1 Land-sea coupling of early Pleistocene glacial cycles in the southern North Sea exhibit

2 dominant Northern Hemisphere forcing

- 3 Timme H. Donders^{1,2}, Niels A.G.M. van Helmond³, Roel Verreussel², Dirk Munsterman⁴,
- 4 Johan Ten Veen⁴, Robert P. Speijer⁵, Johan W.H. Weijers³*, Francesca Sangiorgi³, Francien
- Peterse³, Gert-Jan Reichart^{3,6}, Jaap S. Sinninghe Damsté^{3,6}, Lucas Lourens³, Gesa Kuhlmann⁷
 and Henk Brinkhuis^{3,6}
- 7
- ¹ Department of Physical Geography, Fac. of Geosciences, Utrecht University,
- 9 Heidelberglaan 2, 3584CD, Utrecht, The Netherlands.
- 10 ² TNO Applied Geosciences, Netherlands Organisation of Applied Scientific Research
- 11 Princetonlaan 6, 3584 CB Utrecht, The Netherlands.
- ³ Department of Earth Sciences, Fac. of Geosciences, Utrecht University, Heidelberglaan 2,
- 13 3584CS, Utrecht, The Netherlands.
- ⁴ TNO Geological Survey of the Netherlands, Netherlands Organisation of Applied
- 15 Scientific Research, Princetonlaan 6, 3584 CB Utrecht, The Netherlands.
- ⁵ Department of Earth and Environmental Sciences, KU Leuven, 3001 Heverlee, Belgium
- ⁶ NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB, Den Burg,
- 18 Texel, The Netherlands
- ⁷ BGR Federal Institute for Geosciences and Natural Resources, Geozentrum Hannover
- 20 Stilleweg 2, D-30655 Hannover
- * Currently at: Shell Global Solutions International B.V., Grasweg 31, 1031 HW, Amsterdam,
- 22 The Netherlands
- 23 Correspondence to: t.h.donders@uu.nl
- 24
- 25

26 Abstract

We assess the disputed phase relations between forcing and climatic response in the early 27 Pleistocene with a spliced Gelasian ($\sim 2.6 - 1.8$ Ma) multi-proxy record from the southern 28 North Sea basin. The cored sections couple climate evolution on both land and sea during the 29 intensification of Northern Hemisphere Glaciations (NHG) in NW Europe, providing the first 30 31 well-constrained stratigraphic sequence of the classic terrestrial Praetiglian Stage. Terrestrial signals were derived from the Eridanos paleoriver, a major fluvial system that contributed a 32 large amount of freshwater to the northeast Atlantic. Due to its latitudinal position, the 33 Eridanos catchment was likely affected by early Pleistocene NHG, leading to intermittent 34 shutdown and reactivation of river flow and sediment transport. Here we apply organic 35 36 geochemistry, palynology, carbonate isotope geochemistry, and seismostratigraphy to 37 document both vegetation changes in the Eridanos catchment and regional surface water 38 conditions and relate them to early Pleistocene glacial-interglacial cycles and relative sea-39 level changes. Paleomagnetic and palynological data provide a solid integrated timeframe that ties the obliquity cycles, expressed in the borehole geophysical logs, to Marine Isotope Stages 40 (MIS) 103 to 92, independently confirmed by a local benthic oxygen isotope record. Marine 41 42 and terrestrial palynological and organic geochemical records provide high resolution reconstructions of relative Terrestrial and Sea Surface Temperature (TT and SST), vegetation, 43 44 relative sea level, and coastal influence.

During the prominent cold stages MIS 98 and 96, as well as MIS 94 the record indicates increased non-arboreal vegetation, and low SST and TT, and low relative sea level. During the warm stages MIS 99, 97 and 95 we infer increased stratification of the water column together with higher % arboreal vegetation, high SST and relative sea-level maxima. The early Pleistocene distinct warm-cold alterations are synchronous between land and sea, but lead the relative sea-level change by 3-8 thousand years. The record provides evidence for a

- 51 dominantly NH driven cooling that leads the glacial build up and varies on obliquity
- 52 timescale. Southward migration of Arctic surface water masses during glacials, indicated by
- 53 cool-water dinoflagellate cyst assemblages, is furthermore relevant for the discussion on the
- relation between the intensity of the Atlantic meridional overturning circulation and ice sheet
- 55 growth.
- 56
- 57 **Keywords**: Glacial-interglacial climate, palynology; organic geochemistry; obliquity, land-
- 58 sea correlation, Eridanos delta, southern North Sea

59 **1 Introduction**

60

(Ruddiman et al. 1986; Mudelsee and Raymo, 2005; Ravelo et al., 2004; Ravelo, 2010), with 61 stepwise intensifications between 2.7 and 2.54 Ma ago (e.g., Shackleton and Hall, 1984; 62 Raymo et al., 1989; Haug et al., 2005; Lisiecki and Raymo, 2005; Sosdian and Rosenthal, 63 2009). In the North Atlantic region the first large-scale early Pleistocene glaciations, Marine 64 Isotope Stages (MISs) 100 - 96, are marked by e.g. appearance of ice-rafted debris and 65 southward shift of the Arctic front (see overviews in Naafs et al., 2013; Hennissen et al., 66 2015). On land, the glaciations led to faunal turnover (e.g. Lister, 2004; Meloro et al., 2008) 67 and widespread vegetation changes (e.g. Zagwijn, 1992; Hooghiemstra and Ran, 1994; 68 Svenning, 2003; Brigham-Grette et al., 2013). Many hypotheses have been put forward to 69 70 explain the initiation of these NH glaciations around the Plio-Pleistocene transition interval. Causes include tectonics (Keigwin, 1982, Raymo, 1994; Haug and Tiedemann, 1998; Knies et 71 72 al, 2004; Poore et al., 2006), orbital forcing dominated by obliquity-paced variability (Hays et al., 1976; Maslin et al., 1998; Raymo et al., 2006) and atmospheric CO₂ concentration decline 73 (Pagani et al., 2010; Seki et al., 2010; Bartoli et al., 2011) driven by e.g. changes in ocean 74 stratification that affected the biological pump (Haug et al., 1999). Changes were amplified by 75 NH albedo changes (Lawrence et al., 2010), evaporation feedbacks (Haug et al., 2005), and 76 possibly tropical atmospheric circulation change and breakdown of a permanent El Niño 77 (Ravelo et al., 2004; Brierley and Fedorov, 2010; Etourneau et al., 2010). 78

The build-up of extensive Northern Hemisphere (NH) land ice started around 3.6 Ma ago

79

Key aspects in this discussion are the phase relations between temperature change on land, in
the surface and deep ocean, and ice sheet accretion (expressed through global eustatic sealevel lowering) in both Northern and Southern Hemispheres. According to Raymo et al.

(2006), early Pleistocene obliquity forcing dominated global sea level and δ^{18} O_{benthic}, because 83 84 precession-paced changes in the Greenland and Antarctic ice sheets cancelled each other out. In this view, climate records independent of sea-level variations should display significant 85 variations on precession timescale. Recent tests of this hypothesis indicate that early 86 Pleistocene precession signals are prominent in both Laurentide ice sheet meltwater pulses 87 and iceberg-rafted debris of the East Antarctic ice sheet, and decoupled from marine $\delta^{18}O$ 88 89 (Patterson et al., 2014; Shakun et al., 2016). Alternatively, variations in the total integrated summer energy, which is obliquity controlled, might be responsible for the dominant 90 obliquity pacing of the early Pleistocene (Huybers, 2011; Tzedakis et al., 2017). The 91 92 dominance of the obliquity component has been attributed to feedbacks between high-latitude insolation, albedo (sea-ice and vegetation) and ocean heat flux (Koenig et al., 2011; Tabor et 93 al., 2014). Sosdian and Rosenthal (2009) suggested that temperature variations, based on 94 95 benthic foraminifer magnesium/calcium (Mg/Ca) ratios from the North Atlantic, explain a substantial portion of the global variation in the $\delta^{18}O_{\text{benthic}}$ signal. Early Pleistocene North 96 Atlantic climate responses were closely phased with $\delta^{18}O_{benthic}$ changes, evidenced by 97 dominant 41-kyr variability in North American biomarker dust fluxes at IODP Site U1313 98 (Naafs et al., 2012), suggesting a strong common NH high latitude imprint on North Atlantic 99 100 climate signals (Lawrence et al., 2010). Following this reasoning, glacial build-up should be in phase with decreases in NH sea surface temperatures (SST) and terrestrial temperatures 101 (TT). 102

103

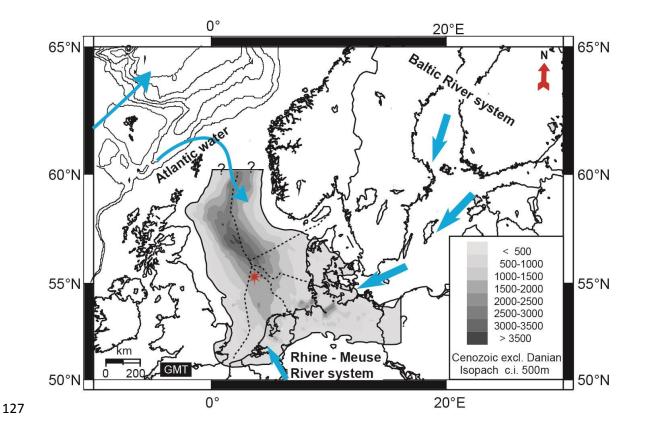
To explicitly test this hypothesis we perform a high-resolution multiproxy terrestrial and
marine palynological, organic geochemical, and stable isotope study on a marginal marine
sediment sequence from the southern North Sea (SNS) during the early Pleistocene "41 kyrworld". We investigate the leads and lags of regional marine vs. terrestrial climatic cooling

during MIS 102-92, and assess the local sea-level response relative to global patterns from the 108 δ^{18} O_{benthic} stack of Lisiecki and Raymo (2005; LR04). In a dominantly, NH obliquity driven 109 scenario, we expect the marine and terrestrial temperature proxies to be in phase on obliquity 110 111 timescales with a short (less than 10 kyr) lead on sea-level variations. In addition, the record can better constrain the signature and timing of the regional continental Praetiglian stage (Van 112 der Vlerk and Florschütz, 1953; Zagwijn, 1960) that is still widely used, although its 113 114 stratigraphic position and original description are not well defined (Donders et al., 2007; Kemna and Westerhoff, 2007). 115

116

117 **2** Geological setting

During the Neogene the epicontinental North Sea Basin was confined by landmasses except 118 towards the northwest, where it opened into the Atlantic domain (Fig. 1) (Bijlsma, 1981; 119 120 Ziegler, 1990). Water depths in the central part were approximately between 100 to 300 m as deduced from seismic geometry (Huuse et al., 2001; Overeem et al., 2001). In contrast, the 121 recent North Sea has an average depth between 20-50 m in the south that deepens only 122 towards the shelf edge towards 200 m in the north-west (e.g., Caston, 1979). From the 123 present-day Baltic region a formidable river system, known as the Eridanos paleoriver, 124 developed which built up the Southern North Sea delta across southern Scandinavia (Sørensen 125 et al., 1997; Michelsen et al., 1998; Huuse et al., 2001; Overeem et al., 2001). 126



128 Figure 1: Geographical map of the present day North Sea region with the superimposed thickness of Cenozoic sediment infill after Ziegler (1990) and the offshore sectors (dashed 129 lines). The reconstructed different water sources (see Gibbard and Lewin, 2016) that 130 influenced the Pliocene and early Pleistocene North Sea hydrography, including the 131 freshwater supply of the Baltic river system, the Rhine-Meuse river system and Atlantic 132 surface waters are indicated with blue arrows. The location of both boreholes A15-3 (UTM X 133 552567.1, Y 6128751.6) and A15-4 (UTM X 557894.4, Y 6117753.5) is marked by an asterisk, 134 see Fig. S1 for details. 135

This delta was characterized by an extensive distributary system that supplied large amounts of freshwater and sediment to the shelf sea during the Neogene and early Pleistocene (Overeem et al., 2001), resulting in a sediment infill of ~1500 m in the central North Sea Basin (Fig. 1). This system was fed by rainfall as well as by melt-water originating from Scandinavian glaciers (Kuhlmann et al., 2004), principally from the Baltic Shield in the east with some contribution from the south (Fig. 1) (Bijlsma, 1981; Kuhlmann, 2004). The
sedimentation rates reached up to 84 cm/kyr at the studied locations (Fig. 2) (Kuhlmann et al.,
2006b). Today, the continental river runoff contributes only 0.5 % of the water budget in the
North Sea (Zöllmer and Irion, 1996) resulting in sedimentation rates ranging between 0.4 to
1.9 cm/kyr in the Norwegian Channel, and 0.5 - 1 cm/kyr in the southern part of the North
Sea (de Haas et al., 1997).

147

148 **3 Material, core description and age model**

149 Recent exploration efforts in the SNS led to the successful recovery of cored sedimentary successions of marine isotope stages (MIS) 102-92 and continuous paleomagnetic logs (Fig. 150 2) (Kuhlman et al, 2006ab). For quantitative palynological and geochemical analyses, discrete 151 152 sediment samples were taken from two exploration wells A15-3 and A15-4 located in the northernmost part of the Dutch offshore sector in the SNS at the Neogene sedimentary 153 depocentre (Fig. 1). An integrated age model is available based on a multidisciplinary 154 geochronological analysis of several boreholes within the SNS (Kuhlmann et al., 2006a,b) 155 and dinocyst biostratigraphy. The magnetostratigraphy, core correlation and age-diagnostic 156 157 dinocyst events used for this age-model are summarized in Fig. 2 and Table S1. The recovered material mainly consists of fine-grained, soft sediments (clayey to very fine sandy), 158 sampled from cuttings, undisturbed sidewall cores and core sections (Fig. 2). Geochemical 159 160 analyses were limited to the (sidewall) core intervals, while the cuttings were to increase resolution of the palynological samples, and are based on larger rock chips that have been 161 cleaned before treatment. Clear cyclic variations in the gamma ray signal and associated 162 163 seismic reflectors across the interval can be correlated across the entire basin (Kuhlman et al., 2006a; Kuhlmann and Wong, 2008; Thöle et al. 2014). Samples from the two boreholes were 164 spliced based on the gamma-ray logs (Figs. 2, S2) and biostratigraphic events to generate a 165

composite record. The age model is mainly based on continuous paleomagnetic logging 166 supported by discrete sample measurements and high-resolution biostratigraphy. There is 167 evidence of small hiatuses above (~2.1 Ma) and significant hiatuses below the selected 168 169 interval (within the early Pliocene and Miocene, particularly the Mid-Miocene Unconformity), which is why we excluded these intervals in this study. The position of the 170 Gauss-Matuyama transition at the base of log unit 6 correlates to the base of MIS 103, the 171 identification of the X-event, at the top of log unit 9, correlates to MIS 96, and the Olduvai 172 magnetochron is present within log units 16-18 (Kuhlmann et al., 2006a,b). These ages are 173 supported by dinocyst and several other bioevents (Table S1, updated from Kuhlmann et al., 174 175 2006a,b). Consistent with the position of the X-event, the depositional model by Kuhlmann and Wong (2008) relates the relatively coarse-grained, low gamma ray intervals to 176 interglacials characterized by high run off. A recent independent study on high-resolution 177 178 stable isotope analyses of benthic foraminifera from an onshore section in the same basin confirmed this phase relation (Noorbergen et al., 2015). Around glacial terminations, when 179 180 sea level was lower but the basin remained fully marine, massive amounts of very finegrained clayey to fine silty material were deposited in the basin, the waste-products of intense 181 glacial erosion. During interglacials with high sea level more mixed, coarser-grained 182 sediments characterize the deposits, also reflecting a dramatically changed hinterland, 183 retreated glaciers, and possibly (stronger) bottom currents (Kuhlmann and Wong, 2008). 184 Based on this phase relation, detailed magneto- and biostratigraphy, grain size measurements, 185 and previous low resolution relative SST indices (Kuhlmann et al., 2004; Kuhlmann et al., 186 2006a,b), the finer grained units are consistently correlated to MIS 102 - 92. Based on this 187 correlation of the GR inflection points to the corresponding LR04 MIS transitions, the 188 189 sequence is here transferred to an age scale through interpolation with a smoothing spline function (Fig. S3). 190

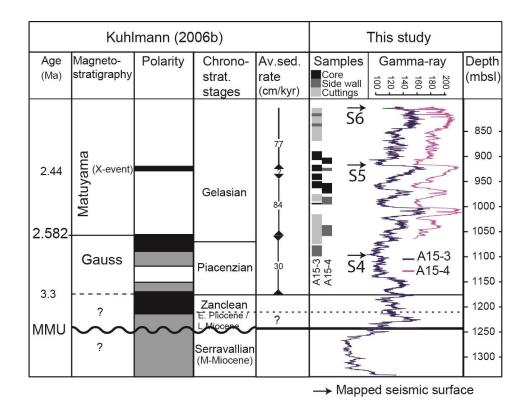


Figure 2: Chronology and mean sedimentation rates as derived from biostratigraphy and
paleomagnetic data (Kuhlmann et al., 2006a,b) in combination with the gamma-ray log of
A15-3 and A15-4 used in this study on a common depth scale. The position of various sample
types and the mapped seismic horizons S4-6 (Fig. S1) are indicated. Material for the sidewall
cores is limited, and used only for palynology and organic geochemistry. Bioevents based on
Kuhlmann et al. (2006a,b) are listed in Table S1.

199

192

The regional structure and development of the delta front across the Plio-Pleistocene transition interval is very well constrained by a high-resolution regional geological model that represents the anatomy of the Eridanos (pro-) delta (Kuhlmann and Wong, 2008; Ten Veen et al., 2013). A total of 25 seismic horizons in the Plio-Pleistocene transition interval were mapped using series of publically available 2D and 3D seismic surveys across the northern part of the Dutch offshore sector. For all these surfaces the distribution of delta elements such as of topset-, foreset- and toeset-to-prodelta has been determined, resulting in zonal maps 207 (250 m grid size) that represent the present day geometry of the surfaces. The 208 paleoenvironmental reconstructions are compared to these maps to constrain the regional 209 setting and aid the interpretations.

210

211 **4** Paleoenvironmental proxies and methods

212 4.1 Benthic oxygen and carbon isotopes ($\delta^{18}O_b$ and $\delta^{13}C_b$)

Oxygen and carbon isotopes were measured on tests of Cassidulina teretis, a cold water 213 species of endobenthic foraminifera that is generally abundant in the samples and common in 214 fine-grained sediment and relatively low salinities (Mackensen and Hald, 1988; Rosoff and 215 Corliss, 1992). Because of their endobenthic habitat, they record isotope compositions of pore 216 waters, which leads to somewhat reduced $(\delta^{13}C_b)$ values compared to the overlying bottom 217 waters. Since the amount of material from the sidewall cores is limited, the isotope data is 218 219 only produced for the cored intervals with the principal aim to confirm the phase relationship described by Kuhlmann and Wong (2008) between facies and climate. Preservation was based 220 221 on a visual inspection and assignment of a relative preservation scale of 1-5, after which the poorest 2 classes were discarded because primary calcite was nearly absent. The best 222 preserved specimens (cat. 1) had shiny tests (original wall calcite) and showed no signs of 223 overgrowth. Category 2 specimens showed signs of overgrowth but were not recrystallized 224 and cat. 3 specimens were dull and overgrown by a thin layer of secondary calcite. Between 225 ~20 and 50 μ g of specimens per sample was weighed after which the isotopes of the 226 carbonate were measured using a Kiel III device coupled to a 253 ThermoFinnigan MAT 227 instrument. Isotope measurements were normalized to an external standard 'NBS-19' ($\delta^{18}O =$ 228 $-2.20\%, \delta^{13}C = 1.95\%)$. 229

230

231 *4.2 Palynological proxies*

In modern oceans, dinoflagellates are an important component of the (phyto-)plankton. About 232 233 15-20% of the marine dinoflagellates form an organic walled cyst (dinocyst) during the life cycle that can be preserved in sediments (Head, 1996). Dinocyst distribution in marine 234 235 surface sediments has shown to reflect changes in the sea surface water properties, mostly responding to temperature (e.g., Rochon et al., 1999; Zonneveld et al., 2013). Down-core 236 changes in dinocyst assemblages are widely used in reconstructing past environmental 237 changes in the Quaternary (e.g., de Vernal et al., 2009), but also in the Neogene and 238 239 Paleogene (e.g., Versteegh and Zonneveld, 1994; Head et al., 2004; Pross and Brinkhuis, 2005; Sluijs et al., 2005; Schreck et al., 2013; De Schepper et al., 2011; 2013; Hennissen et 240 241 al., 2017).

242

Here we use the preference of certain taxa to cold-temperate to arctic surface waters to derive 243 244 sea surface temperature (SST) trends. The cumulative percentage of the dinocysts Filisphaera microornata, Filisphaera filifera, Filisphaera sp., Habibacysta tectata and B. tepikiense on 245 246 the total dinocysts represents our cold surface water indicator (Versteegh and Zonneveld, 1994; Donders et al., 2009; De Schepper et al., 2011). Interestingly, Bitectatodinium 247 tepikiense, the only extant dinocyst among our cold-water species, has been recorded from the 248 249 mixing zone of polar front oceanic waters with cold brackish meltwaters from glacier ice 250 (e.g., Bakken and Dale, 1986) and at the transition between the subpolar and temperate zones 1996). The combined abundance of 251 (Dale, Lingulodinium machaerophorum, Tuberculodinium vancampoae, Polysphaeridium zoharyi and Operculodinium israelianum is 252 253 used here to indicate, coastal waters, although they generally also relate to warmer conditions. In particular, high percentages of L. machaerophorum are typically recorded in eutrophic 254 255 coastal areas where reduced salinity and (seasonal) stratification due to runoff occur (Dale, 1996; Sangiorgi and Donders, 2004; Zonneveld et al., 2009). At present, T. vancampoae, P. 256

zoharyi and *O. israelianum* are also found in lagoonal euryhaline environments (Zonneveld et
al., 2013), and hence could be used to indicate a more proximal condition relative to *L. machaerophorum* (Pross and Brinkhuis, 2005).

260

At present, Protoperidinioid (P) cysts are mostly formed by heterotrophic dinoflagellates and the percentage of P-cysts may be used as indicator of high eukaryotic productivity (cf. Reichart and Brinkhuis, 2003; Sangiorgi and Donders, 2004; Sluijs et al., 2005). Here we use the percentage of P-cysts (*Brigantedinium* spp., *Lejeunecysta* spp., *Trinovantedinium glorianum*, *Selenopemphix* spp., *Islandinium* spp., *Barssidinium graminosum*, and *B. wrennii*) to indicate eukaryotic productivity.

267

Terrestrial palynomorphs (sporomorphs) reflect variations in the vegetation on the 268 269 surrounding land masses and provide information on climate variables such as continental temperatures and precipitation (e.g. Heusser and Shackleton, 1979; Donders et al., 2009; 270 271 Kotthoff et al., 2014). A ratio of terrestrial to marine palynomorphs (T/M ratio) is widely used as a relative measure of distance to the coast and thereby reflects sea-level variations and 272 depth trends in the basin (e.g. McCarthy and Mudie, 1998; Donders et al., 2009; Quaijtaal et 273 274 al., 2014; Kotthoff et al., 2014). Morphological characteristics of late Neogene pollen types 275 can, in most cases, be related to extant genera and families (Donders et al., 2009; Larsson et al., 2011; Kotthoff et al., 2014). In A15-3/4, the relatively long distance between the land and 276 the site of deposition means that the pollen assemblage is not only a reflection of vegetation 277 cover and climate, but includes information on the mode of transport. Assemblages with a 278 relatively high number of taxa, including insect pollinated forms, are indicative of substantial 279 pollen input through water transport (Whitehead, 1983), whereas wind-transported pollen 280 typically show a low-diversity. Sediments of a location proximal to a river delta likely receive 281

a majority of pollen that is water-transported, while distal locations are dominated by wind-282 283 transported pollen and particularly bisaccate taxa (Hooghiemstra, 1988; Mudie and McCarthy, 1994). To exclude these effects, the percentage of arboreal pollen (AP), representing relative 284 terrestrial temperatures, was calculated excluding bisaccate forms. The non-arboreal pollen 285 (NAP; mainly Poaceae and also Artemisia, Chenopodiaceae and Asteraceae) consist only of 286 non-aquatic herbs. High AP percentages indicate warm, moist conditions, whereas open 287 vegetation (NAP and Ericaceae) is indicative for cooler, drier conditions consistent with a 288 glacial climate (Faegri et al, 1989). 289

290

291 *4.3 Palynological processing*

The samples were processed using standard palynological procedures (e.g., Faegri et al., 1989) involving HCl (30%) and cold HF (40%) digestion of carbonates and silicates. Residues were sieved with 15 μ m mesh and treated by heavy liquid separation (ZnCl, specific gravity 2.1 g/cm³). The slides were counted for dinocysts (with a minimum of 100 cysts) and pollen (with a preferable minimum of 200 grains). The dinocyst taxonomy follows Williams et al. (2017). Resulting counts were expressed as percent abundance of the respective terrestrial or marine groups of palynomorphs.

299

300 *4.4 Organic geochemical proxies*

We applied three measures for the relative marine versus terrestrial hydrocarbon sources. The Carbon Preference Index (CPI), based on C_{25} - C_{34} *n*-alkanes, originally devised to infer thermal maturity (Bray and Evans, 1961), has high values for predominantly terrestrial plant sources (Eglinton and Hamilton, 1967; Rieley et al., 1991). Values closer to one indicate greater input from marine microorganisms and/or recycled organic matter (e.g., Kennicutt et al., 1987). Furthermore, peat mosses like *Sphagnum* are characterized by a dominance of the

shorter C₂₃ and C₂₅ n-alkanes (e.g. Baas et al., 2000; Vonk and Gustafsson, 2009), whereas 307 308 longer chain n-alkanes (C_{27} - C_{33}) are synthesized by higher plants (e.g., Pancost et al., 2002; Nichols et al., 2006). Here we express the abundance of Sphagnum relative to higher plants 309 as the proportion of C_{23} and C_{25} relative to the C_{27} - C_{33} odd-carbon-numbered n-alkanes. 310 Finally, the input of soil organic matter into the marine environment was estimated using the 311 relative abundance of branched glycerol dialkyl glycerol tetraethers (brGDGTs), produced by 312 313 bacteria that are abundant in soils, versus that of the marine Thaumarchaeota-derived isoprenoid GDGT crenarchaeol (Sinninghe Damsté et al., 2002), which is quantified in the 314 Branched and Isoprenoid Tetraether (BIT) index (Hopmans et al., 2004). The distribution of 315 316 brGDGTs in soils is temperature dependent (Weijers et al., 2007; Peterse et al., 2012). Annual mean air temperatures (MAT) were reconstructed based on down-core distributional changes 317 of brGDGT and a global soil calibration that uses both the 5- and 6-methyl isomers of the 318 319 brGDGTs (MAT_{mr}; De Jonge et al., 2014a). Cyclisation of Branched Tetraethers (CBT) ratios, was shown earlier to correlate with the ambient MAT and soil pH (Weijers et al., 2007; 320 321 Peterse et al., 2012). The much improved CBT' ratio (De Jonge et al., 2014a), which includes the pH dependent 6-methyl brGDGTs, is used here to reconstruct soil pH. The Total Organic 322 Carbon (TOC) and total nitrogen measurements are used to determine the atomic C/N ratio 323 324 that in coastal marine sediments can indicate the dominant source of organic matter, with marine C/N values at ~10 and terrestrial between 15 and 30 (Hedges et al., 1997). 325

- 326
- 327

4.5 Organic geochemical processing

Organic geochemical analyses were limited to the core and sidewall core samples. For TOC determination ~ 0.3 g of freeze dried and powdered sediment was weighed, and treated with 7.5 ml 1 M HCL to remove carbonates, followed by 4 h shaking, centrifugation and decanting. This procedure was repeated with 12 h shaking. Residues were washed twice with demineralised water dried at 40-50°C for 96 h after which weight loss was determined. ~15 to
20 mg ground sample was measured in a Fisons NA1500 NCS elemental analyzer with a
normal Dumas combustion setup. Results were normalized to three external standards (BCR,
atropine and acetanilide) analyzed before and after the series, and after each ten
measurements. % TOC was determined by %C x decalcified weight/original weight.

337

338 For biomarker extraction ca. 10 g of sediment was freeze dried and mechanically powdered. The sediments were extracted with a Dichloromethane (DCM):Methanol (MeOH) solvent 339 mixture (9:1, v/v, 3 times for 5 min each) using an Accelerated Solvent Extractor (ASE, 340 341 Dionex 200) at 100°C and ca. 1000 psi. The resulting Total Lipid Extract (TLE) was evaporated to near dryness using a rotary evaporator under near vacuum. The TLE then was 342 transferred to a 4 ml vial and dried under a continuous N2 flow. A 50% split of the TLE was 343 344 archived. For the working other half elemental sulfur was removed by adding activated (in 2M HCl) copper turnings to the TLE in DCM and stirring overnight. The TLE was 345 subsequently filtered over Na₂SO₄ to remove the CuS, after which 500 ng of a C₄₆ GDGT 346 internal standard was added (Huguet et al., 2006). The resulting TLE was separated over a 347 small column (Pasteur pipette) packed with activated Al₂O₃ (2 h at 150°C). The TLE was 348 349 separated into an apolar, a ketone and a polar fraction by eluting with n-hexane : DCM 9:1 (v/v), n-hexane : DCM 1:1 (v/v) and DCM : MeOH 1:1 (v/v) solvent mixtures, respectively. 350 The apolar fraction was analyzed by gas chromatography (GC) coupled to a flame ionization 351 detector (FID) and gas chromatography/mass spectroscopy (GC/MS) for quantification and 352 identification of specific biomarkers, respectively. For GC, samples were dissolved in 55 µl 353 hexane and analyzed using a Hewlett Packard G1513A autosampler interfaced to a Hewlett 354 Packard 6890 series Gas Chromatography system equipped with flame ionization detection, 355 using a CP-Sil-5 fused silica capillary column (25 m x 0.32 mm, film thickness 0.12 µm), 356

with a 0.53 mm pre-column. Temperature program: 70°C to 130°C (0 min) at 20°C/min, then
to 320°C at 4°C/min (hold time 20 mins). The injection volume of the samples was 1 µl.

Analyses of the apolar fractions were performed on a ThermoFinnigan Trace GC ultra, interfaced to a ThermoFinnigan Trace DSQ MS using the same temperature program, column and injection volume as for GC analysis. Alkane ratios are calculated using peak surface areas of the respective alkanes from the GC/FID chromatograms.

363

Prior to analyses, the polar fractions, containing the GDGTs, were dissolved in *n*-hexane : 364 propanol (99:1, v/v) and filtered over a 0.45 µm mesh PTFE filter (ø 4mm). Subsequently, 365 analyses of the GDGTs was performed using ultra high performance liquid chromatography-366 mass spectrometry (UHPLC-MS) on an Agilent 1290 infinity series instrument coupled to a 367 6130 quadrupole MSD with settings as described in Hopmans et al. (2016). In short, 368 369 separation of GDGTs was performed on two silica Waters Acquity UHPLC HEB Hilic (1.7µm, 2.1mm x 150mm) columns, preceded by a guard column of the same material. 370 371 GDGTs were eluted isocratically using 82% A and 18% B for 25 mins, and then with a linear gradient to 70% A and 30% B for 25 mins, where A is *n*-hexane, and B = n-372 hexane:isopropanol. The flow rate was constant at 0.2 ml/min. The [M+H]⁺ ions of the 373 374 GDGTs were detected in selected ion monitoring mode, and quantified relative to the peak 375 area of the C₄₆ GDGT internal standard.

376

377 **5 Results**

378 *5.1 Stable isotope data*

The glacial-interglacial range in *Cassidulina teretis* δ^{18} O (δ^{18} O_b) is ~1‰ between MIS 98 and 97, and ~1.3‰ between MIS 95 and 94, but with considerably more variation in especially MIS 95 (Fig. 3). The δ^{13} C_b data co-vary consistently with δ^{18} O_b and have a glacial-interglacial

range of ~1.1‰, besides one strongly depleted value in MIS 94 (-3.5‰). The MIS 95 $\delta^{13}C_{\rm b}$ 382 values are less variable than the $\delta^{18}O_{b}$, pointing to an externally forced signal in the latter. The 383 $\delta^{18}O_b$ confirms the relation between glacial stages and fine grained sediment as proposed by 384 Kuhlman et al. (2006a,b). Although the data are somewhat scattered, the A15-3/4 phase 385 relation to the sediment facies is in agreement with the high-resolution stable isotope benthic 386 foraminifera record of the onshore Noordwijk borehole (Noorbergen et al., 2015). The glacial 387 to interglacial ranges are very similar in magnitude with those reported by Sosdian and 388 Rosenthal (2009) for the North Atlantic, but on average lighter by ~0.5% ($\delta^{18}O_b$) and ~1.8% 389 $(\delta^{13}C_{b}).$ 390

391

392 *5.2 Palynology*

Palynomorphs, including dinocysts, freshwater palynomorphs and pollen, are abundant, 393 394 diverse, and well-preserved in these sediments. Striking is the dominance by conifer pollen. Angiosperm (tree) pollen are present and diverse, but low in abundance relative to conifers. 395 396 During interglacials (MIS 103, 99, 97, 95, and 93) the pollen record generally shows increased and more diverse tree pollen (particularly *Picea* and *Tsuga*), and warm temperate 397 Osmunda spores, whereas during glacials (MIS 102, (100), 98, 96, and 94) herb and heath 398 pollen indicative of open landscapes are dominant (Fig S2). The % arboreal pollen (AP; excl. 399 bisaccate pollen) summarizes these changes, showing maximum values of >40% restricted to 400 just a part of the coarser grained interglacial intervals (Fig. 3). The percentage record of cold 401 water dinocysts is quite scattered in some intervals but indicates generally colder conditions 402 403 within glacial stages, and minima during %AP maxima (Fig. 3). After peak cold conditions and a TOC maximum (see below), but still well within the glacials, the % Protoperidinoid 404 405 consistently increases. Some intervals (e.g., top of MIS 94) are marked by influxes of freshwater algae (*Pediastrum* and *Botryococcus*), indicating a strong riverine input, these data 406

however do not indicate a clear trend. This robust in-phase pattern of glacial-interglacial 407 408 variations is also reflected by high T/M ratios during glacials, indicating coastal proximity, and low T/M during (final phases of) interglacials. The Glacial-Interglacial (G-IG) variability 409 410 in the T/M ratio is superimposed on a long-term increase. The coastal (warm-tolerant) dinocyst maxima are confined to the interglacial intervals and their abundance increases 411 throughout the record. Successive increases of coastal inner neritic Lingulodinium 412 machaerophorum, followed by increases in coastal lagoonal species in the youngest part, 413 mirror the shoaling trend in the T/M ratio, which in time correspond with the gradual 414 progradation of the Eridanos delta front (Fig. S1). 415

416

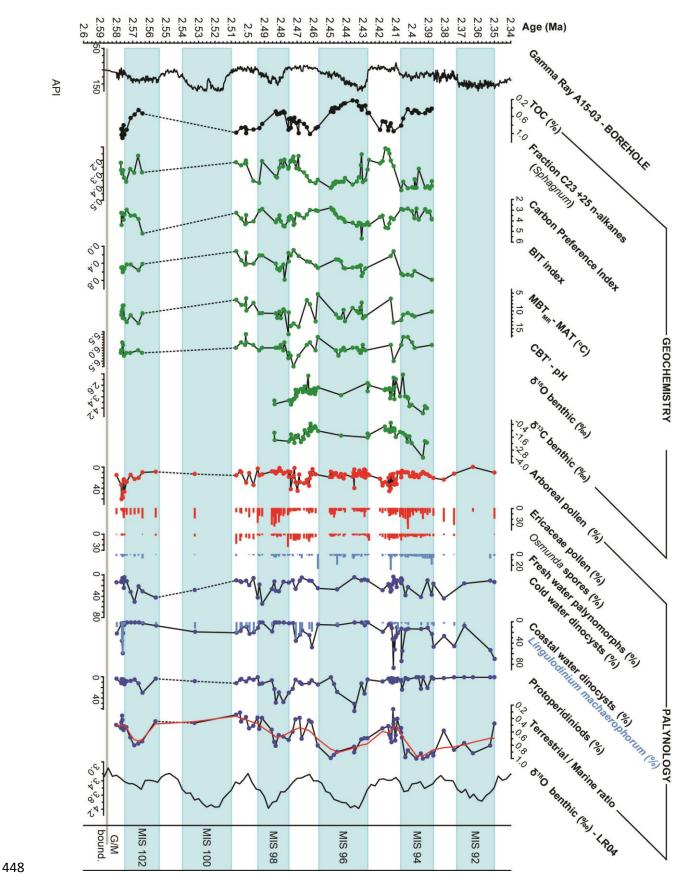
417 *5.3 Organic geochemical proxies*

The lowest TOC contents are reached in the clay intervals, and typically range between 0.5% 418 419 in glacials and 1% in interglacials (Fig. 3). Nitrogen concentrations are relatively stable resulting in C/N ratios primarily determined by organic carbon content, ranging between ~8-9 420 421 (glacials) and ~14 and 17 (interglacials). The Carbon Preference Index (CPI) is generally high, reflecting a continuous input of immature terrestrial organic matter. Minimum CPI 422 values of ~2.8 - 2.9 are reached at the transitions from the coarser sediments to the clay 423 intervals after which they increase to maxima of 4.5 - 5.0 in the late interglacials. The $n-C_{23+25}$ 424 Sphagnum biomarker correlates consistently with the T/M ratio, %AP, and cold water 425 dinocysts (Fig. 3), while the variation in the CPI index is partially out of phase; it is more 426 gradual and lags the % TOC and other signals. Generally lower Branched and Isoprenoid 427 428 Tetraether (BIT) index values during interglacials (Fig. 3) indicate more marine conditions, i.e. larger distance to the coast and relatively reduced terrestrial input from the Eridanos 429 catchment (cf. Sinninghe Damsté, 2016). As both brGDGT input (run off, soil exposure and 430 erosion) and sea level (distance to the coast) vary across G-IG timescales, for example during 431

deglaciation and subsequent reactivation of fluvial transport (Bogaart and van Balen, 2000), 432 the variability of the BIT index is somewhat different compared to the T/M palynomorph ratio 433 (Fig. 3), but is generally in phase with gradual transitions along G-IG cycles. The MAT_{mr}-434 based temperature reconstructions vary between 5 and 17°C, reaching maximum values in 435 MIS 97. However, in the MIS 99/98 and MIS 96/95 transitions the MAT_{mr} shows variability 436 opposite to the identified G-IG cycles and the signal contains much high-order variability. 437 Low values during interglacials generally coincide with low CBT'-reconstructed soil pH of 438 <6.0 (Fig. 3). 439

440

Figure 3: spliced record of A15-3 and A15-4 showing the principal geochemical and palynological indices. Shaded blue intervals represent the identified glacial MIS delimited by the gamma-ray transitions following Kuhlmann et al. (2006a,b). Data density is dependent on type of sample as indicated in Fig. 1. Age scale is based on correlation and LOESS interpolation of the identified MIS transitions to the LR04 benthic stack (Lisiecki and Raymo, 2005) as shown in Fig S3. Data is available in Tables S2 and 3.



451 6 Discussion

452 *6.1 Paleoenvironmental setting and climate signals*

The source area study by Kuhlmann et al. (2004) indicated the Eridanos paleoriver as the 453 principal source of the terrestrial deposits. The detailed seismic interpretations indeed show 454 the advancing Eridanos delta front from the east toward the sites (Fig. S1). This trend is 455 456 captured by the long-term increases in the T/M ratio and the proportion of coastal dinocysts (Fig. 3). In- or exclusion of bisaccate pollen in the T/M index (Fig. S5), the component most 457 sensitive to differential transport processes, indicates no direct influence of differential 458 transport on the T/M ratio. During MIS 103, 99, 97, 95, and 93 the AP% increases indicate 459 generally warmer and more humid conditions than during MIS 102, 98, 96, and 94 (Fig. 3). 460 The cold-water temperature signal based on dinocysts is more variable than the terrestrial 461 cooling signals from the AP%. Pollen assemblages represent mean standing vegetation in the 462 catchment, and also depend on dominant circulation patterns and short-term climate variations 463 464 (Donders et al., 2009). Due to exclusion of bisaccate pollen, the %AP is generally low but eliminates any climate signal bias due to the direct effect of sea level changes (Donders et al., 465 2009; Kotthoff et al., 2014). In the record there are small but significant time lags between 466 proxies, which have important implications for explaining the forcing of G-IG cycles. In the 467 best constrained MIS transition (98 to 97), the G-IG transition is seen first in decreases of the 468 cold water dinocysts and n-C₂₃₊₂₅ n-alkanes predominantly derived from *Sphagnum*. 469 Subsequently the BIT decreases, and MAT_{mr} and the %AP increase, and finally the $\delta^{18}O_{h}$ and 470 471 T/M ratio decrease with a lag of a few thousand years (Fig. 3). Changes in the CPI record are more gradual, but generally in line with T/M. The AP% and T/M proxies have the most 472 extensive record and detailed analysis of several glacial-interglacial transitions shows that the 473 declines in AP% consistently lead the T/M increases by 3-8 kyr based on the present age 474 475 model (Fig. S2). The T/M ratio variability corresponds well to the LR04 benthic stack (Fig.

3), which is primarily an obliquity signal. Within the constraints of the sample availability,
our record captures the approximate symmetry between glaciation and deglaciation typical of
the Early Pleistocene (Lisiecki and Raymo, 2005).

479

The high variability and strongly depleted values in $\delta^{18}O_{\rm b}$ during MIS 95 occur during peak 480 coastal dinocyst abundances, suggesting high run off during maximum warming phases. 481 During cold water dinocysts maxima, the high abundance of Protoperidinioids indicates high 482 nutrient input, and productive spring/summer blooms, which point to strong seasonal 483 484 temperature variations. This productivity signal markedly weakens in MIS 94 and 92 and the gradual T/M increase is consistent with the basin infill and gradually approaching shelf-edge 485 delta (Fig. S1). As Protoperidinioid minima generally occur during TOC maxima there is no 486 487 indication for a preservation overprint since selective degradation typically lowers relative abundances of these P-cysts (Gray et al., 2017). Combined, the high TOC and CPI values, 488 coastal and stratified water conditions, and intervals of depleted $\delta^{18}O_{b}$ document increased 489 Eridanos run-off during interglacials. These suggest a primarily terrestrial organic matter 490 source that, based on mineral provenance studies (Kuhlmann et al., 2004) and high conifer 491 492 pollen abundance documented here, likely originated from the Fennoscandian Shield. The fine-grained material during cold phases is probably transported by meltwater during summer 493 from local glaciers that developed since the late Pliocene at the surrounding Scandinavian 494 495 mainland (Mangerud et al., 1996; Kuhlmann et al., 2004).

496

497 6.2 Temperature reconstruction and brGDGT input

498 Whereas the BIT index reflects the G-IG cycles consistently, the MAT_{mr} record, which is

based on GDGTs, has a variable phase relation with the G-IG cycles and high variability. The

use of MAT_{mr} in coastal marine sediments is based on the assumption that river-deposited 500 501 brGDGTs reflect an integrated signal of the catchment area. As the Eridanos system is reactivated following glacials, glacial soils containing brGDGT are likely eroded causing a 502 503 mixed signal of glacial and interglacial material. The lowest MAT_{mr} and highest variability is indeed observed during periods of deposition of sediments with a higher TOC content and 504 minima of CBT'-derived pH below 6 (Fig. 3), consistent with increased erosion of acidic 505 506 glacial (peat) soil. Additional analysis of the apolar fractions in part of the samples reveals during these periods a relatively high abundance of the C_{31} 17 α , 21 β -homohopanes, which in 507 508 immature soils indicates a significant input of acidic peat (Pancost et al., 2002). This suggests that the variability in the MAT_{mr} record is not fully reliable due to (variable) erosion of glacial 509 soils or peats. Alternatively, the terrestrial brGDGT signal may be altered by a contribution of 510 brGDGTs produced in the marine realm. BrGDGTs were initially believed to be solely 511 produced in soils, but emerging evidence suggests that brGDGTs are also produced in the 512 513 river itself (e.g., Zell et al., 2013; De Jonge et al., 2014b) and in the coastal marine sediments (e.g., Peterse et al., 2009; Sinninghe Damsté, 2016 Based on the modern system, the degree of 514 cyclisation of tetramethylated brGDGTs (#rings_{tetra}) has been proposed to identify a possible 515 516 in situ overprint (Sinninghe Damsté, 2016). The #rings_{tetra} in this sediment core is <0.37, which is well below the suggested threshold of 0.7, and thus suggests that the brGDGTs are 517 primarily soil-derived. However, a ternary diagram of the brGDGT distribution show some 518 offset to the global soil calibration that decreases with increasing BIT values (Fig. S6), 519 pointing to some influence of in-situ GDGT production when terrestrial input is relatively 520 521 low. Finally, selective preservation in the catchment and during fluvial transport may have affected the brGDGT signal, although experimental evidence on fluvial transport processes 522 indicates that these do not significantly affect initial soil-brGDGT compositions (Peterse et 523 524 al., 2015).

526 6.3 Implications for the intensification of Northern Hemisphere glaciations

The classic Milankovitch model predicts that global ice volume is forced by high northern 527 528 summer insolation (e.g. Hays et al., 1976). Raymo et al. (2006) suggested an opposite 529 response of ice sheets on both hemispheres due to precession forcing, cancelling out the signal and amplifying obliquity in the early Pleistocene. That hypothesis predicts that regional 530 climate records on both hemispheres should contain a precession component that is not visible 531 in the sea level and deep sea $\delta^{18}O_{\rm b}$ record, and is supported by evidence from Laurentide Ice 532 Sheet melt and iceberg-rafted debris of the East Antarctic ice sheet (Patterson et al., 2014; 533 Shakun et al., 2016). Alternatively, a dominantly obliquity forced G-IC cycle is supported by 534 a significant temperature component in the temperature deep sea $\delta^{18}O_{\rm b}$ record (Sosdian and 535 536 Rosenthal, 2009) and dominant 41-kyr variability in North American biomarker dust fluxes. Our results show that the regional NH climate on both land and sea surface vary on the same 537 timescale as the local relative sea level which, with the best possible age information so far 538 (Fig. S3), mirrors the global LR04 $\delta^{18}O_b$ record. The temperature changes lead the local sea 539 level by 3-8 kyr, which is consistent with a NH obliquity forcing scenario as cooling would 540 541 precede ice buildup and sea level change. Contrary to the model proposed by Raymo et al. (2006), this suggests that the NH obliquity forcing is the primary driver for the glacial-542 interglacial in the early Pleistocene, although we cannot exclude precession forcing as a 543 contributing factor.. Various studies indicate the importance of gradual CO₂ decline in the 544 545 intensification of NHG (Kürschner et al., 1996; Seki et al., 2010; Bartoli et al., 2011) combined with the threshold effects of ice albedo (Lawrence et al., 2010; Etourneau et al., 546 547 2010) and land cover changes (Koenig et al., 2011). Simulations of four coupled 3-D ice models indicate that Antarctic ice volume increases respond primarily to sea-level lowering, 548 while Eurasian and North American ice sheet growth is initiated by temperature decrease (de 549

Boer et al., 2012). The latter dominate the eustatic sea-level variations during glacials. Our 550 551 observations agree with the modelled temperature sensitivity of NH ice sheet growth. The dominant obliquity signal further suggests a seasonal aspect of the climate forcing. The 552 553 combination of high summer productivity, based on increased Protoperidiniod dinocysts, and increased proportions of cold dinocysts during the glacials in the SNS record indicate a strong 554 555 seasonal cycle. This confirms similar results from the North Atlantic (Hennissen et al., 2015) 556 and is consistent with an obliquity-driven glacial-interglacial signal in a mid-latitudinal setting, likely promoting meridional humidity transport and ice buildup. 557

558

The southward migration of Arctic surface water masses indicated by increases in cold water 559 dinocysts (Fig. 3) is furthermore relevant for understanding the relation between the Atlantic 560 561 meridional overturning circulation (AMOC) intensity and ice sheet growth (e.g. Bartoli et al., 2005; Naafs et al, 2010). Mid-Pliocene increased heat transport and subsequent decrease 562 during NHG due to AMOC intensity changes has been invoked from many proxy records but 563 is difficult to sustain in models (Zhang et al., 2013). Our results indicate that the NW 564 European early Pleistocene climate experienced significant cooling in all temperature-565 sensitive proxies during sea-level lowstands, which is consistent with southward displacement 566 of the Arctic front and decreased AMOC (Naafs et al., 2010). The MAT_{mr} indicates a 4-6 °C 567 568 glacial-interglacial amplitude although the timing is offset relative to the other proxies. The 569 data-model mismatch in AMOC changes might be due to dynamic feedbacks in vegetation or 570 (sea-) ice (Koenig et al., 2011; de Boer et al., 2012) that are prescribed variables in the model comparison by Zhang et al. (2013). 571

572

In addition, our SNS record provides a well-dated early Pleistocene Glacial-Interglacial 573 574 succession integrating marine and terrestrial signals improving on the classic terrestrial Praetiglian stage. While conceptually valid, the earliest Pleistocene glacial stages defined in 575 576 the continental succession of the SE Netherlands (Van der Vlerk and Florschütz, 1953; Zagwijn, 1960) and currently considered text book knowledge, are highly incomplete and 577 578 locally varied (Donders et al., 2007). This shallow marine SNS record provides a much more 579 suitable reflection of large-scale transitions and trends in NW Europe and merits further development by complete recovery of the sequence in a scientific drilling project (Westerhoff 580 et al., 2016). 581

582

583 7 Conclusions

The independently dated late Pliocene-early Pleistocene sedimentary succession of the 584 southern North Sea Basin provides a record that straddles the intensification of Northern 585 586 Hemisphere Glaciation and the subsequent climate fluctuations in a shallow marine setting in great detail. The intensification of the glaciation and the correlation to marine isotope stages 587 103 to 92, including the conspicuous first Pleistocene glacial stages 98, 96 and 94, is well 588 expressed in the marine and terrestrial palynomorph and organic biomarker records of the 589 southern North Sea. The independent relative sea- and land-based temperature records show 590 clearly coeval (at this resolution) expression of glacial-interglacial and sea-level cycles that 591 are well-correlated to the LR04 benthic stack. Critically, both the biomarker signals, % AP, 592 593 and cold water dinocyst variations show consistent in-phase variability on obliquity time scales, leading sea-level changes by 3-8 kyr, which supports a dominantly direct NH 594 595 insolation control over early Pleistocene glaciations. Based on this integrated record, NH 596 obliquity forcing is the primary driver for the glacial-interglacial cycles in the early

Pleistocene. Furthermore, our findings support the hypothesis of temperature sensitivity of NH ice sheet growth. The interglacials are characterized by (seasonally) stratified waters and/or near-shore conditions as glacial-interglacial cycles became more expressive and the Eridanos delta progressed into the region. The strong seasonality at mid-latitudes point to a vigorous hydrological cycling that should be considered as a potential factor in ice sheet formation in further investigations.

603

604 8 Author contributions

THD, HB and GK designed the research. NvH carried out the geochemical analyses under
supervision of JW, GJR, FP and JSSD. RV, DM and THD carried out the palynological
analyses and interpreted the data together with FS. LL and RPS provided stable isotope data
on benthic foraminifera. JtV provided seismic interpretations. THD integrated the data and
wrote the paper with contributions from all authors.

610

611 9 Acknowledgements

We are grateful the constructive comments of Stijn de Schepper and David Naafs and an 612 anonymous referee that helped to improve the manuscript. We gratefully acknowledge the 613 support in providing the offshore samples to this study and permission to publish by 614 Wintershall Noordzee B.V., and project support by partners Chevron Exploration and 615 Production Netherlands B.V., Total E&P Nederland B.V., Dana Petroleum Netherlands B.V., 616 617 Oranje-Nassau Energie B.V., and Energie Beheer Nederland (EBN). Arnold van Dijk is thanked for running C/N and stable isotope analyses, and Giovanni Dammers for processing 618 palynological samples. The work was partly supported by funding from the Netherlands Earth 619

- 620 System Science Center (NESSC) through a gravitation grant (NWO 024.002.001) from the
- 621 Dutch Ministry for Education, Culture and Science to JSSD, GJR, and LL.
- 622

623 10 References

- Baas, M., Pancost, R., van Geel, B. Sinninghe Damsté, J.S., 2000. A comparative study of
- 625 lipids in *Sphagnum* species. Organic Geochemistry 31: 535-539.
- 626 <u>https://doi.org/10.1016/S0146-6380(00)00037-1</u>
- Bakken, K. and Dale, B., 1986. Dinoflagellate cysts in Upper Quaternary sediments from
- southwestern Norway and potential correlations with the oceanic record. Boreas 15: 185-190.
- 629 DOI: 10.1111/j.1502-3885.1986.tb00082.x
- Bartoli, G., Hönisch, B., Zeebe, R.E., 2011. Atmospheric CO₂ decline during the Pliocene
- 631 intensification of Northern Hemisphere glaciations. Paleoceanography 26, PA4213.
- 632 http://dx.doi.org/10.1029/2010PA002055.
- Bijlsma, S., 1981. Fluvial sedimentation from the Fennoscandian area into the Northwest
 European Basin during the Late Cenozoic. Geologie en Mijnbouw 60: 337-345.
- Bogaart, P.W., van Balen, R.T., 2000. Numerical modeling of the response of alluvial rivers
- to Quaternary climate change. Global and Planetary Change 27: 147-163.
- 637 https://doi.org/10.1016/S0921-8181(01)00064-9
- Bray, E.E., and Evans, E.D., 1961. Distribution of n-parrafins as a clue to recognition of
- source beds. Geochimica et Cosmochimica Acta 22: 2-15. https://doi.org/10.1016/0016 7037(61)90069-2
- Brierley, C.M., and Fedorov, A.V., 2010. Relative importance of meridional and zonal sea
- 642 surface temperature gradients for the onset of the ice ages and Pliocene Pleistocene climate
- 643 evolution. Paleoceanography 25: PA2214. DOI:10.1029/2009PA001809.
- Brigham-Grette, J, Melles, M., Minyuk, P.S., Andreev, A.A., Tarasov, P.E., DeConto, R.M.,
- 645 König, S. Nowaczyk, N.R., Wennrich, V., Rosén, P., Haltia-Hovi, E., Cook, T.L., Gebhardt,
- 646 C., Meyer-Jacob, C., Snyder, J.A., Herzschuh, U., 2013. Pliocene warmth, polar
- amplification, and stepped Pleistocene cooling recorded in NE Arctic Russia. Science 340:
- 648 1421-1427. DOI: 10.1126/science.1233137
- 649 Caston, V.N.D., 1979. The Quaternary sediments of the North Sea. In: Banner, F.T., Collins,
- M.B., Massie, K.S. (Eds.), The north-west European shelf seas: the sea bed and the sea in
- motion. I. Geology and Sedimentology, Elsevier Oceanographic Series 24A, p. 195-270.

- Dale, B., 1996. Dinoflagellate cyst ecology: modelling and geological applications. In: J.M.G.
- Jansonius, D.C. (Editor), Palynology: Principles and Application, vol. 3. American
- Association of Stratigraphic Palynologists Foundation, College Station, TX: 1249-1275.
- de Boer, B., van de Wal, R.S.W., Lourens, L.J., Bintanja, R., Reerink, T.J., 2012. A
- continuous simulation of global ice volume over the past 1 million years with 3-D ice-sheet
 models. Climate Dynamics 41, 1365. doi:10.1007/s00382-012-1562-2
- de Haas, H., Boer, W., van Weering, T.C.E., 1997. Recent sediment and organic carbon burial
 in a shelf sea; the North Sea. Marine Geology 144, 131–146. https://doi.org/10.1016/S00253227(97)00082-0.
- De Jonge, C, Hopmans, A.C, Zell, C.I., Kim, J.-H., Schouten, S., Sinninghe Damsté, J.S.,
- 662 2014a. Occurrence and abundance of 6-methyl branched glycerol dialkyl glycerol tetraethers
- in soils: Implications for palaeoclimate reconstruction. Geochimica et Cosmochimica Acta
- 664 141: 97-112. https://doi.org/10.1016/j.gca.2014.06.013.
- 665 De Jonge. C., Stadnitskaia, A., Hopmans, E.C., Cherkashov, G., Fedotov, A. and Sinninghe
- Damsté, J.S., 2014b. In-situ produced branched glycerol dialkyl glycerol tetraethers in
- suspended particulate matter from the Yenisei River, Eastern Siberia. Geochimica et
- 668 Cosmochimica Acta 125: 476-491. https://doi.org/10.1016/j.gca.2014.06.013.
- 669 De Schepper, S., Head, M.J., and Louwye, S., 2009. Pliocene dinoflagellate cyst stratigraphy,
- palaeoecology and sequence stratigraphy of the Tunnel-Canal Dock, Belgium, Geological
- 671 Magazine 146: 92-112. DOI: 10.1017/S0016756808005438.
- De Schepper, S., Fischer, E.I., Groeneveld, J., Head, M.J., Matthiessen, J., 2011. Deciphering
- the palaeoecology of Late Pliocene and Early Pleistocene dinoflagellate cysts.
- Palaeogeography, Palaeoclimatology, Palaeoecology 309: 17–32.
- 675 https://doi.org/10.1016/j.palaeo.2011.04.020.
- De Schepper, S., Groeneveld, J., Naafs, B.D.A., Van Renterghem, C., Hennissen, J., Head,
- 677 M.J., Louwye, S., Fabian, K., 2013. Northern Hemisphere glaciation during the globally
- warm early Late Pliocene. PLoS ONE 8 (12), e81508.
- 679 http://dx.doi.org/10.1371/journal.pone.0081508.
- de Vernal, A., 2009. Marine palynology and its use for studying nearshore environments,
- 681 From Deep-Sea to Coastal Zones: Methods Techniques for Studying Paleoenvironments,
- 682 IOP Conference Series: Earth and Environmental Science, 5, 012002.DOI:10.1088/1755-
- 683 1307/5/1/012002.
- 684 Donders, T.H., Kloosterboer-van Hoeve, M.L., Westerhoff, W., Verreussel, R.H.C.M. &
- 685 Lotter, A.F., 2007. Late Neogene continental stages in NW Europe revisited. Earth-Science
- 686 Reviews 85: 161-186. https://doi.org/10.1016/j.earscirev.2007.06.004.
- 687 Donders, T.H., Weijers, J.W.H., Munsterman, D.K., Kloosterboer-van Hoeve, M.L., Buckles,
- L.K., Pancost, R.D., Schouten, S., Sinninghe Damsté, J.S. & Brinkhuis, H., 2009. Strong

- climate coupling of terrestrial and marine environments in the Miocene of northwest Europe.
- Earth and Planetary Science Letters 281 (3-4): 215-225.
- 691 https://doi.org/10.1016/j.epsl.2009.02.034.
- Eglinton, G., Hamilton, R.J., 1967. Leaf epicuticular waxes. Science 156, 1322-1335. DOI:
- 693 10.1126/science.156.3780.1322.
- Etourneau, J., Schneider, R., Blanz, T., Martinez, P., 2010. Intensification of the Walker and
 Hadley atmospheric circulations during the Pliocene-Pleistocene climate transition. Earth and
- 696 Planetary Science Letters 297: 103-110. http://dx.doi.org/10.1016/j.epsl.2010.06.010.
- Faegri, K., Iversen, J., Kaland, P.E., Krzywinski, K., 1989. Text book of pollen analysis, IV
 Edition. The Blackburn Press, 328 pp.
- Gibbard P.L., and Lewin, J., 2016. Filling the North Sea Basin: Cenozoic sediment sources
 and river styles. Geologica Belgica 19: 201-217. http://dx.doi.org/10.20341/gb.2015.017
- Gray, D. D., Zonneveld, K.A., & Versteegh, G.J., 2017. Species-specific sensitivity of
- dinoflagellate cysts to aerobic degradation: A five-year natural exposure experiment. Review
 of Palaeobotany and Palynology 247, 175-187. DOI: 10.1016/j.revpalbo.2017.09.002
- Head, M.J., 1996. Modern dinoflagellate cysts and their biological affinities. In: Jansonius, J.,
- 705 McGregor, D.C. (Eds.), Palynology: Principles and Application, vol. 3. American Association
- of Stratigraphic Palynologists Foundation, College Station, TX, pp. 1197-1248.
- Haug, G.H. and Tiedemann, R., 1998. Effect of the formation of the Isthmus of Panama on
 Atlantic Ocean thermohaline circulation. Nature 393 (6686): 673- 676. DOI:10.1038/31447.
- Haug, G.H., Sigman, D.M., Tiedemann, R., Pedersen, T.F. & Sarnthein, M., 1999. Onset of
- permanent stratification in the subarctic Pacific Ocean. Nature 40: 779–782.
- 711 DOI:10.1038/44550
- Haug, G.H., Ganopolski, A., Sigman, D.M., Rosell-Mele, A., Swann, G. E. A, Tiedemann, R.,
- 713Jaccard, S. L., Bollmann, J., Maslin, M.A., Leng, M.J. and Eglinton, G., 2005. North Pacific
- seasonality and the glaciation of North America 2.7 million years ago. Nature 433: 821-825.
- 715 DOI: 10.1038/nature03332.
- Hays, J. D., Imbrie, J. & Shackleton, N. J., 1976. Variations in the Earth's orbit: pacemaker of
 the ice ages. Science 194; 1121–1132. doi: 10.1126/science.194.4270.1121.
- Head, M.J., Riding, J.B., Eidvin, T., Chadwick, R.A., 2004. Palynological and foraminiferal
- biostratigraphy of (Upper Pliocene) Nordland Group mudstones at Sleipner, northern North
- Sea. Marine and Petroleum Geology 21:277-297.
- 721 http://dx.doi.org/10.1016/j.marpetgeo.2003.12.002.
- Hedges, J.I., Keil, R.G., & Benner, R., 1997. What happens to terrestrial organic matter in the
 ocean? Organic Geochemistry 27: 195-212. https://doi.org/10.1016/S0146-6380(97)00066-1

- Hennissen, J.A.I., Head, M.J., De Schepper, S., Groeneveld, J., 2015. Increased seasonality
- during the intensification of Northern Hemisphere glaciation at the Pliocene-Pleistocene
- transition ~2.6 Ma. Quaternary Science Reviews 129: 321–332.
- 727 <u>https://doi.org/10.1016/j.quascirev.2015.10.010</u>.
- Hennissen, J.A.I., Head, M.J., De Schepper, S., Groeneveld, J., 2017. Dinoflagellate cyst
- paleoecology during the Pliocene–Pleistocene climatic transition in the North Atlantic.
- Palaeogeography, Palaeoclimatology, Palaeoecology 470: 81-108.
- 731 https://doi.org/10.1016/j.palaeo.2016.12.023.
- Heusser, L.E., and Shackleton, N.J., 1979. Direct marine-continental correlation: 150,000-
- year oxygen isotope-pollen record from the North Pacific. Science 204: 837-839. DOI:
 10.1126/science.204.4395.837.
- Hooghiemstra, H., 1988. Palynological records from Northwest African marine sediments: a
- 736 general outline of the interpretation of the pollen signal. Philosophical Transactions of the
- Royal Society of London, Series B Biological Sciences 318 (1191): 431–449. DOI:
- 738 10.1098/rstb.1988.0018.
- Hooghiemstra, H., Ran, E.T.H., 1994. Late Pliocene-Pleistocene high resolution pollen
 sequence of Colombia: An overview of climatic change. Quaternary International, 21: 63-80
- 741 Hopmans, E.C., Weijers, J.W.H., Schefuss, E., Herfort, L., Sinninghe Damsté, J.S., Schouten,
- S., 2004. A novel proxy for terrestrial organic matter in sediments based on branched and
- isoprenoid tetraether lipids. Earth and Planetary Science Letters 24: 107–116.
- 744 https://doi.org/10.1016/j.epsl.2004.05.012.
- 745 Hopmans, E.C., Schouten, S., Sinninghe Damsté, J.S., 2016. The effect of improved
- chromatography on GDGT-based palaeoproxies. Organic Geochemistry 93: 1-6.
- 747 https://doi.org/10.1016/j.orggeochem.2015.12.006.
- Huuse, M., Lykke-Andersen, H., Michelsen, O., 2001. Cenozoic evolution of the eastern
- North Sea Basin new evidence from high-resolution and conventional seismic data. Marine
 Geology 177: 243-269.
- Huybers, P., 2011. Combined obliquity and precession pacing of late Pleistocene
 deglaciations. Nature 480: 229–232. DOI:10.1038/nature10626.
- Keigwin, L. D., 1982. Isotope paleoceanography of the Caribbean and east Pacific: role of
- Panama uplift in late Neogene time. Science 217: 350–353. DOI:
- 755 10.1126/science.217.4557.350.
- Kemna, H.A., Westerhoff, W.E., 2007. Remarks on the palynology-based chronostratigraphic
- subdivision of the Pliocene terrestrial deposits in NW-Europe. Quaternary International 164–
- 758 165: 184–196. https://doi.org/10.1016/j.quaint.2006.10.017.

- 759 Kennicutt II, M.C., Barker, C., Brooks, J.M., DeFreitas, D.A., Zhu, G.H., 1987. Selected
- 760 organic matter source indicators in the Orinoco, Nile and Changjiang deltas. Organic
- 761 Geochemistry 11: 41-51. https://doi.org/10.1016/0146-6380(87)90050-7.
- Knies, J., Cabedo-Sanz, P., Belt, S.T., Baranwal, S., Fietz, S., Rosell-Mele, A., 2014. The
- remergence of modern sea ice cover in the Arctic Ocean. Nature Communications 5:
 http://dx.doi.org/10.1038/ncomms6608.
- Koenig, S.J., DeConto, R.M. & Pollard, D., 2011. Late Pliocene to Pleistocene sensitivity of
- the Greenland Ice Sheet in response to external forcing and internal feedbacks. Climate
- 767 Dynamics 37: 1247. DOI:10.1007/s00382-011-1050-0.
- Kotthoff, U., Greenwood, D., McCarthy, F., Müller-Navarra, K., Prader, S., Hesselbo, S.,
- 769 2014. Late Eocene to middle Miocene (33 to 13 million years ago) vegetation and climate
- development on the North American Atlantic Coastal Plain (IODP Expedition 313, Site
- 771 M0027). Climate of the Past 10: 1523-1539. https://doi.org/10.5194/cp-10-1523-2014.
- Kuhlmann, G. & Wong, T.E., 2008. Pliocene paleoenvironment evolution as interpreted
- from 3D-seismic data in the southern North Sea, Dutch offshore sector. Marine and Petroleum
- Geology 25: 173-189. https://doi.org/10.1016/j.marpetgeo.2007.05.009.
- Kuhlmann, G., Pedersen, R.-B., de Boer, P., Wong, T.E., 2004. Provenance of Pliocene
- sediments and paleoenvironmental change in the southern North Sea region using Sm/Nd
- (samarium-neodymium) provenance ages and clay mineralogy. Sedimentary Geology 171:
- 778 205-226. DOI: 10.1016/j.sedgeo.2004.05.016.
- Kuhlmann, G., Langereis, C.G., Munsterman, D., van Leeuwen, R.-J., Verreussel, R.,
- 780 Meulenkamp, J., Wong, T.E., 2006a. Chronostratigraphy of Late Neogene sediments in the
- southern North Sea Basin and paleoenvironmental interpretations. Palaeogeography,
- 782 Palaeoclimatology, Palaeoecology 239: 426–455.
- 783 https://doi.org/10.1016/j.palaeo.2006.02.004.
- Kuhlmann, G., Langereis, C.G., Munsterman, D., van Leeuwen, R.-J., Verreussel, R.,
- 785 Meulenkamp, J.E., Wong, Th.E., 2006b. Integrated chronostratigraphy of the Pliocene–
- 786 Pleistocene interval and its relation to the regional stratigraphical stages in the southern North
- 787 Sea region. Netherlands Journal of Geosciences Geologie en Mijnbouw 85 (1): 19–35.
- 788 https://doi.org/10.1017/S0016774600021405.
- 789 Kürschner, W.A., van der Burgh, J., Visscher, H., and Dilcher, D.L., 1996. Oak leaves as
- biosensors of late Neogene and early Pleistocene paleoatmospheric CO₂ concentrations.
- 791 Marine Micropaleontology 27: 299-312. https://doi.org/10.1016/0377-8398(95)00067-4.
- 792 Larsson, L.M., Dybkjaer, K., Rasmussen, E.S., Piasecki, S., Utescher, T., and Vajda, V.,
- 2011. Miocene climate evolution of northern Europe: A palynological investigation from
- 794 Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology 309: 161-175.
- 795 https://doi.org/10.1016/j.palaeo.2011.05.003.

- The Lawrence, K.T., Sosdian, S., White, H.E., Rosenthal, Y., 2010. North Atlantic climate
- evolution through the Plio-Pleistocene climate transitions. Earth and Planetary Science Letters
 300: 329-342. http://dx.doi.org/10.1016/j.epsl.2010.10.013.
- 799 Lisiecki, L.E., and Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally
- 800 distributed benthic δ^{18} O records. Paleoceanography 20: PA1003.
- 801 DOI:10.1029/2004PA001071.
- 802 Lister, A.M., 2004. The impact of Quaternary Ice Ages on mammalian evolution.
- 803 Philosophical Transactions of the Royal Society of London, Series B Biological Sciences 359,
- 804 221-241. DOI: doi: 10.1098/rstb.2003.1436.
- 805 Mackensen, A. & Hald, M., 1988. *Cassidulina teretis* Tappan and *C. laevigata* d'Orbigny:
- their modern and late Quaternary distribution in northern seas. Journal of Foraminiferal
 Research 18 (1): 16-24. DOI: https://doi.org/10.2113/gsjfr.18.1.16.
- 808 Mangerud, J., Jansen, E., Landvik, J., 1996. Late Cenozoic history of the Scandinavian and
- Barents Sea ice sheets. Global and Planetary Change 12: 11-26. https://doi.org/10.1016/0921-
- 810 8181(95)00009-7.
- 811 Maslin, M.A., Li, X. S., Loutre M. F., & Berger A. 1998. The contribution of orbital forcing
- to the progressive intensification of Northern Hemisphere Glaciation. Quaternary Science
- 813 Reviews 17: 411-426. https://doi.org/10.1016/S0277-3791(97)00047-4.
- 814 McCarthy, F.M.G. and Mudie, P., 1998. Oceanic pollen transport and pollen: dinocyst ratios
- as markers of late Cenozoic sea level change and sediment transport. Palaeogeography,
- Palaeoclimatology, Palaeoecology 138: 187-206. https://doi.org/10.1016/S0031-
- 817 0182(97)00135-1.
- 818 Meijer, T., Cleveringa, P., Munsterman, D.K., and Verreussel, R.M.C.H., 2006. The Early
- 819 Pleistocene Praetiglian and Ludhamian pollen stages in the North Sea Basin and their
- relationship to the marine isotope record. Journal of Quaternary Science 21: 307–310. DOI:
- 821 10.1002/jqs.956.
- Meloro, C., Raia, P., Carotenuto, F., Barbera, C., 2008. Diversity and turnover of Plio-
- 823 Pleistocene large mammal fauna from the Italian Peninsula. Palaeogeography,
- Palaeoclimatology, Palaeoecology 268: 58-64. https://doi.org/10.1016/j.palaeo.2008.08.002.
- Michelsen, O., Thomsen, E., Danielsen, M., Heilmann-Clausen, C., Jordt, H., Laursen, G-V.,
- 1998. Cenozoic sequence stratigraphy in eastern North Sea. In: P.-C. de Graciansky, T.
- Jacquin, P.R. Vail and M.B. Farley (Eds), Mesozoic and Cenozoic sequence stratigraphy of
- 828 European Basins: SEPM (Society for Sedimentary Geology) Special Publications 60, 91-118.
- 829 DOI: https://doi.org/10.2110/pec.98.02.0091.
- 830 Mudelsee, M. and Raymo, M.E., 2005. Slow dynamics of the Northern Hemisphere
- 831 glaciation. Paleoceanography 20, PA4022. DOI: 10.1029/2005PA001153.

- 832 Mudie, P.J. and McCarthy, F.M.G., 1984. Late Quaternary pollen transport processes, western
- 833 North Atlantic: Data from box models, cross-margin and N-S transects. Marine Geology, 118:
- 834 79-105. https://doi.org/10.1016/0025-3227(94)90114-7.
- Naafs, B.D.A., Stein, R., Hefter, J., Khelifi, N., De Schepper, S., Haug, G.H., 2010. Late
- Pliocene changes in the North Atlantic current. Earth and Planetary Science Letters 298: 434442. http://dx.doi.org/10.1016/j.epsl.2010.08.023.
- 838 Naafs, B.D.A., Hefter, J., Acton, G., Haug, G.H., Martínez-Garcia, A., Pancost, R., Stein, R.,
- 839 2012. Strengthening of North American dust sources during the late Pliocene (2.7 Ma). Earth
- and Planetary Science Letters 317-318. 8-19, doi:10.1016/j.epsl.2011.11.026
- Naafs, B.D.A., Hefter, J., Stein, R., 2013. Millennial-scale ice rafting events and Hudson
- 842 Strait Heinrich(-like) Events during the late Pliocene and Pleistocene: a review. Quaternary
- 843 Science Reviews 80: 1-28. doi: 10.1016/j.quascirev.2013.08.014.
- Nichols, J.E., Booth, R.K., Jackson, S.T., Pendall, E.G. & Huang, Y., 2006. Paleohydrologic
- reconstruction based on n-alkane distributions in ombrotrophic peat. Organic Geochemistry
- 846 37: 1505-13. <u>https://doi.org/10.1016/j.orggeochem.2006.06.020</u>.
- 847 Noorbergen, L.J., Lourens, L.J., Munsterman, D. K., Verreussel, R.M.C.H., 2015. Stable
- 848 isotope stratigraphy of the early Quaternary of borehole Noordwijk, southern North Sea
- 849 .Quaternary International 386: 148 157. DOI:10.1016/j.quaint.2015.02.045.
- 850 Overeem, I., Weltje, G. J., Bishop-Kay, C., and Kroonenberg, S. B., 2001. The Late Cenozoic
- 851 Eridanos delta system in the Southern North Sea Basin: a climate signal in sediment supply?
- Basin Research 13: 293-312. DOI: 10.1046/j.1365-2117.2001.00151.x.
- Pagani, M., Liu, Z., LaRiviere, J., Ravelo, A.C., 2010. High Earth-system climate sensitivity
 determined from Pliocene carbon dioxide concentrations. Nature Geoscience. 3: 27-30.
 http://dx.doi.org/10.1038/NGEO724.
- Pancost, R.D., Baas, M., van Geel, B., and Sinninghe Damsté, J.S., 2002. Biomarkers as
- proxies for plant inputs to peats: an example from a sub-boreal ombrotrophic bog. Organic
 Geochemistry 33(7): 675-690.
- Pancost, R.D., Baas, M., van Geel, B., and Sinninghe Damsté, J.S., 2003. Response of an
 ombrotrophic bog to a regional climate event revealed by macrofossil, molecular and carbon
 isotopic data. The Holocene, 13(6): 921-932. https://doi.org/10.1016/S0146-6380(02)00048-7.
- 862 Patterson, M.O., McKay, R., Naish, T., Escutia, C., Jimenez-Espejo, F.J., Raymo,
- 863 M.E., Meyers, S.R., Tauxe, L., Brinkhuis, H. & IODP Expedition 318 Scientists 2014. Orbital
- forcing of the East Antarctic ice sheet during the Pliocene and Early Pleistocene. Nature
- 865 Geoscience 7: 841. DOI: 10.1038/ngeo2273.
- Peterse, F., Moy, C.M., and Eglinton, T.I., 2015. A laboratory experiment on the behaviour of
 soil-derived core and intact polar GDGTs in aquatic environments. Biogeosciences 12: 933–
 943. DOI:10.5194/bg-12-933-2015.

- 869 Peterse, F., Kim, J.-H., Schouten, S., Kristensen, D.K., Koç, N. & Sinninghe Damsté, J.S.
- 870 2009. Constraints on the application of the MBT/CBT palaeothermometer at high latitude
- environments (Svalbard, Norway). Organic Geochemistry 40 (6): 692-699.
- 872 https://doi.org/10.1016/j.orggeochem.2009.03.004.
- Poore, H.R., Samworth, R., White, N.J., Jones, S.M., McCave, I.N., 2006. Neogene overflow
- of Northern Component Water at the Greenland–Scotland Ridge. Geochemistry Geophysics
- 875 Geosystems 7. http://dx.doi.org/10.1029/2005gc001085.Q06010.
- 876 Pross, J. and Brinkhuis, H., 2005. Organic-walled dinoflagellate cysts as paleoenvironmental
- indicators in the Paleogene; a synopsis of concepts. Paläontologische Zeitschrift, 79(1): 53-
- 878 59.
- 879 Quaijtaal, W., Donders, T.H., Persico, D. & Louwye, S., 2014. Characterising the middle
- 880 Miocene Mi-events in the Eastern North Atlantic realm A first high-resolution marine
- palynological record from the Porcupine Basin. Palaeogeography, Palaeoclimatology,
- 882 Palaeoecology 399: 140-159. https://doi.org/10.1016/j.palaeo.2014.02.017.
- 883 Ravelo, A.C., Andreasen, D.H., Lyle, M., Lyle, A.O., Wara, M.W., 2004. Regional climate
- shifts caused by gradual global cooling in the Pliocene epoch. Nature 429 (6989): 263-267.
- 885 DOI:10.1038/nature02567
- Ravelo, A.C., 2010. Palaeoclimate: Warmth and glaciation. Nature Geoscience 3: 672–674.
 DOI:10.1038/ngeo965
- 888 Raymo, M.E., 1994. The initiation of Northern Hemisphere glaciation. Annual Review of
- Earth and Planetary Sciences 22, 353-383.
- 890 http://dx.doi.org/10.1146/annurev.ea.22.050194.002033.
- Raymo, M.E., Ruddiman, W.F., Backman, J., Clement, B. M., and Martinson, D.G., 1989.
- 892 Late Pliocene variation in Northern Hemisphere ice sheets and North Atlantic Deep Water
- circulation. Paleoceanography 4: 413–446. DOI: 10.1029/PA004i004p00413.
- 894 Raymo, M. E., Lisiecki, L. & Nisancioglu, K. 2006. Plio–Pleistocene ice volume, Antarctic 895 climate, and the global δ^{18} O record. Science 313: 492–495. DOI: 10.1126/science.1123296.
- Reichart, G.J., Brinkhuis, H., 2003. Late Quaternary *Protoperidinium* cysts as indicators of
- paleoproductivity in the northern Arabian Sea. Marine Micropaleontology 49 : 303-315.
 https://doi.org/10.1016/S0377-8398(03)00050-1.
- 899 Rieley, G., Collier, R.J., Jones, D.M., Eglinton, G., 1991. The biogeochemistry of Ellesmere
- 900 Lake, U.K. I: source correlation of leaf wax inputs to the sedimentary lipid record. Organic
- 901 Geochemistry 17: 901–912. https://doi.org/10.1016/0146-6380(91)90031-E.
- Rochon, A., de Vernal, A., Turon, J.L., Mathiessen, J., Head, M.J., 1999. Distribution of
- 903 recent dinoflagellate cysts in surface sediments from the North Atlantic Ocean and adjacent
- seas in relation to sea-surface parameters: American Association of Stratigraphic
- Palynologists Foundation Contributions Series 35, 150 pp.

- Rosoff, D.B., and Corliss, B.H., 1992. An analysis of Recent deep-sea benthic foraminiferal
- 907 morphotypes from the Norwegian and Greenland seas. Palaeogeography, Palaeoclimatology,
- 908 Palaeoecology 91, 13-20. https://doi.org/10.1016/0031-0182(92)90028-4.
- Ruddiman, W.F., Raymo, M., McIntyre, A., 1986. Matuyama 41,000-year cycles: North
- Atlantic Ocean and northern hemisphere ice sheets: Earth and Planetary Science Letters 80:
- 911 117-129. https://doi.org/10.1016/0012-821X(86)90024-5.
- 912 Sangiorgi, F. and Donders, T.H., 2004. Reconstructing 150 years of eutrophication in the
- 913 north-western Adriatic Sea (Italy) using dinoflagellate cysts, pollen and spores. Estuarine,
- 914 Coastal and Shelf Science 60: 69-79. https://doi.org/10.1016/j.ecss.2003.12.001.
- Sangiorgi, F., Fabbri, D., Comandini, M., Gabbianelli, G. & Tagliavini, E., 2005. The
- 916 distribution of sterols and organic-walled dinoflagellate cysts in surface sediments of the
- 917 North-western Adriatic Sea (Italy). Estuarine, Coastal and Shelf Science 64: 395-406.
- 918 Shakun, J.D., Raymo, M.E., Lea, D.W., 2016. An early Pleistocene Mg/Ca-δ¹⁸O record from
- the Gulf of Mexico: Evaluating ice sheet size and pacing in the 41-kyr world.
- 920 Paleoceanography 31: 1011-1027. DOI: 10.1002/2016PA002956.
- 921 Seki, O., Foster, G.L., Schmidt, D.N., Mackensen, A., Kawamura, K., Pancost, R.D., 2010.
- Alkenone and boron-based Pliocene pCO₂ records. Earth and Planetary Science Letters 292:
 201-211. http://dx.doi.org/10.1016/j.epsl.2010.01.037.
- 924 Shackleton, N.J. and Hall, M.A., 1984. Oxygen and carbon isotope stratigraphy of Deep Sea
- 925 Drilling Project Hole 552A: Plio- Pleistocene glacial history. D-G. Roberts. D. Schnitker et al.
- 926 initial Reports of the Deep Sea Drilling Project 81: 599-609. U.S. Govt. Printing Office,
- 927 Washington.
- 928 Schreck, M., Meheust, M., Stein, R. and Matthiessen, J., 2013. Response of marine
- palynomorphs to Neogene climate cooling in the Iceland Sea (ODP Hole 907A). Marine
 Micropaleontology 101: 49-67. https://doi.org/10.1016/j.marmicro.2013.03.003.
- 931 Sinninghe Damsté, J.S., Schouten, S., Hopmans, E.C., van Duin, A.C.T., Geenevasen, J.A.J.,
- 932 2002. Crenarchaeol: the characteristic core glycerol dibiphytanyl glycerol tetraether
- 933 membrane lipid of cosmopolitan pelagic crenarchaeota. Journal of Lipid Research 43: 1641-
- 934 1651. doi: 10.1194/jlr.M200148-JLR200
- 935 Sinninghe Damsté, J.S., 2016. Spatial heterogeneity of sources of branched tetraethers in shelf
- 936 systems The geochemistry of tetraethers in the Berau River delta (Kalimantan, Indonesia).
- 937 Geochimica et Cosmochimica Acta 186: 13-31. https://doi.org/10.1016/j.gca.2016.04.033.
- 938 Sluijs, A., Pross, J., and Brinkhuis, H., 2005. From greenhouse to icehouse; organic-walled
- dinoflagellate cysts as paleoenvironmental indicators in the Paleogene. Earth Science
- 940 Reviews 68: 281-315. https://doi.org/10.1016/j.earscirev.2004.06.001.
- Sørensen, J. C., Gregersen, U., Breiner, M. and O. Michelsen, 1997. High-frequency sequence
 stratigraphy of Upper Cenozoic deposits in the central and southeastern North Sea areas.

- Marine and Petroleum Geology 14 (2): 99-123. https://doi.org/10.1016/S02648172(96)00052-9
- Solution Solution Science Scien
- 946 Pliocene-Pleistocene climate transitions. Science 325: 306-310.
- 947 DOI:10.1126/science.1169938 pmid:19608915.
- Tabor, C.R., Poulsen, C.J., Pollard, D., 2014. Mending Milankovitch's theory: obliquity
 amplification by surface feedbacks. Climate of the Past 10: 41–50. DOI: 10.5194/cp-10-412014.
- 951 Thöle, H., Gaedicke, C., Kuhlmann, G., and Reinhardt, L., 2014. Late Cenozoic sedimentary
- evolution of the German North Sea A seismic stratigraphic approach. Newsletters on
- 953 Stratigraphy 47: 299–329. DOI: 10.1127/0078-0421/2014/0049.
- Tzedakis, P.C., Crucifix, M., Mitsui, T., Wolff, E.W, 2017. A simple rule to determine which insolation cycles lead to interglacials. Nature 542: 427–432 DOI:10.1038/nature21364.
- 956 Svenning, J.-C., 2003. Deterministic Plio-Pleistocene extinctions in the European cool-
- 957 temperate tree flora. Ecology Letters 6: 646–653. DOI: 10.1046/j.1461-0248.2003.00477.x.
- Westerhoff, W., Donders, T.H. & Luthi, S.M., 2016. Report on ICDP workshop CONOSC
 (COring the NOrth Sea Cenozoic). Scientific Drilling 21: 47-51. https://doi.org/10.5194/sd-
- 960 21-47-2016.
- 961 Whitehead, D.R., (1983). Wind pollination: some ecological and evolutionary perspectives.
- 962 In: Real, L. (Ed.), Pollination Biology. Academic Press, Orlando, pp.
- 963 Williams, G.L., Fensome, R.A., and MacRae, R.A., 2017. The Lentin and Williams index of
- 964 fossil dinoflagellates 2004 edition. American Association of Stratigraphic Palynologists,
- 965 Contributions Series 48, College Station, TX, 1097 pp. 97–108
- 966 Van der Vlerk, I.M, Florschütz, F. 1953. The palaeontological base of the subdivision of the
- 967 Pleistocene in the Netherlands. Verhandelingen Koninklijke Nederlandse Akademie van
- 968 Wetenschappen, Afdeling Natuurkunde, 1e Reeks XX(2): 1–58.
- 969 Versteegh, G.J.M., Zonneveld, K.A.F., 1994. Determination of (palaeo-)ecological
- 970 preferences of dinoflagellates by applying detrended and canonical correspondence analysis
- to late Pliocene dinoflagellate cyst assemblages of the south Italian Singa section. Review of
- 972 Palaeobotany and Palynology 84: 181–199. https://doi.org/10.1016/0034-6667(94)90050-7.
- 973 Vonk, J.E., Gustafsson, Ö, 2009. Calibrating n-alkane *Sphagnum* proxies in sub-Arctic
- 974 Scandinavia. Organic Geochemistry 40: 1085-1090.
- 975 https://doi.org/10.1016/j.orggeochem.2009.07.002.
- 276 Zagwijn, W.H., 1960. Aspects of the Pliocene and early Pleistocene vegetation in The
- 977 Netherlands. Mededelingen van de Geologische Stichting, Serie C III-1–5, 1–78.

- 978 Zell, C., Kim, J.-H., Moreira-Turcq, P., Abril, G., Hopmans, E.C., Bonnet, M.-P., Sobrinho,
- 979 R. L., and Sinninghe Damsté, J.S., 2013. Disentangling the origins of branched tetraether
- 980 lipids and crenarchaeol in the lower Amazon River: implications for GDGT-based proxies,
- 981 Limnology and Oceanography. 58, 343–353. DOI: 10.4319/lo.2013.58.1.0343.
- 282 Zhang, Z.-S., Nisancioglu, K. H., Chandler, M. A., Haywood, A. M., Otto-Bliesner, B. L.,
- 983 Ramstein, G., Stepanek, C., Abe-Ouchi, A., Chan, W.-L., Bragg, F. J., Contoux, C., Dolan, A.
- 984 M., Hill, D. J., Jost, A., Kamae, Y., Lohmann, G., Lunt, D. J., Rosenbloom, N. A., Sohl, L. E.,
- and Ueda, H., 2013. Mid-pliocene Atlantic Meridional Overturning Circulation not unlike
- 986 modern. Climate of the Past 9, 1495-1504.DOI :10.5194/cp-9-1495-2013
- Ziegler, P.A., 1990. Geological Atlas of Western and Central Europe (2nd edition).Shell
 Internationale Petroleum Maatschappij B.V.; Geological Society Publishing House (Bath),
 239 pp.
- 200 Zöllmer, V. and Irion, G., 1996. Tonminerale des Nordseeraumes ihr Verteilungsmuster in
- 891 kreidezeitlichen bis pleistozänen Sedimentabfolgen und in den Oberflächensedimenten der
- heutigen Nordsee: Courier Forschungsinstitut Senckenberg, 190. Frankfurt am Mainz, 72 p.
- 201 Zonneveld, K.A.F., Marret, F., Versteegh, G.J.M., Bogus, K., Bonnet, S., Bouimetarhan, I.,
- 994 Crouch, E., de Vernal, A., Elshanawany, R., Edwards, L., Esper, O., Forke, S., Grøsfjeld, K.,
- 995 Henry, M., Holzwarth, U., Kielt, J.-F., Kim, S.-Y., Ladouceur, S., Ledu, D., Chen, L.,
- 996 Limoges, A., Londeix, L., Lu, S.-H., Mahmoud, M.S., Marino, G., Matsouka, K.,
- 997 Matthiessen, J., Mildenhal, D.C., Mudie, P., Neil, H.L., Pospelova, V., Qi, Y., Radi, T.,
- 998 Richerol, T., Rochon, A., Sangiorgi, F., Solignac, S., Turon, J.-L., Verleye, T., Wang, Y. &
- 999 Young, M., 2013. Atlas of modern dinoflagellate cyst distribution based on 2405 data points.
- 1000 Review of Palaeobotany and Palynology 191: 1-197.
- 1001 https://doi.org/10.1016/j.revpalbo.2012.08.003.