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Seasonal climate variations in the Baltic Sea during the Last Interglacial based on foraminiferal geochemistry

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A B S T R A C T

Climate during the Last Interglacial period (LIG, Marine Isotope Stage 5e) was on average warmer than the present, with a higher global sea level but also more unstable conditions. Today, the Baltic Sea interacts strongly with conditions in the North Atlantic region, and this interaction was likely even stronger during the LIG. We here present a reconstruction of seawater conditions during the LIG based on benthic foraminiferal geochemistry (stable isotopes and trace elements) and compare these records with modern marine monitoring data to evaluate seasonal hydrographic conditions in the western and southern Baltic Sea during the first half of the LIG (130–123 ka BP). Our reconstructions reflect the evolution of seasonal temperature and salinity, rather than annual mean conditions. The spring LIG bottom water temperatures in the Skagerrak and Kattegat were ~2–3 °C higher compared to the modern spring bottom water temperatures. During the LIG, there was an increase in seasonality in bottom water temperature (progressively warmer summers and cooler springs) in the southern Baltic Sea, which can be linked to seasonal insolation changes. Moreover, our data suggest a decreased gradient of bottom water salinity along a transect through the Skagerrak-Kattegat-Danish Straits-southern Baltic Sea, supporting previous investigations inferring a stronger ocean-water influx into the Baltic Sea during the LIG than at present.

1. Introduction

The Baltic Sea region is located at a glaciation-sensitive high latitude, and it has been strongly impacted by glacial-interglacial variability (Andrén et al., 2011). The advancing and retreating glaciers have resulted in extensive isostatic movement during glacial-interglacial cycles, facilitating the deposition of lacustrine and marine sediments during the interglacial periods (e.g. Berglund and Lagerlund, 1981; Andrén et al., 2011). The Last Interglacial period (LIG), Marine Isotope Stage (MIS) 5e, referred to as the Eemian stage in Europe (130–115 ka BP) separated the two glacial periods of the Saalian (~300–130 ka BP, MIS 6–8) and the Weichselian (~115–11.7 ka BP, MIS 5 d – MIS 2), and has been described from a range of marine and terrestrial sites in the northern European region (e.g. Cheddadi et al., 1998; Brewer et al., 2008; Knudsen et al., 2009; Andrén et al., 2011). The LIG stage at high northern latitudes was characterized by rapid changes in ocean circulation and polar front movement (Seidenkrantz et al., 1995; Fronval and Jansen, 1996; Seidenkrantz and Knudsen, 1997; Fronval et al., 1998; Knudsen et al., 2002; Andrén et al., 2011; Hoffman et al., 2017; Clark et al., 2020; Kessler et al., 2020).

The hydrography and geographic configuration of the Baltic Sea during the LIG were very different from the Holocene and the present (e.g. Funder et al., 2002). The surface water in the western Baltic during the LIG is believed to have been warmer and considerably more saline than today (e.g. Konradi, 1976; Kristensen et al., 2000; Funder et al., 2002; Head et al., 2005; Knudsen et al., 2012). During the early LIG, the Baltic Sea was connected to the North Sea through Schleswig-Holstein in northern Germany (Knudsen, 1985a, 1992; Knudsen, 1985a; Knudsen, 1992; Funder et al., 2002) and to

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the White Sea and the Arctic Ocean through Karelia (Funder et al., 2002; Miettinen et al., 2014; Knudsen, 1984, 1985b; Seidenkrantz, 1993a, b; Seidenkrantz et al., 1995; Seidenkrantz and Knudsen, 1997; Kristensen et al., 1998). Global sea level rose rapidly in the early LIG due to the rapid and extensive melting of ice sheets (Kopp et al., 2009; Dutton and Lambeck, 2012; Rohling et al., 2019). In the Baltic region, the relative sea-level rise was further accentuated through the delayed isostatic uplift after the Saalian glaciation. The relative sea-level highstand lasted for about 6 kyr (Kristensen and Knudsen, 2006; Miettinen et al., 2014) until it fell from the middle LIG (Seidenkrantz, 1993a; Waelbroeck et al., 2002; Eiríksson et al., 2006), probably due to a combination of isostatic rebound and decreasing global sea level caused by a new rapid built-up of northern hemisphere glaciers (Hearty et al., 2007). During most of the LIG, the North Atlantic Current was presumably stronger than today as a result of a more vigorous Atlantic conveyor (Weaver and Hughes, 1994; Seidenkrantz et al., 2000; Tzedakis et al., 2018) and might have had a more westerly located current front during the LIG than the present (Larsen et al., 1995; Fronval et al., 1998; Bauch et al., 1999; Seidenkrantz et al., 2000; Grøsfjeld et al., 2006). The only exceptions were likely during the cooling events, which interrupted the overall warmer-than-present LIG climate in the northern regions of the North Atlantic (e.g. Seidenkrantz et al., 1995; Fronval and Jansen, 1996; Martrat et al., 2014).

The marine sediments from the LIG in the western Baltic Sea in many cases consist of dislocated deposits glacially thrust up onto the present Baltic coastline in southeastern Denmark, northern Germany and Poland (Fig. 1) (e.g. Knudsen, 1985a; Seidenkrantz and Knudsen, 1994, 1997; Glaister and Gibbard, 1998; Kristensen et al., 2000; Funder et al., 2002; Head et al., 2005; Funder and Balic-Zunic, 2006; Kristensen and Knudsen, 2006; Knudsen et al., 2009, 2011, 2012). In contrast, in the Kattegat and Skagerrak region, a relatively deep trough existed during the LIG (Lykke-Andersen et al., 1993) with deposition of sediments at ~100–300 m palaeo water depth (Knudsen, 1984; Knudsen, 1985b; Seidenkrantz, 1993a, b; Seidenkrantz et al., 1995; Seidenkrantz and Knudsen, 1997; Kristensen et al., 1998).

Today, the surface waters of the Skagerrak and the Kattegat are characterized by an inflow of North Atlantic Current-derived water passing north of Scotland, mixed with a minor inflow through the English Channel into the North Sea (Svansson, 1975). In the Kattegat, this inflow is mixed with low-saline surface water outflow from the Baltic Sea. The mixture of the saline water inflowing from the Atlantic with the outflowing low-salinity surface water in the Kattegat causes a strong vertical stratification (Rodhe, 1987; Seidenkrantz et al., 2000; Ricker and Stanev, 2020).

The geochemical composition of benthic foraminiferal calcite (i.e. trace elements and stable isotopes) is a well-established and widely used method for reconstructing past seawater conditions (e.g. Elderfield et al., 2006; Hönisch et al., 2011; Pearson, 2012; Groeneveld and Filipsson, 2013). The Mg content of the foraminiferal calcium carbonate ($CaCO_3$) (as Mg/Ca) is mainly a function of the temperature at which $CaCO_3$ was precipitated, and therefore, the Mg/Ca in foraminiferal calcite has been used as a temperature proxy (e.g. Nürnberg et al., 1996; Rosenthal et al., 1997), including in the Baltic (Groeneveld et al., 2018; Ni et al., 2020). Calibrations for species-specific Mg/Ca vs. temperature relationships are available for several benthic foraminiferal species, including the ones used in this study, *Bulimina marginata, Hyalinea balthica,* and *Ammonia batava* (e.g. Kristjánsdóttir et al., 2007; Rosenthal et al., 2011; Toyofuku et al., 2011; Grunert et al., 2018). The foraminiferal oxygen isotopic composition ($\delta^{18}O$) reflects both temperature and seawater

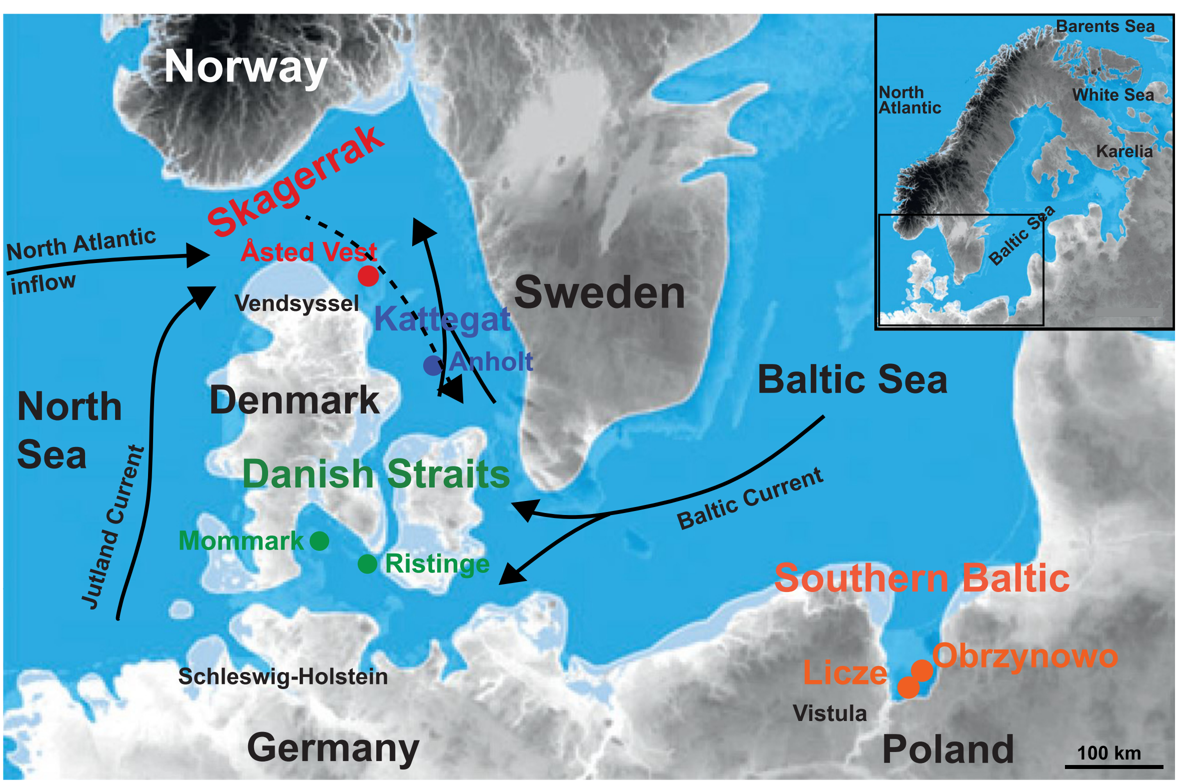

Fig. 1. Location map of the western and southern Baltic Sea with an indication of the presumed LIG coastline modified from Ehlers et al. (2013). The present-day coastline is shown as a paler-blue shadow and the modern hydrographical circulation pattern, the inflow of water from the North Sea into the Baltic Sea is shown as solid-line arrows, Baltic Sea brackish water outflow is indicated by a dashed-line arrow. The six sites presented in this study are indicated by colored dots. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

$\delta^{18}O$, which varies with regional hydrography and with ice volume on glacial and interglacial timescales. The Mg/Ca and $\delta^{18}O$ of the foraminiferal calcite are often used together in paleoceanography for the reconstruction of temperature and absolute salinity (Wolff et al., 1999; Nürnberg et al., 2000).

The Ba/Ca of foraminiferal calcite has been recently used as a salinity/runoff proxy in coastal regions (Lea and Boyle, 1991; Hönisch et al., 2011; Bahr et al., 2013; Groeneveld et al., 2018). This is specifically suitable in areas where salinity is mainly controlled by changes in runoff and thus precipitation, such as in the Baltic Sea, implying that an increase in barium is an indication for decreasing salinity. Redox-sensitive elements such as Mn and its incorporation into $CaCO_3$ are used as a proxy for the dissolved oxygen conditions in seawater where the organisms calcified (e.g., Glock et al., 2012; Groeneveld and Filipsson, 2013; Koho et al., 2015; Petersen et al., 2018). Under oxic conditions, Mn directly precipitates as an oxide, but when dissolved oxygen concentrations decrease and become hypoxic, dissolved Mn concentrations increase and can be increasingly incorporated into the calcite of the foraminifera (Froelich et al., 1979; Tribovillard et al., 2006). The Mn/Ca values in benthic foraminiferal tests are therefore relatively higher under hypoxic conditions. Stable carbon isotopes ($\delta^{13}C$) in foraminifera are influenced by productivity, carbon cycling, and water mass exchanges (e.g., Schmiedl and Mackensen, 2006; Filipsson and Nordberg, 2010). Both Mn/Ca and $\delta^{13}C$ in benthic foraminifera can therefore be used for understanding past seawater circulation and ventilation conditions. Benthic foraminiferal species have the potential to be used to reconstruct seasonal bottom water conditions (e.g. Boltovskoy and Lena, 1969; Gooday and Rathburn, 1999; Loubere and Fariduddin, 1999; Gustafsson and Nordberg, 1999, 2000, 2001; Filipsson et al., 2004; Sun et al., 2006; Schönfeld and Numberger, 2007a, b; Groeneveld et al., 2018). The relative abundance of different species may vary due to their response to seasonally varying "food input", through phytoplankton blooms, or hydrographic changes in temperature or dissolved oxygen content. Assuming that the largest amount of $CaCO_3$ is formed when foraminifera show the highest population density, the foraminiferal calcite may provide valuable high resolution records of seasonal variations.

Our study aims to investigate the seasonal variation of bottom water conditions during the LIG in the Baltic Sea region and the influence and interplay of seasonal insolation, sea-level change and water exchange. To achieve this goal, we applied a multiproxy approach to generate high-resolution reconstructions of LIG bottom water conditions at six sites in the southern and western Baltic using foraminiferal geochemistry (Mg/Ca, Ba/Ca, Mn/Ca, $\delta^{18}O_c$ and $\delta^{13}C_c$). The sites are located in northern Denmark/the Skagerrak (site Åsted Vest), the Kattegat (site Anholt), the Danish Straits (sites Ristinge and Mommark) and northern Poland/the Vistula River (sites Licze and Obrzynowo) (Fig. 1). The samples contain marine sediments from four boreholes and two outcrops spanning different time intervals within the LIG (spanning time intervals from ~0.3–15 kyr after the beginning of the LIG).

2. Modern hydrographic conditions

As all the studied sites are today above sea level, we could not directly compare them to modern hydrographical conditions at the actual sites. Instead, we used monthly monitoring hydrographic data recorded between 1926 and 2020 in the Skagerrak, Kattegat, Danish Straits and the southern Baltic area (Fig. 2) to compare the present hydrography with that of the LIG period. Surface water was classified as the upper 20 m of the water column in the relatively deep Skagerrak and as the upper 10 m at the shallower sites (Kattegat, Danish Straits and southern Baltic) due to varying depths of the halocline at different sites. Hydrographical data from the deepest available level in the water column of ~120 m were used for the Skagerrak, while we used data from ~60 m water depth for the Kattegat and the Danish Straits, to facilitate comparisons with LIG bottom water. The bottom water is represented by data from below the halocline to the seafloor, i.e. ~25–60 m depth in the Kattegat and the Danish Straits, and ~50–120 m in the Skagerrak. Because a steep bathymetric gradient occurs to ~120 m depth off the coast directly north of our southern Baltic sites at Licze and Obrzynowo, and as no hydrographical data exists for the water depth (<20 m; Knudsen et al., 2012) represented in these LIG deposits in this area, we used data from a relatively shallow depth in the water column (20–50 m) in this region to represent bottom water.

The modern surface- and deep-water temperatures in these four zones obtained from the Baltic Nest Institute (Stockholm University Baltic Sea Centre) show a comparable and large temperature seasonality (Fig. 2). The largest difference in average monthly SST between spring and summer (MAM and JJA) is ~11 °C in the Kattegat, while in the Skagerrak it is ~9 °C. The difference between spring and summer BWT (MAM and JJA) in the Straits and the southern Baltic is ~5 °C, while the difference is ~2 and ~4 °C in the Skagerrak and Kattegat, respectively. The highest SSTs occur in July and August, reaching ~15–18 °C, whereas the warmest bottom water conditions appear one or two months later. There is a similar time lag for the minimum water temperatures, i.e. the lowest temperatures occur in February and March for the surface water and March and April for the bottom water. The spring BWTs are in general lower than the spring SSTs, with the largest spring temperature difference noted for the Straits, where the spring BWTs are typically ~2 °C lower than the SSTs, while in the Kattegat the BWTs are very similar to the SSTs during the coldest months.

The salinity measurements show a distinct gradient from the Skagerrak through the Kattegat and the Danish Straits into the Baltic Sea, with the largest seasonal change occurring in the Straits. In the Skagerrak, which has nearly fully marine conditions, salinities are ~33 in the surface water and ~35 in the bottom water throughout the year. The southern Baltic salinities are about 7–8 for both SSS and BWS. However, in the North Sea-Baltic Sea transition area, the seasonal differences between SSS and BWS are larger, with a difference of ~12 in the Kattegat and ~6 in the Straits (Fig. 2).

The bottom water is generally fully oxygenated with a weak seasonality at all sites except for the Straits, where seasonal hypoxia periodically occurs between August and October. During these months, 26–41% of the measurements (daily average) were hypoxic ($[O_2] < 1.4$ ml/l).

3. Materials and methods

3.1. Study area and age model

All sites included in this study have been dated to the LIG based on the generally well-known foraminiferal and/or pollen stratigraphy of the region. The more precise age models for some of the sites are based on correlation to the regional pollen zonation (Müller, 1974; Andersen, 1975; Menke and Tynni, 1984), which provide a floating chronology (Table 1). The foraminiferal-based geochemistry data from the sites are all generated within this study, whereas the foraminiferal faunal data and age models have been published previously (Table 1).

The LIG marine deposits from the Skagerrak-Kattegat and Baltic Sea region have been studied extensively for more than a century, with the first studies by Madsen et al. (1908), Nordmann (1908) and Jessen et al. (1910). Originally, the age allocation was based on the stratigraphical location of these deposits, as they underly glacial

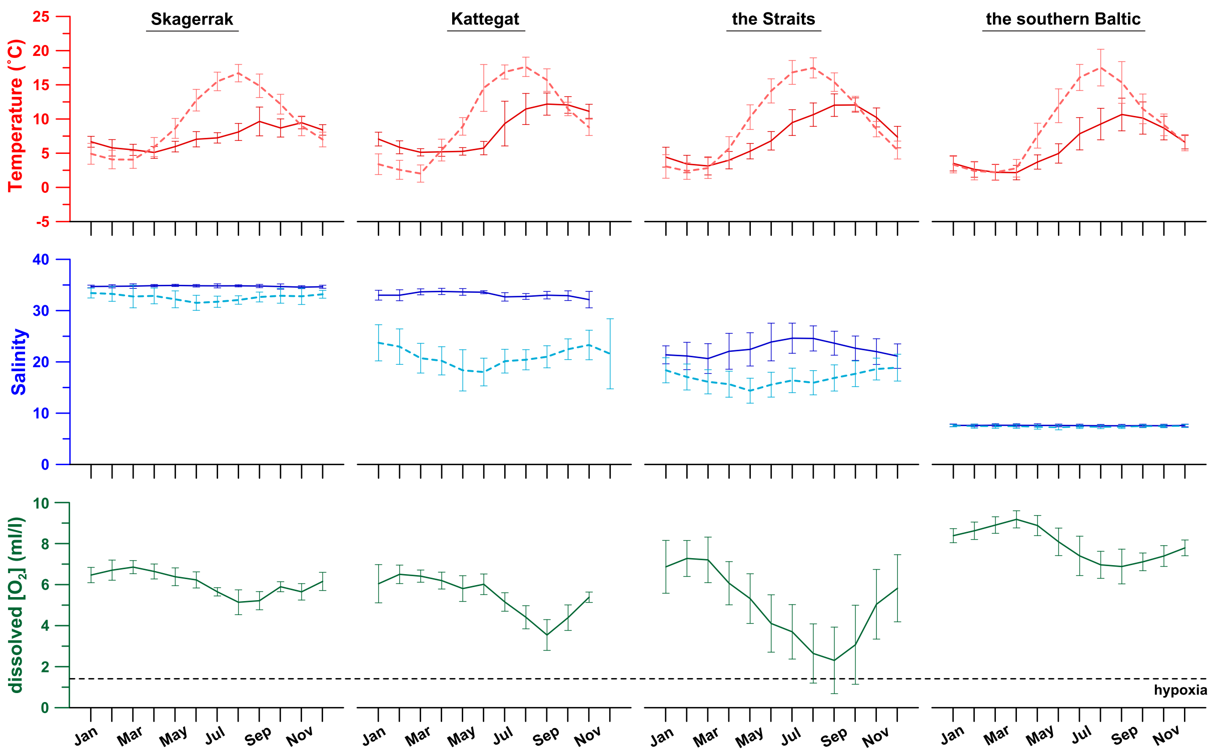

Fig. 2. Monthly variations in surface (dashed lines) and bottom water (solid lines) temperature (°C), salinity and oxygen concentrations (ml/l) in the Skagerrak, the Kattegat, the Danish Straits and the southern Baltic Sea. The black dashed line indicates the hypoxic level ([O_2] <1.4 ml/l). Error bars are ±1SD. Data source: the Baltic Nest Institute, Stockholm University Baltic Sea Centre.

Table 1
The maximum time span (years since the start of the LIG) with generated foraminiferal geochemistry data in each site in four regions. The local pollen zones were correlated with regional pollen zones in northern Germany with the ages of the zonal boundaries (years from the Saalian–Eemian Stage boundary) based on Müller (1974). The time span for Åsted Vest is based on Knudsen et al. (2009), with reference to the marine isotope stages (MIS; Shackleton and Updyke, 1973).

Region	Site Name and type	Longitude	Latitude	Modern Elevation (m)	Paleo-water depth (m)	Age (ka BP)	Time span (yrs in the LIG)	Local pollen zones based on
Skagerrak	Åsted Vest (borehole)	10°22.58 E	57°26.01 N	+60	100–200	130–115	15000	–
Kattegat	Anholt (Anholt III borehole)	11°31′E	56°43′N	+2	75–100	130–121	9077	–
The Danish Straits	Mommark (outcrop)	10°02.7′E	54°55.7′N	+10	<30	128–119	10504	Gibbard and Glaister, (2006)
	Ristinge (outcrop)	10°22.9′E	54°30.7′N	+12	<30	130–127	3462	Kristensen et al., (2000)
The southern Baltic	Licze (borehole)	19°07′E	53°73′N	+87	<20	130–123	7000	Head et al., (2005)
	Obrzynowo (borehole)	19°15′E	53°46′N	+105	<20	130–127	3241	Knudsen et al., (2011)

deposits and have a fossil content showing a warmer-than-present climate (e.g. Knudsen, 1984; Seidenkrantz, 1993a; Head et al., 2005; Knudsen et al., 2011). Internal correlation of deposits was based on biostratigraphical data, with foraminiferal specific species only found in these LIG deposits (e.g. Nordmann, 1928; Konradi, 1976; Knudsen, 1984, 1985b; Seidenkrantz, 1993a, b; Kristensen et al., 2000). More recently, Optically Stimulated Luminescence (OSL) dating carried out at selected sites has supported this chronology (Murray and Funder, 2003; Eiríksson et al., 2006).

The pollen stratigraphy of the LIG deposits (Müller, 1974; Andersen, 1975; Menke and Tynni, 1984) is unique for this interglacial, making it possible to allocate a LIG age and perform relatively long-distance correlations (Funder et al., 2002). A detailed correlation to this established pollen zonation from NW Europe has been used in this study. Previously published pollen chronologies (Table 1) are available for the studied sites in the Danish Straits (Mommark and Ristinge) and the southern Baltic (Licze and Obrzynowo). The local pollen zones in these sediment sequences are correlated to the regional pollen zones in northern Germany (Menke and Tynni, 1984) and Denmark (Andersen, 1975) and assigned to a chronology by integration with the annually laminated lacustrine sequence from Bispingen, northern Germany (Müller, 1974) (Table 1).

However, it is difficult to determine the marine sequence zones based on pollen stratigraphy in northern Denmark due to the large proportion of reworked pollen grains present in these sediments (Glaister and Gibbard, 1998). Consequently, at sites Åsted Vest and Anholt, constant sedimentation rates were assumed between the age zone boundaries throughout the whole record (3 mm/yr at Åsted Vest (Knudsen et al., 2009) and 0.3 mm/yr at Anholt (Seidenkrantz, 1993a), respectively. Sedimentation rates were calculated for Åsted Vest assuming a nearly complete LIG record, while at Anholt, one-tenth of the sedimentation rate of Vendsyssel (Knudsen, 1984) was used based on foraminiferal density. However, the foraminiferal faunal succession in Åsted Vest indicates that the lowermost part of the interglacial sequence may be missing (Knudsen et al., 2009). Therefore, we should keep in mind that the reconstructed record in Åsted Vest may lack the earliest part of LIG. In the Anholt core (Anholt III borehole), the end of the LIG is missing (Seidenkrantz, 1993a).

The studied sites encompass LIG palaeoenvironments ranging from near-coastal shallow-water sites (0–30 m water depth) in the southern Baltic and the Danish Straits to relatively deep-water environments reaching water depths in excess of 100 m in the Kattegat-Skagerrak region. This is also observable in the types of lithologies found, where the shallow sites are characterized by coarse-grained sediments which grade into clays. The marine section of the southern Baltic sites of Licze and Obrzynowo encompass fine sand to silt and silty clay (Knudsen et al., 2012). The Danish Strait sites of Ristinge and Mommark are both composed of non-laminated greenish-gray silty clay to clay (the *Cyprina* Clay), with silty clays occurring in the lower transitional part of the marine sequence (Eiríksson et al., 2006; Kristensen et al., 2006, 2008; Knudsen et al., 2011). The deeper Kattegat and Skagerrak sites are composed of non-laminated clay and silty clay (Seidenkrantz, 1993a, b; Larsen et al., 2009).

3.2. Trace metal/Ca in foraminifera

For analysis of Ba/Ca, Mg/Ca and Mn/Ca in foraminiferal calcite, we selected 8–24 specimens of the benthic foraminiferal species *Bulimina marginata* in 36 samples, 10–15 specimens of *Hyalinea balthica* in 25 samples, 20–40 specimens of *Ammonia batava* in 60 samples and 30–100 specimens of the combined *Elphidium clavatum-Elphidium selseyensis* taxon group in 124 samples (these latter two species were combined to the *Elphidium clavatum-selseyensis* complex; following Groeneveld et al., 2018). The species selected depended on which one was present at each site; as the range of salinity at each site was large, no species was present at all sites. The size ranged mostly between 125 and 355 μm for *B. marginata*, *H. balthica* and *A. batava*, and 125–250 μm for the *E. clavatum-selseyensis* complex. We gently crushed the foraminiferal tests and cleaned the fragments according to the standard cleaning protocol for foraminiferal Mg/Ca analyses (Boyle and Keigwin, 1985), which includes a reductive cleaning step. The samples were analyzed with an ICP-OES (Agilent Technologies, 700 Series with autosampler (ASX-520 Cetac) and micro-nebulizer) at the MARUM – Centre for Marine Environmental Sciences, University of Bremen, Germany. We used a limestone standard (ECRM752-1) with a Mg/Ca content of 3.75 mmol/mol to allow inter-laboratory comparison (Greaves et al., 2008). Analytical precision based on three replicate measurements of each sample for all species at all stations is shown in Supplementary Table A1. At least two replicate samples per site were measured for testing data reliability and replicability. The average relative standard deviation (RSD, %) of replicates in each site is shown in Supplementary Table A2.

We employed species-specific Mg/Ca-temperature calibrations (Table 2) for *B. marginata, H. balthica* and *A. batava* for BWT reconstructions, and used the calibration established for *Melonis barleeanus* (Williamson, 1858) for semi-quantitative temperature reconstruction of *E. clavatum-selseyensis* (cf. Kristjánsdóttir et al., 2007) following Groeneveld et al. (2018) and Ni et al. (2020).

3.3. Stable oxygen and carbon isotopes in foraminifera

We picked 6–20 specimens of *A. batava* in 26 samples and 20–35 specimens of the *E. clavatum-selseyensis* complex in 31 samples from sites Licze and Obrzynowo for the analysis of stable oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopes. The measurements were performed on a Thermo Fisher Scientific 253plus gas isotope ratio mass spectrometer (IRMS) with a Kiel IV automated carbonate preparation device at MARUM, University of Bremen. The stable isotopic data are reported relative to the Vienna Peedee belemnite (V-PDB) using the NBS19 standard. The analytical standard deviation based on the internal laboratory standard (Solnhofen limestone) was 0.07‰ for $\delta^{18}O$ and 0.03‰ for $\delta^{13}C$. For the other four sites, we used existing published oxygen and carbon isotope data (Seidenkrantz, 1993a; Kristensen and Knudsen, 2006; Knudsen et al., 2009, 2011; Knudsen et al., 2009; Knudsen et al., 2011).

To estimate bottom water salinity (BWS), we first applied the reconstructed bottom water temperature (BWT), based on foraminiferal Mg/Ca ($T_{Mg/Ca}$), and the measured $\delta^{18}O$ to a paleotemperature equation (Shackleton, 1974) to calculate seawater $\delta^{18}O$:

$$\delta^{18}O_{water,\ SMOW} = 0.25 * T\ (^{\circ}C) + \delta^{18}O_{calcite,V-PDB} - 3.955 \qquad \text{Eq. 1}$$

and used the $\delta^{18}O$/salinity relationship for modern seawater of the North Sea-Baltic Sea transition (Ni et al., 2020):

$$\text{Salinity} = (\delta^{18}O_{water,\ SMOW} + 8.14)\ /\ 0.24 \qquad \text{Eq. 2}$$

to calculate the BWS. The uncertainties of this salinity reconstruction include the foraminiferal Mg/Ca-based temperature estimates and the fact that the LIG $\delta^{18}O$/salinity mixing line might have differed compared with the modern one. An average error of 1 °C in BWT, due to the calibration uncertainty, will induce an error of 1 salinity unit. We also note that the absolute BWS data based on *E. clavatum-selseyensis* should be interpreted with caution since the calculations include uncertainties due to the semi-quantitative temperature reconstruction using a non-species-specific calibration.

3.4. Statistical analyses

We applied *t*-test to analyze if the difference between the two datasets is statistically significant. We used Mann-Kendall trend test to look for a monotonic trend within the time series. P value was considered significant at <0.05. Because the sampling depth intervals in this study differ for trace element and stable isotopes for some sites, we interpolated between data points in higher-resolution datasets to calculate water salinities.

4. Results

We first present the reconstructed bottom water temperatures (BWTs) and salinities (BWSs) for the LIG in the Skagerrak-Kattegat-Baltic Sea region. The quantitative reconstruction is based on geochemical analyses of four benthic foraminiferal species (Skagerrak and Kattegat: *B. marginata* and *H. balthica;* the Danish Straits and the southern Baltic coast: *A. batava* and *E. clavatum-selseyensis*).

4.1. Benthic foraminiferal TE/Ca distribution

Ba/Ca, Mg/Ca and Mn/Ca values in the foraminiferal calcite were more variable when comparing different species from the same site than for the same species from different locations. This supported our use of species-specific calibrations (Fig. 3). Our results show that *H. balthica* incorporated higher proportions of trace elements (TE) into its calcite than *B. marginata*. The Ba/Ca values of

Table 2
Species-specific Mg/Ca-temperature calibrations for the species we used in this study.

Site	Species	Equation	Reference
Åsted Vest; Anholt	*B. marginata* d'Orbigny 1826	T (°C) = (Mg/Ca (mmol/mol) - (0.938 ± 0.08))/(0.114 ± 0.012); 3°C[1]	Grunert et al., (2018)
Åsted Vest; Anholt	*H. balthica* (Schroeter 1783)	T (°C) = Mg/Ca (mmol/mol)/(0.488 ± 0.03); 1°C[1]	Rosenthal et al., (2011)
Ristinge; Licze; Obrzynowo	*A. batava* (Linné 1758)	T (°C) = 18.8 * ln (1.74 * Mg/Ca (mmol/mol))	Toyofuku et al., (2011)
Mommark; Ristinge; Licze; Obrzynowo	*E. clavatum* (Cushman, 1930) *E. selseyensis* (Heron-Allen and Earland, 1911)	T (°C) = ln (Mg/Ca (mmol/mol)/(0.658 ± 0.07))/(0.137 ± 0.02); 3 °C[1]	Kristjánsdóttir et al., (2007)

[1] The range of calibration uncertainty within 95% of confidence. The uncertainty in the Mg/Ca vs temperature regression is determined by the uncertainty in the calibration equation, which has no impact on specific trends revealed by those data points (Dolman et al., 2021).

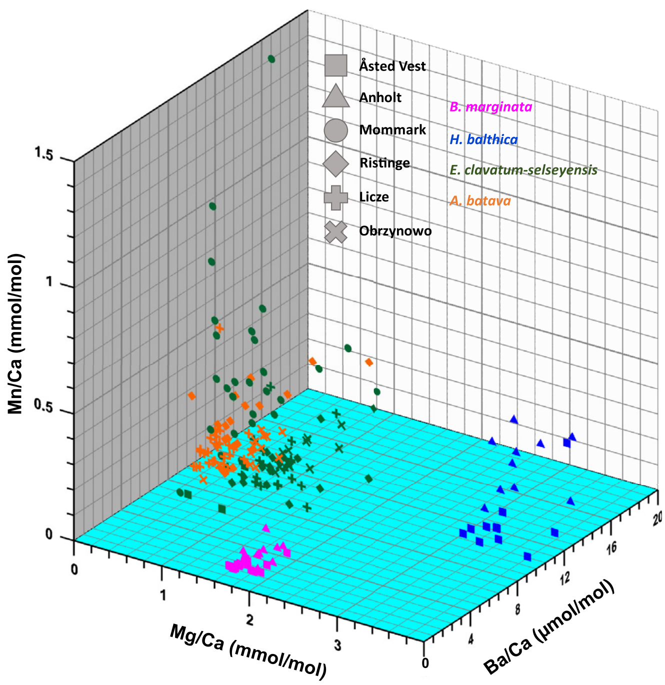

Fig. 3. TE/Ca distribution of the four foraminiferal species from the six sites in the Baltic Sea during the LIG. The symbol shapes indicate sites, while the colors indicate species. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

B. marginata were the lowest among all the species (0.9–3.9 μmol/mol), while *H. balthica* incorporated relatively more Mg into its calcite than the other species (3.6–4.5 mmol/mol). The Mn/Ca values of *H. balthica* ranged between 0.2 and ~0.7 mmol/mol and were more variable than those of *B. marginata* (0.02–~0.1 mmol/mol). For both species, the Mn incorporation in the foraminiferal calcite in specimens from Anholt (Kattegat) was higher than in specimens from Åsted Vest (Skagerrak). Trace elemental incorporation in *E. clavatum-selseyensis* and *A. batava* was similar (Fig. 3, green and orange symbols). Mn/Ca values of *E. clavatum-selseyensis* from Mommark were the highest of all our studied species and sites, with a mean value of 0.55 mmol/mol, and were ~3–4 times higher than those from the other sites of the Straits and the southern Baltic.

4.2. Benthic foraminiferal stable isotopes in the southern Baltic coastal area

The records of oxygen and carbon isotopes ($\delta^{18}O$ and $\delta^{13}C$) of *A. batava* and *E. clavatum-selseyensis* in the southern Baltic Sea sites Licze and Obrzynowo are shown in Fig. 4. At Licze, the *A. batava* isotope values varied between −5.71 and −4.59‰ for $\delta^{18}O$ and between −4.68 and −2.09‰ for $\delta^{13}C$, and in *E. clavatum-selseyensis*, between −2.86 and −1.96‰ for $\delta^{18}O$ and between −4.87 and −3.13‰ for $\delta^{13}C$. At Obrzynowo, $\delta^{18}O$ and $\delta^{13}C$ values showed relatively larger ranges compared to those from Licze. The Obrzynowo $\delta^{18}O$ values varied between −5.93 and −4.55‰ for *A. batava* and between −3.71 and −1.91‰ for *E. clavatum-selseyensis*. The $\delta^{13}C$ values of *A. batava* varied between −3.98 and −0.79‰, and of *E. clavatum-selseyensis* varied between −4.13 and −1.45‰.

4.3. Proxy-based reconstruction of seawater conditions

4.3.1. Skagerrak and Kattegat

In general, the trace elemental compositions of the foraminifera at Åsted Vest and Anholt (Skagerrak and Kattegat) were less variable during the LIG than those from the two other areas. The Mg/Ca values of *B. marginata* and *H. balthica* from these two sites were relatively stable, with ranges of 1.6–2.1 mmol/mol and 3.6–4.5 mmol/mol, respectively (Supplementary Fig. A1). This gives a reconstructed BWTs range of 5.9–9.9 °C and 7.3–9.3 °C, respectively. The BWTs of Skagerrak and Kattegat showed no significant trend during the LIG. The BWT was relatively high at Åsted Vest in the early LIG (~128–127 ka BP) and in the late LIG (~120–115 ka BP).

The LIG mean bottom water salinities (BWSs) at Åsted Vest and Anholt were 35.6 and 34.2, respectively, based on our $\delta^{18}O$ and Mg/Ca data (Fig. 5). The LIG BWS in the Kattegat showed no significant temporal trend and the average value was lower than the Skagerrak BWS. The salinity variations in the Skagerrak (Åsted Vest) can be divided into four stages: 1) during the early LIG (~130–128 ka BP), a net salinity increase occurred (Fig. 5a blue shadow), indicated by increasing foraminiferal $\delta^{18}O$, which was followed by 2) a short freshening period from ~128 to 126 ka BP. 3) BWS was relatively stable at ~34.8 between ~126 and 121 kyr. 4) During the late LIG (~121-115 kyr), the BWS again increased from ~35 to ~38, together with increasing BWT (~8–~10 °C) and Mn/Ca from 0.02 to 0.06 mmol/mol (Fig. 5a yellow shadow).

4.3.2. The Danish Straits

The Mg/Ca values of *A. batava* from Ristinge show a significant increasing trend over the LIG, corresponding to a reconstructed Mg/

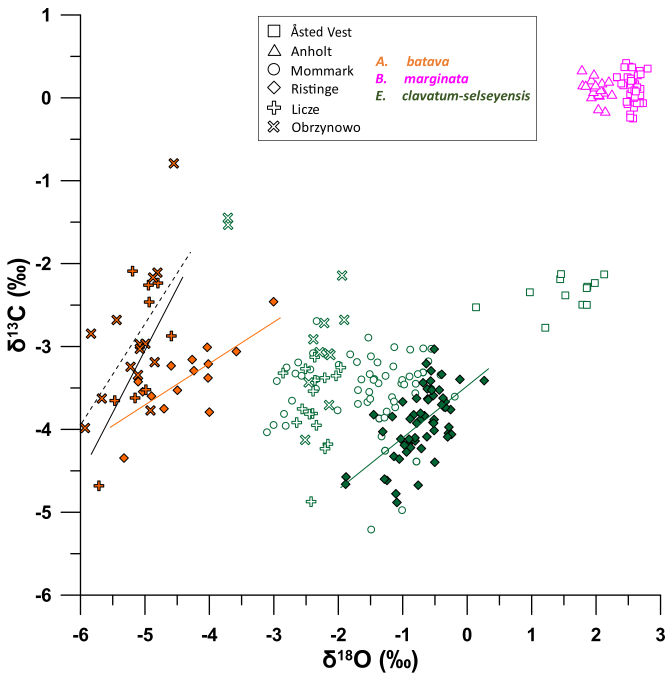

Fig. 4. Foraminiferal $\delta^{13}C$ and $\delta^{18}O$ of three species in six sites from the Baltic Sea: Licze and Obrzynowo (this study), Åsted Vest (Knudsen et al., 2009), Anholt (Seidenkrantz, 1993a), Mommark (Kristensen and Knudsen, 2006) and Ristinge (Knudsen et al., 2011). The symbols indicate different sites, while colors indicate foraminiferal species. The solid symbols show species and sites with significant correlations between $\delta^{13}C$ and $\delta^{18}O$, including *E. clavatum-selseyensis* and *A. batava* from Ristinge (Knudsen et al., 2011), and *A. batava* from Licze and Obrzynowo (this study). The green and orange solid lines are the trend lines of Ristinge, the solid and dashed black lines are the trend lines of Licze and Obrzynowo, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Ca temperature increase from 4 to 14 °C in pollen zones E1-4 (Fig. 6a). However, the *E. clavatum-selseyensis* Mg/Ca values showed no significant trend in BWT at Ristinge. The difference between the reconstructed BWT based on *A. batava* and *E. clavatum-selseyensis* (average ΔT = ~5.0 °C) increased through the LIG. The BWT in Mommark was generally relatively stable, except during pollen zone E6, when the BWT was relatively higher and more variable (Fig. 6b).

The Ba/Ca values for both *A. batava* and *E. clavatum-selseyensis* show decreasing trends through time in pollen zones E1 – early E5 at Ristinge, indicating a salinity increase during the early LIG (Fig. 6a). The salinity increased rapidly from ~4 to ~10 in the Straits 500–700 yrs after the start of the LIG (pollen zone E3) (blue shadow in Fig. 6a). Salinity continued to increase in pollen zone E4 and early E5 by ~5 units at Ristinge until ~21.8 at 126–127 ka BP. The BWS showed a significant decreasing trend during pollen zones E5 to E7 at the Mommark site (Fig. 6b). BWS was relatively high from 128 to 124 ka BP at Mommark (pollen zones late E4 and E5), followed by a salinity drop at 123 ka BP. After that, the BWS decreased by 6 units, reaching a stable low salinity (~9.5) in pollen zone E7. The Mn/Ca was more variable during the late LIG (123–119 ka BP, 0.1–1.3 mmol/mol).

4.3.3. *The southern Baltic coast*

The average BWT during the time interval 130–127 ka BP at Obrzynowo reconstructed from *A. batava* and *E. clavatum-selseyensis* were 12 and 4 °C, respectively (Fig. 7a). The difference between the BWTs reconstructed with two species shows no significant trend at Obrzynowo during the early LIG. At Licze in the southern coastal Baltic, the average LIG (130–123 ka BP) temperature was ~4.1 °C based on Mg/Ca in *E. clavatum-selseyensis* and ~10.5 °C in *A. batava.* Similar to the conditions at Ristinge, the differences between the BWTs at Licze (average ΔT = ~6.4 °C) reconstructed from *A. batava* and *E. clavatum-selseyensis* increased in the first half of the LIG (Fig. 7b).

The Ba/Ca values of *A. batava* and *E. clavatum-selseyensis* in the southern Baltic are rather stable (Supplementary Fig. A1). Ba/Ca of Obrzynowo are higher than at Licze for both species (Supplementary Fig. A1). The average Licze LIG salinity calculated from Mg/Ca and $\delta^{18}O$ of *A. batava* was ~7.2, and salinity based on *E. clavatum-selseyensis* was ~11.6 during the time interval 130–123 ka BP. The BWS at Obrzynowo was relatively stable that the average BWS based on *A. batava* Mg/Ca and $\delta^{18}O$ was 8.9 and based on *E. clavatum-selseyensis* was 11.6 in early LIG (~130–~127 ka BP).

5. Discussion

5.1. *Seasonal reconstruction*

There is a large benefit of using multiple foraminifera species at the same study sites, when possible, as it can help us to understand seasonality. Late winter to spring is the time when species of Buliminae are typically most abundant (Gooday and Rathburn, 1999; Gustafsson and Nordberg 2000, 2001; Gustafsson and Nordberg, 2000; Gustafsson and Nordberg, 2001; Duchemin et al., 2008). Hence, it is likely that *B. marginata* are mostly calcified during spring and that they thus record LIG spring temperatures for the Skagerrak and Kattegat. There is a lack of studies with regard to the seasonal abundance of *H. balthica* and this species needs further investigation. *Ammonia* is typically the most abundant taxon between June and August (Boltovskoy and Lena, 1969; Saad and Wade, 2017), suggesting that *Ammonia* reproduces during summer, while *E. clavatum-selseyensis* reproduces rapidly in connection with phytoplankton blooms during late winter/early spring (i.e. at lower temperatures) (Gustafsson and Nordberg, 1999, 2001; Schönfeld and Numberger, 2007a, b). Thus, we use *A. batava* for the reconstruction of summer conditions, while *E. clavatum-selseyensis* represents spring conditions at sites in the Straits and the southern Baltic. Consequently, the Mg/Ca-based BWT reconstructions in the Straits and southern Baltic coast, based on *A. batava* and *E. clavatum-selseyensis*, not only give us quantitative temperature data but also provide information on seasonal temperature and salinity differences. Our study provides valuable quantitative estimates of seasonal bottom-water salinity and temperature that are a vital complement to previous climate reconstructions and may be particularly useful in future modeling studies focused on the LIG.

5.2. *Temperature*

5.2.1. *Skagerrak and Kattegat*

The average spring LIG BWTs based on *B. marginata* were 1.6 °C higher in the Skagerrak and 3.0 °C higher in the Kattegat than modern average spring (MAM) BWTs (Fig. 5; *t*-test $p < 0.001$ for both sites). The seasonally warmer conditions in the Skagerrak and Kattegat were also indicated by foraminiferal faunal assemblage results (Seidenkrantz and Knudsen, 1994). In addition, a LIG annual SST reconstruction at 125 ka BP based on $\delta^{18}O$ of the gastropod *Littorina littorea* showed temperatures ranging between 8 and 26 °C for the Kattegat (Burman and Påsse, 2008), which is 6–8 °C warmer than the present seasonal SST variation (~2–18 °C).

Our results are further supported by the qualitative results from the foraminiferal faunal assemblage studies performed in the region. The foraminiferal assemblages in Åsted Vest suggest a deep-

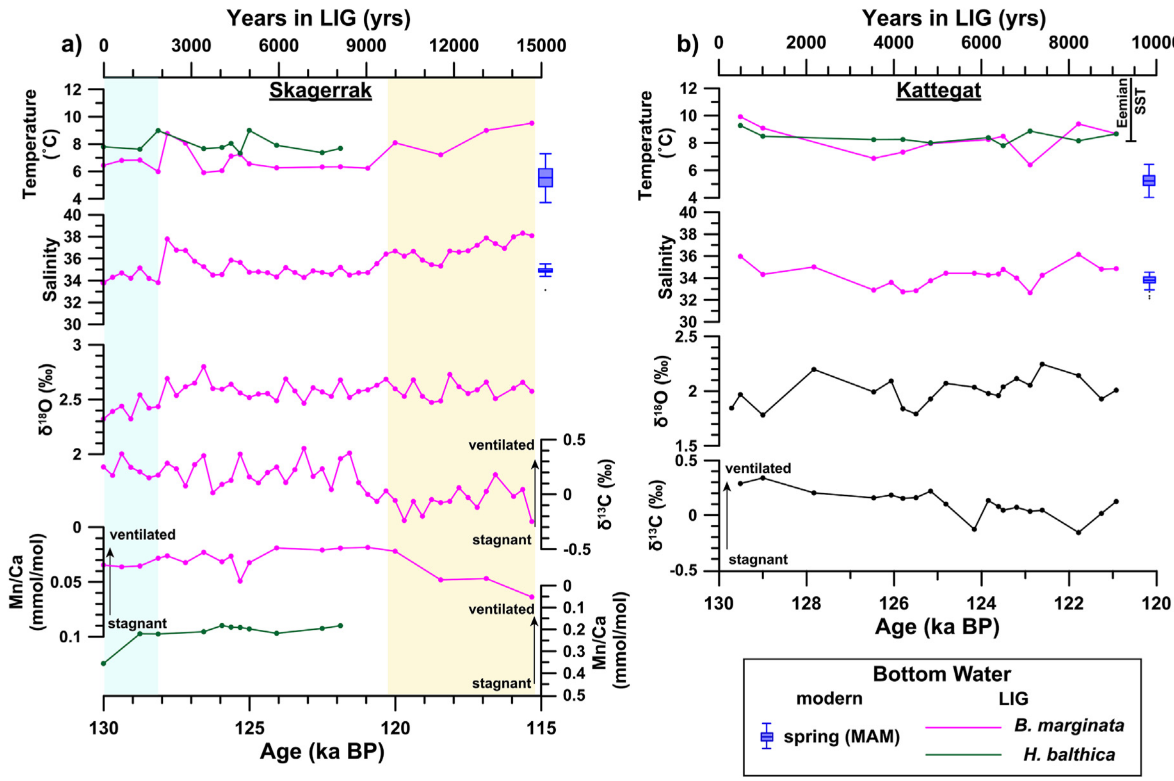

Fig. 5. Foraminiferal Mg/Ca-based BWT, absolute BWS calculated from $T_{Mg/Ca}$ and $\delta^{18}O_c$, Mn/Ca from sites located in the a) Skagerrak and b) Kattegat. Kattegat LIG SST and SSS shown in panel b are based on the gastropod $\delta^{18}O$ study of Burman and Påsse (2008). $\delta^{18}O$ and $\delta^{13}C$ data for *B. marginata* (pink lines; Skagerrak) and *Bulimina aculeata* (black lines; Kattegat) are taken from Knudsen et al. (2009) and Seidenkrantz (1993a), respectively. The box plots indicate the distribution of spring temperatures and salinities at present (Fig. 2). Yellow and blue shadows in Fig. 5a indicate two periods that are described in the text. Note that Y axes of Mn/Ca and $\delta^{13}C$ (‰) are reversed. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

water environment, with ~150–200 m water depth (Larsen et al., 2009), similar to the northern part of the North Sea (Feyling-Hanssen, 1981; Sejrup and Knudsen, 1993), and a comparatively high water temperature associated with an enhanced North Atlantic Current (Knudsen et al., 2009). The LIG marine transgression covered extended areas in the western and northern parts of Vendsyssel (northern Denmark), resulting in a relatively more open connection to the North Atlantic Ocean at that time. The water depth at Anholt was shallower than that of the northern Danish sites, reflecting decreasing water depths toward the south in the paleo-trough (Seidenkrantz, 1993a). The foraminiferal faunas in the Kattegat suggest higher water temperatures during the LIG than at present. This was also indicated by faunas from outcrops and borings in the eastern North Atlantic region (Mangerud et al., 1981; Knudsen, 1985b, 1988; Sejrup, 1987; Penney, 1989; Sejrup and Larsen, 1991).

5.2.2. The Straits and the southern Baltic Sea

The average spring BWT was ~4.4 °C throughout the first 3 kyr during the LIG recorded at Ristinge, which is similar to the modern spring BWT in the Danish Strait (~4.1 °C; *t*-test $p = 0.5$). The average summer BWT at Ristinge was ~8.9 °C; the first two kyr the BWT was lower than the modern summer BWT, while after the first two kyr, i.e. since ~128 ka BP, the summer BWT of Ristinge surpassed the modern summer BWT (~9.0 °C) in the Straits. There was an increasing seasonal temperature difference between spring (MAM) and summer (JJA) during the early LIG from 129 to 126 ka BP (pollen zone E3-E5) at Ristinge, with summers warming over time (trend $p = 0.001$), while springs stayed cool in general. During the time interval (128.4–126.5 ka BP), the spring BWT showed an increasing trend ($p = 0.01$), coinciding with the relatively high BWT in the Skagerrak in the early LIG. It may suggest warm NA inflow from two entrances (Skagerrak and southern Denmark, Fig. 1) into the Baltic Sea and reached these two sites. The reconstructed BWT at Mommark indicates a slightly lower spring temperature (~2.9 °C) compared to the modern day spring BWT (*t*-test $p < 0.001$). There was no significant trend of BWT at Mommark during the recorded time interval during the LIG (130–119 ka BP), however, during the pollen zone E6 (Fig. 6b, yellow shadow), the BWT was relatively high and more variable.

The average spring BWT was 1.4 °C higher than modern spring BWT, and *A. batava* Mg/Ca BWT was ~3 °C higher than the modern summer BWT at Licze in the southern Baltic (*t*-test $p < 0.001$ for both seasons). The seasonality at Licze increased, with increasing summer BWT in pollen zone E4 and E5 (trend $p = 0.002$) and decreasing spring BWT over time (trend $p = 0.019$). In addition to the increasing seasonality trend during the LIG, the average seasonal differences (summer-spring) in BWT in the southern Baltic ($\Delta T = $ ~6.4 °C) during the LIG were higher than during the present ($\Delta T = $ ~4.7 °C), which can be attributed to higher summer temperature and/or larger seasonal water depth changes than today. In contrast, there was no significant trend of seasonal BWT at Obrzynowo. The average BWT difference between spring and summer in the first three kyr of the LIG at Obrzynowo was ~8.1 °C, which was ~1.7 °C higher than the seasonal difference at Licze (Fig. 7), indicating a shallower water depth at Obrzynowo due to the different local bathymetry allowing for a more direct effect of atmospheric summer warming and spring cooling.

For both Ristinge (Danish Straits) and Licze (southern Baltic), our Mg/Ca data infer a clear increase in summer BWTs through the

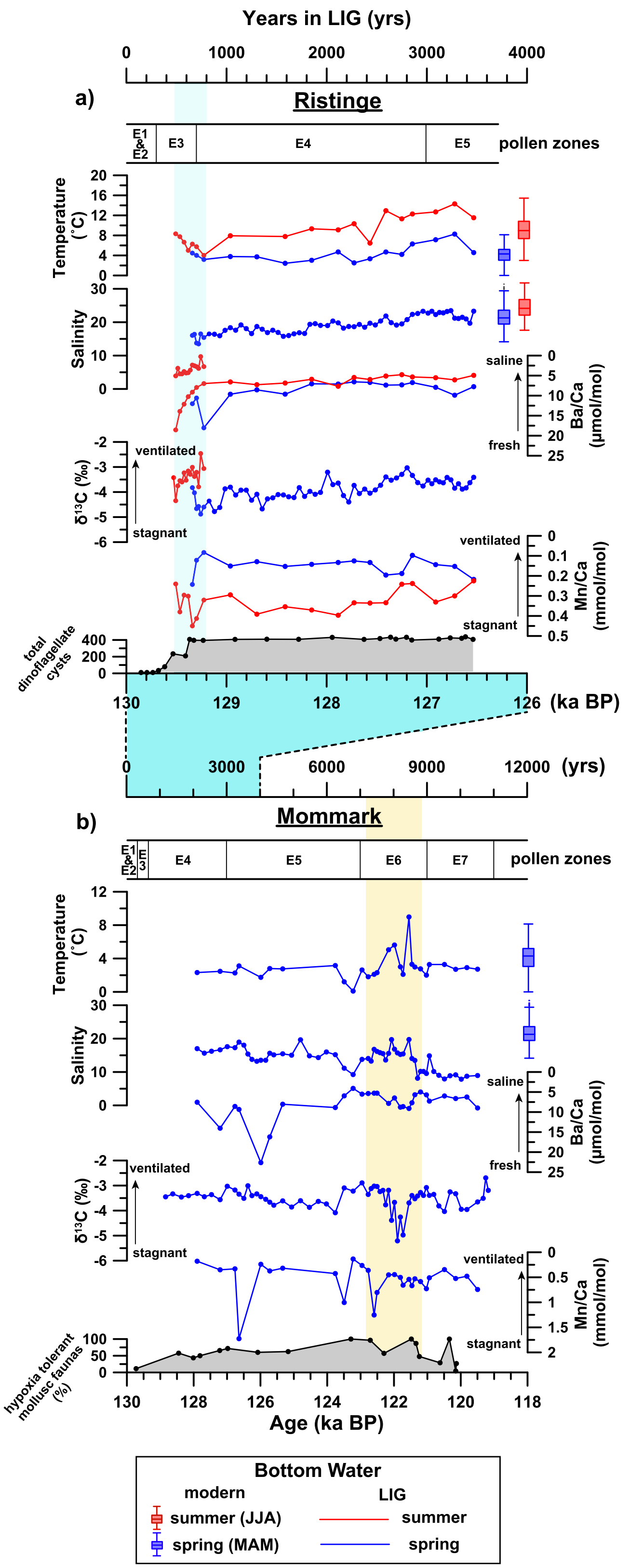

Fig. 6. Foraminiferal (*A. batava* and *E. clavatum-selseyensis*) Mg/Ca-based BWT, absolute BWS calculated from $T_{Mg/Ca}$ and $\delta^{18}O_c$, TE/Ca, $\delta^{18}O$ and $\delta^{13}C$ from the Straits (a) Ristinge and b) Mommark) (Kristensen and Knudsen, 2006; Knudsen et al., 2011), dinoflagellate cyst assemblage (Head, 2007) from Ristinge, as well as mollusc faunas (Funder and Balic-Zunic, 2006) from Mommark. The box plots indicate the distribution of modern seasonal mean temperatures and salinities (Fig. 2). Yellow and blue shadows in Fig. 5a indicate two periods that are described in the text. Note that Y axes of Ba/Ca, Mn/Ca and $\delta^{13}C$ (‰) are reversed, X axes of age and years in LIG are in different scales in a and b. The same time span of a and b is shown with blue zones with diagonal dashed lines on X axes. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

early part of the LIG, while cold-season (spring) underwent a cooling observed at Licze. This suggests that changes in seasonal insolation had a significant impact on Baltic conditions, because summer insolation increased significantly from 130 to 123 ka BP and spring insolation decreased at 55°N (Fig. 8, Laskar et al., 2004), which led to increasing seasonality during the LIG.

The larger seasonal temperature differences between spring and summer in the Baltic Sea during the first half of the LIG compared with modern conditions were mainly caused by higher summer temperatures (Figs. 6 and 7) rather than colder spring temperatures. This suggests that increased summer insolation and corresponding higher summer BWTs played a more important role than spring insolation in the increased LIG seasonality. Due to the higher obliquity and eccentricity states during the early LIG, seasonal differences in insolation were globally larger during the LIG, leading to warmer boreal summers (Berger and Loutre, 1991; Laskar et al., 2004; Lunt et al., 2013; Bova et al., 2021). This is also supported by previous studies, as further discussed below. The records of dinoflagellate cyst assemblages from Licze suggest that the summer SST may have reached as high as ~27 °C during the early LIG (Head et al., 2005), while molluscs indicate a winter SST of ~9 °C from the northern Polish coast (Funder et al., 2002). This seasonal difference in SST based on dinoflagellate cysts and molluscs is larger than the maximum differences between seasons seen today. A similar stronger-than-present seasonality during the early LIG is also recorded in northern Finland (Salonen et al., 2018). The covariance of temperature seasonality with insolation seasonality in the Baltic region agrees also with the findings in the tropical Atlantic Ocean (Felis et al., 2015; Brocas et al., 2016) and Mediterranean Sea (Milner et al., 2012). The SST seasonality in the tropical North Atlantic Ocean, based on coral Sr/Ca within the mid-LIG (4.9 °C at 126 ka) was also significantly higher than the modern SST seasonality (2.9 °C), with the SST seasonal difference (ΔT ~2 °C) in the tropical North Atlantic Ocean (Brocas et al., 2016) being similar to the BWT seasonality in the southern Baltic Sea observed in our study. Our seasonality data from the Baltic Sea are further supported by a coupled atmosphere-ocean general circulation model (COSMOS, see Brocas et al., 2016), showing enhanced mid-LIG SST seasonality in the tropical Atlantic Ocean. The results from our work and the above-mentioned studies demonstrate that increasing insolation-induced summer warming and stronger seasonal temperature differences during the early half of the LIG impacted the boreal area and the wider tropical and North Atlantic region.

5.3. Salinity

5.3.1. Skagerrak and Kattegat

The $\delta^{18}O$ of foraminifera from the six sites shows a general decreasing trend along the Skagerrak-Kattegat-the Danish Straits-Southern Baltic transect, indicating a decreasing trend of BWS from the Skagerrak to the Baltic Proper similar to the present. The $\delta^{18}O$ of foraminifera at Åsted Vest varied between 2.3 and 2.8‰ (Knudsen et al., 2009) and at Anholt it varied between 1.8 and 2.2‰ (Seidenkrantz, 1993a). The reconstructed LIG mean BWSs of Skagerrak and Kattegat (35.6 and 34.2, respectively) were slightly higher than the modern spring mean BWS at these two sites (34.9 and 33.7, respectively) (*t*-test $p < 0.001$ and $p = 0.04$, respectively). The water depth might have shallowed due to isostatic rebound

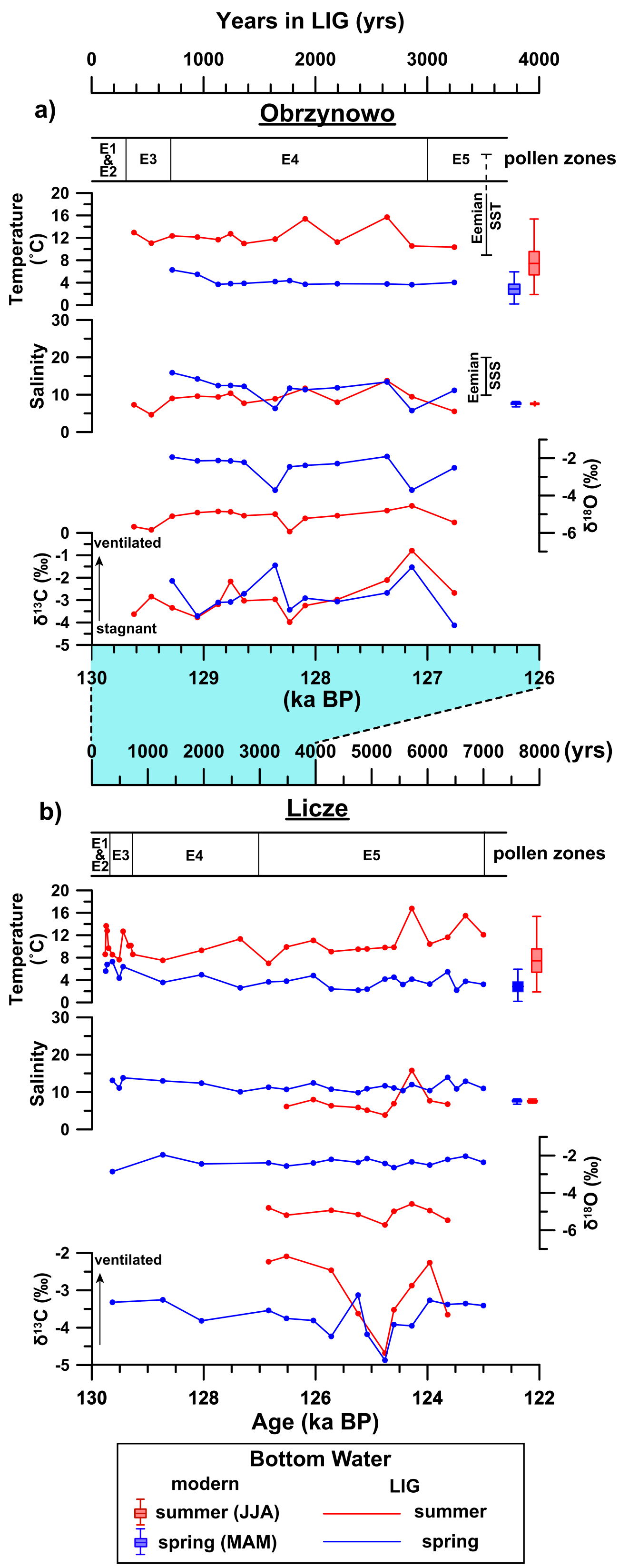

Fig. 7. Foraminiferal (*A. batava* and *E. clavatum-selseyensis*) Mg/Ca-based BWT, absolute BWS calculated from $T_{Mg/Ca}$ and $\delta^{18}O_c$, TE/Ca, $\delta^{18}O$ and $\delta^{13}C$ from the southern Baltic Sea (a) Licze and b) Obrzynowo). LIG SST and SSS estimations are based on Funder et al. (2002) and Head et al. (2005). The box plots indicate the distribution of modern seasonal mean temperatures and salinities (Fig. 2). Note that Y axes of Ba/Ca and $\delta^{13}C$ (‰) are reversed, X axes of age and years in LIG are in different scales in a and b. The same time span of a and b is shown with blue zones with diagonal dashed lines on X axes. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and corresponding sea level regression, which would have resulted in a smaller volume of deep water. A study using the $\delta^{18}O$ of gastropod shells estimated the SSS in the Kattegat to be ~29 at 125 ka BP (Burman and Påsse, 2008), while reconstructions based on mollusc faunas suggest salinities of ~25 (Funder et al., 2002), which is ~4 units higher than the modern annual mean SSS (~21). This is in overall agreement that during the LIG both BWS and SSS were higher than the modern conditions suggesting more inflow of open marine water from the North Atlantic. During the late LIG (121–115 ka BP), the BWS in the Skagerrak increased from ~35 to ~38, coinciding with slightly increasing temperature and more stagnant bottom water conditions (Fig. 5a, yellow shadow). However, it is unlikely that the Skagerrak salinity reached 38; rather, this anomalously high salinity value could be a result of errors in the Mg/Ca-based temperature reconstruction (1 °C error may induce one-unit salinity uncertainty), together with uncertainties in the $\delta^{18}O$ mixing line we used for salinity calculation and species calibration.

5.3.2. The Straits and the southern Baltic Sea

During the beginning of the LIG, the rapid salinity increase at Ristinge may be related to the early LIG transgression and water depth increase in the North Sea – Baltic transition area. This may correspond to a wider/greater-than-previous opening of the Danish Straits due to sea-level rise and major alteration in current activity in the early stage of the LIG. This salinity increase affected the entire water body, as indicated by an increasing $\delta^{18}O_c$ (Kristensen and Knudsen, 2006; Knudsen et al., 2011), decreasing Ba/Ca, and changed diatom and dinoflagellate cyst assemblages (Fig. 6a) (Head et al., 2007; Knudsen et al., 2011). The BWS at Ristinge ~126–127 ka BP reached a salinity (~21.8) that is similar to modern spring salinity (~21.7). The wider and deeper passage for water transport from the North Sea to the Kattegat and the wider straits across Denmark, combined with a relatively stronger North Atlantic Current, may have allowed persistently higher salinities and temperatures in the Danish Straits and western Baltic throughout the LIG (Head et al., 2005; Knudsen et al., 2012). This also created a stronger water exchange between the Baltic Sea and the North Atlantic than today.

The Ba/Ca data in the southern Baltic sites imply lower salinity at Obrzynowo than Licze, supporting our BWT-based evaluation of a shallower water depth at Obrzynowo (see discussion in 5.2). The LIG summer BWS (7.2) was similar to the modern summer (JJA) BWS (~7.6), while the LIG spring BWS (11.6) was ~4 units higher than the modern spring (MAM) BWS (~7.6) at Licze. The salinity differences at Licze between seasons suggest a larger seasonal variability during the mid-LIG (~127–124 ka BP) than at present. The BWSs of spring and summer at Obrzynowo were also significantly different (*t*-test $p = 0.02$), the difference between seasons was significantly larger than the modern seasonal difference. The trend of seasonal difference during the recorded time interval at Obrzynowo was not significant, probably due to the different local bathymetry and location. The water depth at Obrzynowo was probably shallower compared to the water depth at Licze based on the larger seasonal temperature difference at Obrzynowo. In addition, the average seasonal difference (spring-summer) for the whole recorded time interval at Obrzynowo was smaller (2.7) than at Licze (4.4), which may be ascribed to a greater influence of river input or closer distance to the Vistula river for Licze. At Licze, both surface and bottom waters freshened through the LIG, which

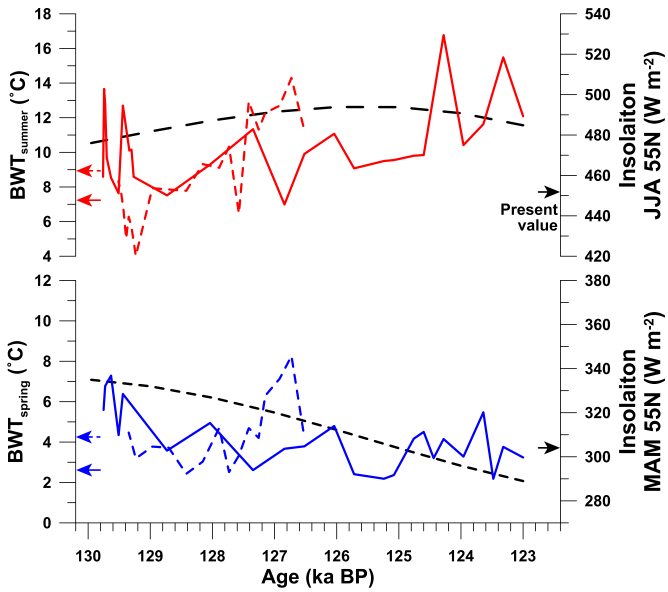

Fig. 8. BWTs reconstructed from *A. batava* and *E. clavatum-selseyensis* Mg/Ca in Licze (solid, colored lines) and Ristinge (dashed colored lines). The colored arrows indicate modern values of BWTs. Dashed lines indicate 55°N averaged spring (MAM) and summer (JJA) insolation, and the black arrows indicate modern values of insolation (Laskar et al., 2004).

coincided with a marked increase in the number of freshwater diatoms and green algae (Head et al., 2005; Knudsen et al., 2012), suggesting increasing river input to the Vistula estuary and/or a water depth decrease with accordingly less saline bottom water. The Licze and Obrzynowo sites are located in an area with shallow LIG water depth. This area was presumably a brackish estuary environment with no distinct halocline and with bottom water characteristics similar to those for the surface waters, i.e. summer salinity slightly lower than the spring salinity.

5.4. Oxygen conditions

The $\delta^{13}C$ of three foraminifera species from the six sites show large variations, varying from 0.42‰ at Åsted Vest (Knudsen et al., 2009) to −5.2‰ at Mommark (Kristensen and Knudsen, 2006). The $\delta^{13}C$ variation during the LIG mainly indicates bottom-water ventilation. But the $\delta^{13}C$ data may also be influenced by the habitat depth of foraminifera (Tachikawa and Elderfield, 2002; Mackensen et al., 2017), which needs to be further investigated regarding foraminifera species-specific microhabitat. The bottom-water in Skagerrak became more stagnant during the late LIG (Fig. 5 yellow shadow), indicated by increased Mn/Ca and more negative benthic foraminiferal $\delta^{13}C$ values. In the Kattegat, a generally decreasing trend occurred in foraminiferal $\delta^{13}C$, which was associated with increasing TOC (Seidenkrantz, 1993a), indicating enhanced nutrients and less oxygenated bottom water. More stagnant bottom-water in Skagerrak during late LIG can be linked to comparatively restricted water exchange and reduced current velocity, and possibly warm-climate-induced higher primary productivity resulting in more organic matter deposition.

The difference between maximum and minimum values of *E. clavatum-selseyensis* $\delta^{13}C$ in the Danish Straits and the southern Baltic Sea region suggests that the ventilation conditions at Mommark and Obrzynowo were worse than at the other two sites. Seasonal hypoxia may have taken place during spring. Higher foraminiferal Mn/Ca and more negative $\delta^{13}C$ occurring together with more variable and occasionally high BWT and BWS indicate more stratified water conditions and seasonal hypoxia during pollen zone E6 (yellow shadow in Fig. 6b) at Mommark. Furthermore, during this period, the total foraminiferal flux (Kristensen and Knudsen, 2006) and the abundance of hypoxia tolerant mollusc fauna in the *Cyprina* Clay (Funder and Balic-Zunic, 2006) were high, suggesting high productivity and related bottom water oxygen stress.

Foraminiferal $\delta^{13}C$ at Ristinge increased during the early LIG and showed a significant positive correlation with $\delta^{18}O$ (Fig. 4), indicating a gradually increasing water exchange from the North Sea, likely due to a greater water depth and wider waterways through the Straits and/or across northern Germany during the early LIG. The increasing $\delta^{13}C$ also suggests increasing bottom-water ventilation and well-oxygenated bottom water conditions occurred during the early LIG due to greater connectivity with the North Sea in the Straits. At the southern Baltic sites, the $\delta^{13}C$ and $\delta^{18}O$ of *A. batava* showed a significant positive correlation, similar to that observed at Ristinge. This indicates the presence of a different water mass with very negative $\delta^{13}C$ and $\delta^{18}O$ during the summer, which may be linked to changing of salinity and water depth in the estuary.

6. Conclusions

We applied benthic foraminifera-based geochemistry records from six sites in the western and southern Baltic to provide quantitative reconstructions of bottom water temperature and salinity, and relative oxygen and ventilation conditions during the Last Interglacial (LIG) and to investigate the Last Interglacial climate seasonality in the Baltic region.

The average LIG bottom-water temperatures (BWTs) during spring based on Mg/Ca were 1.6 °C higher in the Skagerrak and 3.0 °C higher in the Kattegat when compared to the modern spring (MAM) BWTs. Due to the relatively greater water depth, the bottom-water salinities (BWSs) showed no clear seasonal variation; the reconstructed BWSs in the Skagerrak and the Kattegat were ~1 unit higher than the modern annual mean BWS. In general, there was an increasing trend in bottom-water salinity in the Skagerrak during the LIG, suggesting both a relatively more open connection to the North Atlantic Ocean than today and a gradual increase in water depth through the LIG. During the late LIG, the bottom water in the Skagerrak and the Kattegat experienced a decrease in dissolved oxygen due to a sea level decline and high primary production. In the Danish Straits, the summer BWTs increased over time during early LIG, while the spring BWTs were similar to modern spring BWTs. There was a rapid salinity increase during the earliest LIG (~500–800 yrs after LIG started) in the Danish Straits, which may be due to the early LIG transgression and opening of the connection between the North Sea and the Baltic Sea.

The most notable feature of our climate reconstructions is the distinct increasing seasonal difference in BWT (warming summer and cooling spring) in our reconstructed time series during the first half of the LIG in the Straits and southern Baltic Sea. This can be ascribed to the increase in summer (JJA) insolation and potentially also the reduced spring (MAM) insolation shown in other studies. In such a complex environment as the western and southern Baltic, changes in sea level, water depth and runoff, as well as land-cover influences, should of course also be considered. Nevertheless, our proxy records are significant as they support previously published evidence for the increased seasonality during the LIG compared to today at mid-to high latitudes, as would also be expected from the insolation record (Berger and Loutre, 1991; Laskar et al., 2004). Regional modeling experiments may help further explain and test the mechanism of seasonality in the Baltic region during the LIG.

Author contribution

S. Ni: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Funding acquisition, Visualization, Investigation, Formal analysis. N. B. Quintana Krupinski: Conceptualization, Methodology, Writing – review & editing. J. Groeneveld: Writing – review & editing, Methodology, Formal analysis. J. Chonewicz: Writing – review & editing, Investigation. K. L. Knudsen: Writing – review & editing, Resources. M.S. Seidenkrantz: Writing – review & editing, Funding acquisition, Project administration, H.L. Filipsson: Conceptualization, Writing – review & editing, Supervision, Funding acquisition, Project administration

Data availability

Datasets related to this article are available at: https://data.mendeley.com/datasets/4x2w5f63zx/1.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2021.107220.

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