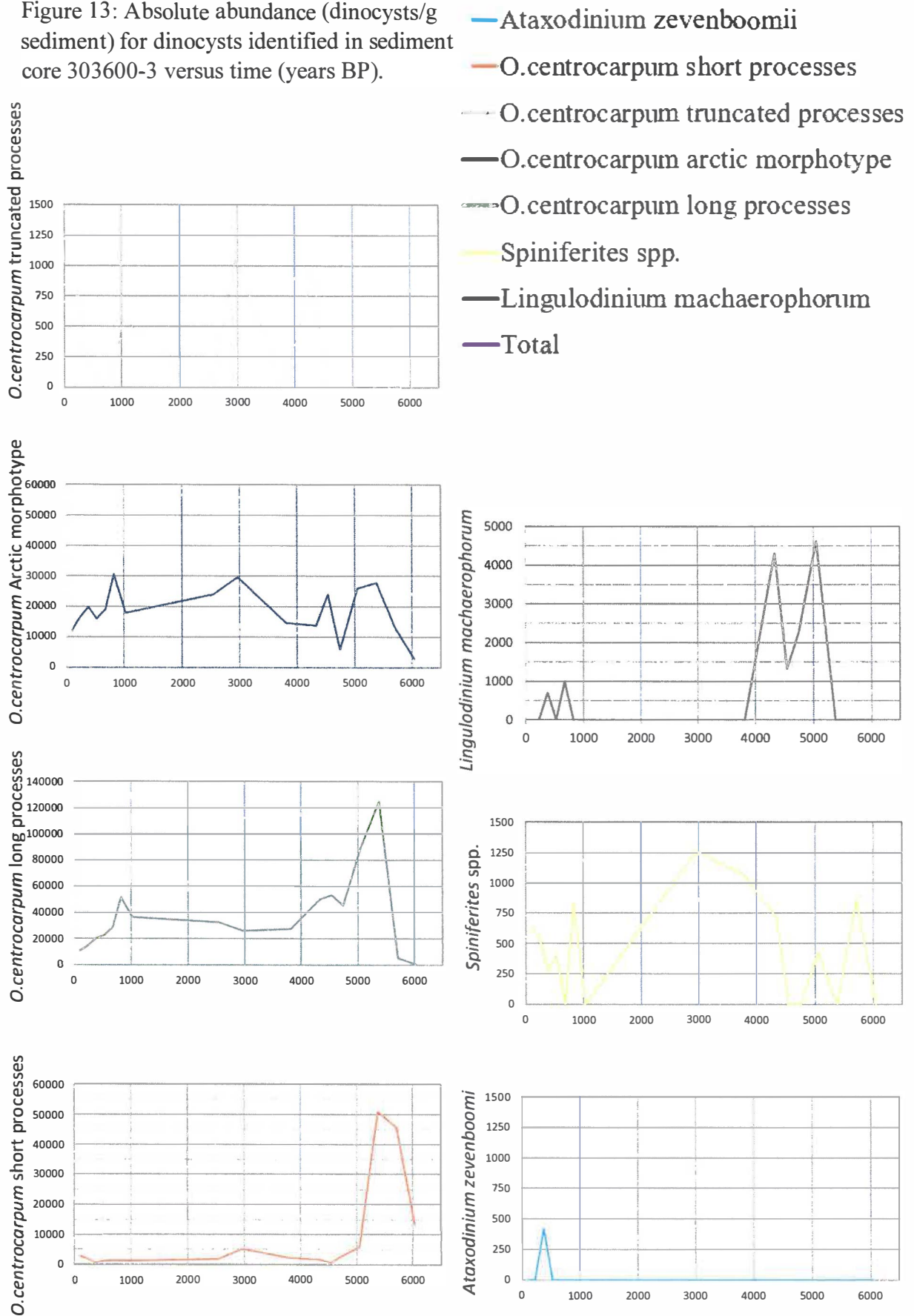


Figure 13: Absolute abundance (dinocysts/g sediment) for dinocysts identified in sediment core 303600-3 versus time (years BP).



4.1.3 Late Littorina Sea/B

1000 years BP - Recent

From 1000-100 years BP, there is a decrease in the relative abundance of *O.centrocarpum* long processes (65% to 40%) and a concurrent increase in cf. Arctic morphotype (32 to 45%) and short processes (1-10%). *L.machaerophorum* re-appears in low concentrations from 800-250 years BP. *Spiniferites* spp. are present in low concentrations from 1000 -100 years BP, with one gap at 700 years BP. *O.centrocarpum* truncated processes are present in low concentrations (<3%, <1500 dinocysts/g sediment) at 1000 years BP and 700 – 100 years BP.

From 1000 – 800 years BP, there is an increase in total dinocyst abundance from 56 000 – 84000 dinocyst/g sediment. This is followed by a steady decrease in total dinocyst abundance, with concentrations of 25000 dinocysts/g sediment by 100 years BP. The total dinocyst abundance peak at 800 years BP is driven by 1000 – 800 years BP increases in *O.centrocarpum* long processes and Arctic morphotype absolute abundance. In addition, *Spiniferites* spp. is present in low concentrations at 800, 500 – 100 years BP after being absent since 3000 years BP. *Ataxodinium zevenboomi* is uniquely present in low concentration (1%, <500 dinocysts/g sediment) at 700 years BP.

5. Discussion

5.1 Timeline of hydrographic changes

Dinocyst assemblages are commonly analyzed in Baltic Sea Holocene sediments (Brenner, 2004; Yu and Berglund, 2007; Verleye et al., 2012; Ning et al., 2017). In particular, taxonomic and morphological variations in dinoflagellate cysts reflect the sea-surface summertime environmental conditions in which they lived (Brenner, 2004). The semi-enclosed nature of the Baltic Sea ensures that the locally buried assemblage reflects the local population.

5.1.1 Littorina Sea Transgression/A

6000 – 4750 years BP

In the oldest sediments analyzed (6000 years BP/ 201 cm), dinoflagellate assemblages are dominated by *O.centrocarpum*. Mertens et al. (2011) established the current understanding of the relationship between *O.centrocarpum* process length and water salinity; showing the strong positive correlation through sampling of recent dinocysts. This correlation, and other similar morphological variations in dinocysts are used worldwide to interpret changes in salinity (Verleye et al., 2012; Zonneveld et al., 2013; Sildever et al., 2015; Ning et al., 2017). In this phase, increasing process length in *O.centrocarpum* assemblage is interpreted as an increase in salinity from 6000 – 4750 years BP, the entire phase. This salinity increase is interpreted as the mixing of the Baltic Sea with marine waters flowing into the Sea via the Kattegat. This is likely a continuation of the Littorina Transgression, whereby eustatic rise reconnected the North and Baltic Seas approximately 7800 years BP (Brenner, 2004; Ning et al., 2017). During this time, freshwater runoff into the Baltic Sea stayed relatively stable (Gustafsson and Westman, 2002). Because our sampling resolution does not show the interval preceding the transgression, the salinity increase observed from 6000 – 4750 years BP is interpreted as a maximum seawater input, not the original marine transgression. This is consistent with a paleosalinity reconstruction in the Gotland Basin by Emeis et al. (2003), showing increasing salinity from before 6000 – 5000 years BP, before remaining in a state of “+/- stable high salinity” until 4000 years BP. In addition, Westman and Sohlenius (1999) analyzed Baltic Sea diatom assemblages and interpreted 7000-4500 years BP as the time of increasing salinity caused by increasing marine input through the Kattegat, with erosion of the straits reaching a maximum by 6000 years BP. *L. machaeorophorum* can only exist in conditions with salinity of 8+ practical salinity units (psu) (Pankow, 1990;

Brenner, 2004), therefore the salinity must have reached this point by 5400 years BP and remained above it until 3800 years BP. Emeis et al. (2003) found salinity of 8+ psu from 5300 – 4200 years BP, with the 4200-3800 years BP interval at 7-8 psu. A multi-proxy study by Gustafsson and Westman (2002) also found salinity of 8+ psu during this interval, with salinity staying above or at 8 psu from 6200 – 2000 years BP. Ning et al. (2017) reconstructed paleosalinity using Sr isotopes in mollusc shells and found a salinity maximum at 4600 years BP, and salinity >8 psu from before 6000 – 4000 years BP, where their record ends. This interval of increasing salinity is also correlated with dark laminae in the sediment core from before 6000 – 4500 years BP.

The maximum of 205 000 dinocyst/g sediment is the largest concentration observed throughout the section analyzed. Brenner (2004) observed a maximum concentration of approximately 400 000 dinocysts/g sediment just before 5000 years BP, and concentrations remained >200 000 dinocysts/g sediment until 3000 years BP. The lower concentrations observed in this study compared with a similar Gotland Basin dinocyst investigation by Brenner (2004) are interpreted as lower nutrient availability further from coastal runoff. The rapid rise of dinocyst absolute abundance from 6000 – 5400 years BP is significant but not unusual. Rapid temperature and precipitation fluctuations from 6000 – 4000 years BP resulted in warmer summers and wetter winters (Dahl and Nesje, 1996). Because warmer summers allow more time for dinoflagellates to bloom, short term variations in average summer temperature can lead to greatly increased concentrations of dinocysts (Brenner, 2004). As such, the absolute abundance maximum at 5400 is interpreted as an anomalously warm period during Mid Holocene warming. A higher resolution of dinocyst counts from 5500 – 4750 years BP would allow further analysis by showing if the absolute abundance maximum at 5400 years BP is a local peak or part of a longer period with similar concentrations.

This phase is the Littorina Sea A (LTS-A, Figure 14), where eustatic rise had recently re-established a North Sea-Baltic marine-freshwater connection. This event caused significant change to the hydrology of the Baltic, with saline bottom waters stratifying throughout to establish the permanent halocline that has persisted ever since. Mixing between the marine and fresh waters created the brackish conditions of Baltic Sea during the last 7800 years BP. These hydrographic changes are reflected in the constant change in dinocyst assemblage towards a more saline assemblage. This is consistent with increasing marine water input through eroding straits between the Baltic Sea and the Kattegat and relatively low freshwater input (Gustafsson and Westman, 2002; Andr en et al., 2011). Establishing the absolute and relative timing of the transgression maximum throughout the Baltic Sea will allow more accurate regional interpretations of the evolution of the Littorina Sea.

5.1.2 Littorina Sea Stabilization/A->B

4750 – 1000 years BP

From 4750 – 3000 years BP there is an overall decrease in the relative and absolute abundance of *O.centrocarpum* long processes, and a concurrent increase in *O.centrocarpum* cf. Arctic morphotype and short processes. This is interpreted as a decrease in salinity. However, this trend is relatively weak and *O.centrocarpum* long processes concentrations never go below 40% or 25 000 dincysts/g sediment. As such, the salinity decrease from 4750 – 3000 years BP is interpreted as gradual and minor. This is consistent with Gustafsson and Westman (2002) and Emeis et al. (2003), who observed decreasing salinity from 5000 – 3100 years BP. A local interruption in this trend at 4500 is interpreted as a local salinity low, possibly caused by an increase in freshwater continental runoff (Dahl and Nesje, 1996). The presence of *L.machaeorporum* until 3800 years BP suggests that the salinity is >8 psu during that time.

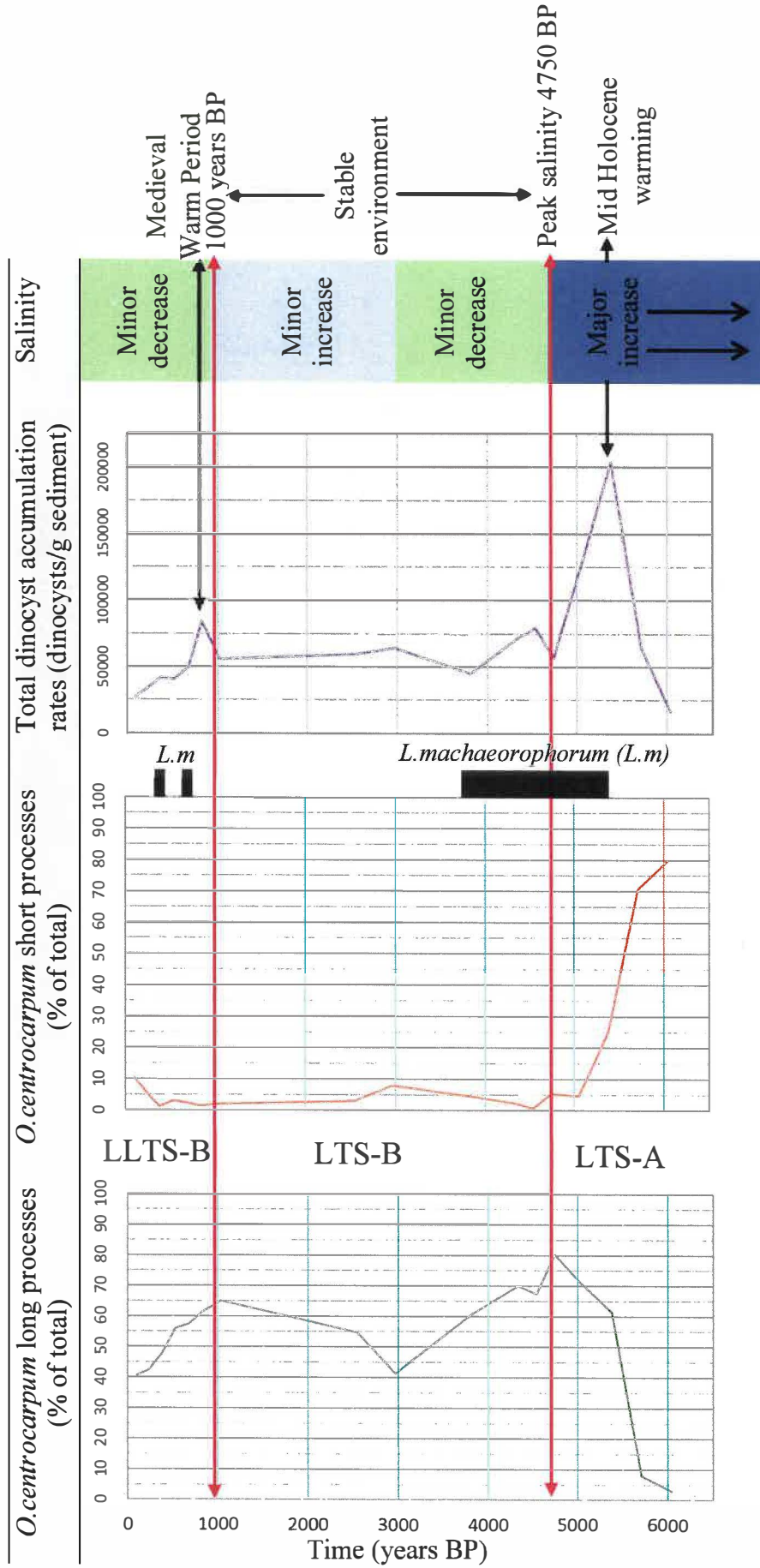


Figure 14: Discussion summary of the Mid-to Late-Holocene dinocyst assemblage from sediment core 303600-3, showing interpreted Littorina Sea phases, qualitative paleosalinity and some significant factors of discussion.

LTS-A = Littorina Sea A LTS-B = Littorina Sea B LLTS-B = Late Littorina Sea B

From 3000-1000 years BP, a gradual increase in *O.centrocarpum* long processes relative abundance and concurrent decrease in *O.centrocarpum* cf. Arctic morphotype and short processes is interpreted as a salinity increase. Again, this trend is relatively weak and *O.centrocarpum* Arctic morphotype concentrations at 1000 years BP are still relatively high at 30% and 18 000 dincysts/g sediment. Because of this, the salinity increase from 3000 – 1000 years BP is interpreted as gradual and minor. This is again consistent with Emeis et al. (2003), who observed increasing salinity from 3100 years BP to present. Conversely, Gustafsson and Westman (2002) records a stable or slightly decreasing salinity from 3000 – 1000 years BP.

Absolute abundances of dinocysts, especially *O.centrocarpum* are relatively stable during this phase at concentrations an order of magnitude lower than observed at 5400 years BP. This is consistent with Brenner (2004), Yu and Berglund (2007) and Ning et al. (2017), who all observed similar trends of decreasing abundance from 4500 years BP to stable low abundance assemblages by 3000 years BP, with little change in *O.centrocarpum* process length from 4000 – 1000 years BP. The decreased dinocyst abundance during this time is interpreted as a consequence of shorter, cooler summers during the Neoglacial period from 4000 years BP onwards (Dahl and Nesje, 1996). The presence of *Spiniferites* spp., observed in this study at 5700, 5000, 4300 – 2500, 800 and 500 – 100 years BP is interpreted by Yu and Berglund (2007) as an increase in dinoflagellate primary productivity due to an increase in warm, saline marine input.

From 4750 – 1000 BP, a remarkable lack of environmental change is reflected in the dinocyst assemblage. Dark clay laminae associated with hypoxia in bottom waters are less common in this phase than LTS-A. This phase is the Littorina Sea B (LTS-B, Figure 14), where the North Sea connection had stabilized into a source of consistent marine input.

5.1.3 Late Littorina Sea/B

1000 years BP – Recent

From 1000-100 years BP, there is an overall decrease in the relative and absolute abundance of *O.centrocarpum* long processes, and a concurrent increase in *O.centrocarpum* cf. Arctic morphotype and short processes. This is interpreted as a gradual, minor decrease in salinity caused by decreasing marine input and increasing freshwater runoff (Gustafsson and Westman, 2002). The appearance of *L.machaerophorum* from at 600, 250 years BP suggests a salinity of >8psu during that time (Brenner, 2004). Similarly, the lack of *L.machaerophorum* since 250 years BP is interpreted as salinity falling below 8psu. This is consistent with Gustafsson and Westman (2002), who defined a stable salinity of 7-8 psu during the last 1000 years BP. However, this trend is the opposite of that suggested by Emeis et al. (2003), who interpreted a rising salinity of 8-11 psu from 1100 years BP to present. Because of the discrepancies in quantitative paleosalinity reconstructions, qualitative indicators such as the *O.centrocarpum* assemblage analysis presented in this paper are useful contextual data for Baltic Sea studies.

From 1000 – 800 years BP, there is a sharp increase in total dinocyst abundance. However, this is associated with little change in the dinocyst assemblages. This is not interpreted as a major hydrologic change, which would affect the salinity and *O.centrocarpum* assemblage, but as a period of high productivity during elevated temperatures. Known as the Medieval Warm Period (MWP) or the Medieval Climate Anomaly, a period in Europe from 1100 – 650 years BP with stable climatic conditions and temperatures up to 0.8 C above the 20th century average, as shown in Figure 15 (Büntgen et al., 2011; Fig. 3.1 BACC II Author Team, 2015).

These elevated temperatures may have enabled higher concentrations of dinocysts to accumulate during longer, warmer growth seasons. There is only a relatively

small salinity increase (Emeis et al., 2003) or stagnation (Gustafsson and Westman, 2002) during the MWP. It has also been suggested that increased anthropogenic land use during the MWP contributed to higher nutrient runoff into the Baltic Sea (Zillén and Conley, 2010; Andrén et al., 2011). This would also lead to higher dinocyst concentrations. However, the correlation between land use and nutrient availability in the Baltic Sea surface waters is not yet well understood. Increases in absolute abundance of *O.centrocarpum* long processes and Arctic morphotype, as well as *Spiniferites* spp. from 1000-800 years BP during the MWP

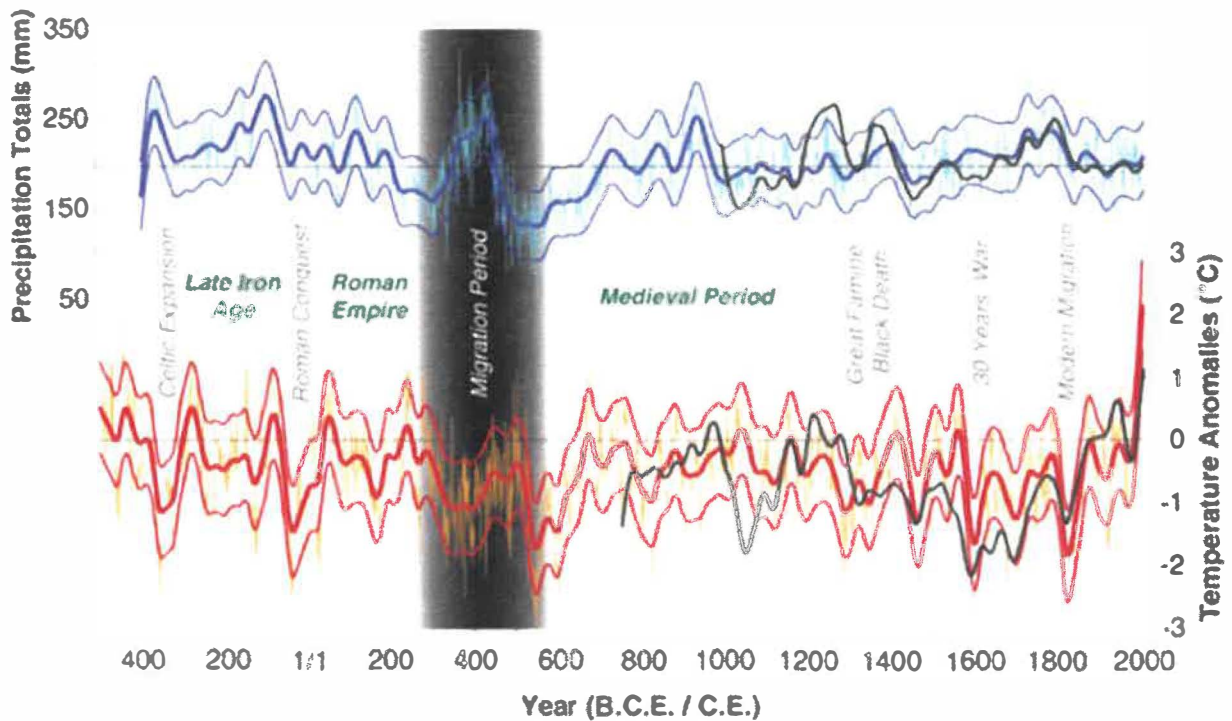


Figure 15: June-August average temperature (thick red) and April-June precipitation totals (thick blue) throughout central Europe for the last 2500 years reconstructed from tree rings, relative to their respective 20th century average. ± 1 Root Mean Squared Error (RMSE) bars and 60-year low pass filters (thin red and blue) are shown along the main trendlines. Additionally, black lines show independent Swiss temperature (Büntgen et al., 2006) and German precipitation (Büntgen et al., 2010) reconstructions (Büntgen et al., 2011; Fig 3.1 BACC II Author Team, 2015).

culminate in an abundance maximum of 84 000 dinocysts/g sediment at 800 years BP. Brenner (2004) observed a similar trend, with stable dinocyst concentrations

from 3000 – 1000 years BP, peaking just after 1000 years BP. Andrén (1999) recorded high diatom productivity during the MWP from 950 – 800 years BP. From this abundance maximum at 800, the absolute abundance of dinocysts decreases rapidly to 100 years BP levels of 27 000 dinocysts/g sediment. This stagnant then decreasing trend in salinity and dinocyst abundance from 800-100 years BP is consistent with Brenner (2004), Head (2007), Yu and Berglund (2007) and Ning et al., (2017). Andrén (1999) interpreted a similar change in diatom assemblages beginning at 850 – 750 years BP as influenced by colder, wetter conditions during the Little Ice Age.

This is the Late Littorina Sea B (LLTS-B, Figure 14), where the marine connection persists, but time between marine water inputs is higher. This is likely correlated with isostatic rise being slightly greater than erosion in the straits connecting the Baltic and Kattegat (Ning et al., 2017; Andrén et al., 2011).

5.2 Geochronology Considerations

The chronological framework for sediment core 303600-3 is based on AMS-14C dating of the bulk sediment (Fig. 4, Virtasalo et al., 2011). However, it has been shown by Hedenström and Possnert (2001) that bulk sediment dating in the Baltic Sea may overestimate dates by 700-1500 years when compared to *in situ* terrestrial macrofossils due to the reworking of older reservoir sediment into younger sea bottom stratigraphy. Comparison of palynological data including dinocyst assemblages combined with C-14 dates would help further resolve the timing of environmental changes in the Holocene Baltic Sea. For example, when considered as a coherent data set, it is possible to observe how the timing of maximum salinity varied throughout the region during the Littorina Sea A (interpreted in this study as 4750 years BP in the Gotland Basin) as inferred from dinocyst assemblages.

5.3 Future studies

Palynological slides sampled from sediment core 303600-3 preserve diverse organic material, including dinocysts. Among others, algae, invertebrate mandibles and pollen are all well represented. Analyzing each micropaleontological assemblage in the core would be valuable in their own unique ways, but a multi-proxy study of several microfossils as well as geochemical data (carbon or oxygen isotopes) along with radiocarbon dates such as Brenner (2004) would allow a more sophisticated discussion of environmental change.

6. Conclusion

Holocene dinoflagellate cyst assemblages in the Baltic Sea reflect well the hydrographic conditions they experienced, allowing for qualitative analysis of the salinity. The Littorina Transgression was already underway in the eastern Gotland Deep by 6000 years BP. Dinoflagellate cysts show increasing saline influence from 6000 – 4750 years BP, when the transgression reached a maximum. This is likely correlated with increasing marine volume input as well as decreasing or stable freshwater runoff from continental Europe and Scandinavia. Temperature and precipitation fluctuations during Mid Holocene warming lead to high concentrations (205 000 dinocysts/g sediment) of dinocysts at 5400 years BP.

From 4750 – 1000 years BP, only minor changes in salinity are reflected in the dinocyst assemblage. From 4000 – 1000 years BP, low concentrations (<80 000 dinocysts/g sediment) of dinocysts are observed due to shorter ‘Neoglacial’ summers. This is the most stable phase of the Holocene Baltic Sea.

Dinocyst abundance increases prominently from 1000 – 800 years BP during the MWP before declining from 800 – 100 years BP to very low concentrations (25 000 dinocysts/g sediment). This is correlated with longer, warmer summers during the MWP and shorter, cooler summers during the Little Ice Age. In addition, it is

plausible that anthropogenic land use during the MWP released higher nutrient runoff into the Baltic Sea, leading to increased dinocyst abundance.

During the entire 1000 – 100 years BP period, dinocyst assemblages show gradually decreasing salinity, interpreted as rising freshwater runoff and decreasing marine input.

Appendix A

Dinocyst counts

Sediment Core 303600N	Depth (cm)	Radiocarbon Age (Year BP)	Total Dinocysts	Dinocyst																	
				Lycopodium	Morphotype	Short/absent	Truncated	Arctic	>3 um	Spiniferites	Lingulodinium	Species	zevenboomii	centrocarpum	spp.	marhaerophorum					
	0-1	96	300			31	5	135	122												
	10-11	230	300			17	7	144	127												
	20-21	379	300	199		3	2	141	143												
	30-31	528	300	278		9	1	119	168												
	40-41	677	300	265		7		115	172												
	50-51	826	300	192		4		109	184												
	60-61	1027	300	207		6	3	96	195												
	90-91	2544	300	217		9		122	164												
	100-101	2967	300	249		24	5	141	124												
	120-121	3813	300	237		14		97	182												
	140-141	4333	300	254		7	4	58	210												
	150-151	4539	300	261		2		91	202												
	160-161	4745	300	316		16		31	241												
	170-171	5050	300	289		14		62	212												
	180-181	5380	300	268		75		41	184												
	190-191	5710	300	254		212		60	24												
	200-201	6040	300	789		239		52	9												

Appendix A: Sediment core depth and age alongside the associated assemblage of dinocysts counted.

Appendix B

Palynological Slide Data

Depth (cm)	Trendline Age (year BP)	# of tablets added (t)	# of counted <i>Lycopodium</i>		weight (g) of dried sediment (w)	# of <i>Lycopodium</i> /tablet (L)
			(/c)			
0-1	96	4	1107		0.749	18584
10-11	230	4	678		0.9655	18584
20-21	379	2	399		0.6629	18584
30-31	528	2	378		0.7301	18584
40-41	677	2	265		0.841	18584
50-51	826	2	292		0.4537	18584
60-61	1027	2	207		0.9629	18584
90-91	2544	2	217		0.8659	18584
100-101	2967	2	249		0.7091	18584
120-121	3813	2	237		1.0401	18584
140-141	4333	2	254		0.6116	18584
150-151	4539	2	261		0.5387	18583
160-161	4745	3	316		0.9338	18583
170-171	5050	2	289		0.3063	18583
180-181	5380	2	268		0.2043	18583
190-191	5710	2	254		0.6785	18583
200-201	6040	2	789		0.8574	18583

Appendix B: Sediment core depth and age alongside the number of counted *Lycopodium* and the associated palynological slide parameters used to calculate the absolute abundance of dinocysts in the sediment.

Sediment Core
303600N

Appendix C

Dinocyst Relative Abundance

Sediment Core 303600N	Depth (cm)	Trendline Age (year BP)	Dinocyst		Spiriferites		Lingulodinium			
			Genus	Species	zeverboomii	centrocarpum	spp.	machaerophorum		
	0-1	96			10	2	45	41	2	0
	10-11	230			6	2	48	42	2	0
	20-21	379			1	1	47	48	1	2
	30-31	528			3	0	40	56	1	0
	40-41	677			2	0	38	57	0	2
	50-51	826			1	0	36	61	1	0
	60-61	1027			2	1	32	65	0	0
	90-91	2544			3	0	41	55	2	0
	100-101	2967			8	2	47	41	2	0
	120-121	3813			5	0	32	61	2	0
	140-141	4333			2	1	19	70	1	6
	150-151	4539			1	0	30	67	0	2
	160-161	4745			5	0	10	80	0	4
	170-171	5050			5	0	21	71	0	4
	180-181	5380			25	0	14	61	0	0
	190-191	5710			71	0	20	8	1	0
	200-201	6040			80	0	17	3	0	0

% of total

Appendix C: Sediment core depth and age alongside the associated assemblage of dinocysts, showing the relative abundance of each taxonomically and/or morphologically distinct group (% of total).

Appendix D

Dinocyst Absolute Abundance

Sediment Core 3036G0N	Depth (cm)	Trendline Age (year BP)	Dinocyst		Spiriferites		Total			
			Genus	Species	Genus	Species				
	0-1	96	0	2779	448	12203	10938	628	0	26896
	10-11	230	0	1930	795	16352	14422	568	0	34067
	20-21	379	422	422	281	19814	20095	281	703	42016
	30-31	528	0	1212	135	16027	22626	404	0	40403
	40-41	677	0	1167	0	19179	28685	0	1001	50032
	50-51	826	0	1122	0	30580	51622	842	0	84166
	60-61	1027	0	1119	559	17901	36362	0	0	55942
	90-91	2544	0	1780	0	24132	32440	989	0	59342
	100-101	2967	0	5052	1053	29681	26103	1263	0	63151
	120-121	3813	0	2111	0	14826	27442	1055	0	45234
	140-141	4333	0	1675	957	13877	50244	718	4307	71778
	150-151	4539	0	529	0	24055	53396	0	1322	79301
	160-161	4745	0	3023	0	5857	45532	0	2267	56678
	170-171	5050	0	5878	0	26031	89010	420	0	125957
	180-181	5380	0	50910	0	27831	124899	0	0	203640
	190-191	5710	0	45719	0	12939	5176	863	0	64697
	200-201	6040	0	13131	0	2857	494	0	0	16482

Appendix D: Sediment core depth and age alongside the associated assemblage of dinocysts, showing the absolute abundance of each taxonomically and/or morphologically distinct group (dinocysts/g sediment).

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