1	Global warming leads to Early Triassic nutrient stress across
2	northern Pangea
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25 ABSTRACT

The largest extinction in Earth history, in the latest Permian, was followed throughout most of 26 the Early Triassic by a prolonged period of ecologic recovery. What factors delayed biotic 27 recovery are still under debate and partly revolve around impacts of global warming on primary 28 marine productivity. We examined N isotope records from the Festningen section on Spitsbergen 29 to examine changes in nutrient availability through the Early to Middle Triassic along the 30 northern margin of Pangea. Our results show progressive decline in N availability throughout the 31 Griesbachian, leading to severe nutrient limitations through the remainder of the Early Triassic, 32 33 until returning to a highly productive continental margin in Middle Triassic time. These results are consistent with other studies from northern and western Pangea and thus show regional 34 nutrient limitations occurred in what should have been the main zone of marine primary 35 productivity. Such nutrient limitation likely stressed primary production and consequently 36 contributed to prolonged marine recovery. We suggest this was driven by high ocean 37 temperatures depressing the marine nutricline. 38

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41 INTRODUCTION

The Early Triassic represents a period of extreme global warming and severely stressed 42 environments (Tribovillard et al., 2006; Chen and Benton, 2012; Joachimski et al., 2012; Sun et 43 al., 2012; Grasby et al., 2013), that followed the Latest Permian Extinction (LPE), the most 44 severe in Earth history (Erwin et al., 2002; Chen and Benton, 2012; Bond and Grasby, 2017). 45 Marine environments were affected by the globally disrupted carbon cycle (Payne et al., 2004; 46 Galfetti et al., 2007; Grasby et al., 2013), and recurrent anoxia (Grasby et al., 2013; Wignall et 47 al., 2016), associated with numerous gaps in the sedimentary record including: absence of 48 49 biogenic chert and metazoan reefs (Chen and Benton, 2012 and references therein), as well as nitrogen deficiency and absence of phosphorite deposition (Trappe, 1994; Kidder and Worsley, 50 2004; Grasby et al., 2016b). Terrestrial systems were also highly stressed, with a noted gap in 51 coal deposition (Retallack et al., 1996), and evidence of enhanced continental denudation 52 (Sephton et al., 2005; Algeo and Twitchett, 2010; Midwinter et al., 2017). These severe Early 53 54 Triassic conditions extended for 5–9 Ma after the LPE, until final return in the Middle Triassic to normal marine conditions (Bottjer et al., 2008; Chen and Benton, 2012; Grasby et al., 2013) and 55 sea water temperature (Sun et al., 2012). 56

57 What prolonged the Early Triassic recovery has been under active debate, one that partly revolves around primary productivity of global oceans at that time. Some researchers have 58 suggested high post LPE bioproductivity (e.g. Meyer et al., 2011; Schobben et al., 2015; Shen et 59 60 al., 2015) while others have argued for oceans with low primary productivity (e.g. Schoepfer et 61 al., 2013; Song et al., 2013; Winguth et al., 2015; Grasby et al., 2016b). Examination of nitrogen isotope records can help elucidate nutrient availability, and thus constraints on primary 62 productivity in Early Triassic oceans. A detailed nitrogen isotope profile through the Smithian 63 64 stratotype, in the Sverdrup Basin, Canadian High Arctic, showed evidence for progressively

increased nutrient limitation following the LPE, leading to an Early Triassic 'nutrient gap' and 65 associated bioproductivity crisis (Grasby et al., 2016b). Whether or not this was local nutrient 66 limitation in the Sverdrup Basin, or a more widespread event, remains uncertain. Here we test the 67 regional extent of N-limited oceans by examining the broader northern Pangea margin. We 68 analysed N isotope data, along with key nutrients (P, N) and bioproductivity proxies (Ba, Ni, and 69 70 Cu) (Dymond et al., 1992; Steiner et al., 2017) from the Festningen section, Spitsbergen (Fig. 1), that was deposited in an open marine environment (Fig. 2). We show that trends in stable 71 nitrogen isotope values are similar to those observed in the Sverdrup Basin, confirming 72 73 widespread N-limited conditions across northern Pangea throughout the Early Triassic.

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75 UPWELLING AND N LIMITATION IN THE PANTHALASSA OCEAN

Upwelling zones of the world oceans, that transport nutrients to the photic zone, form major 76 regions of bioproductivity, mainly along the western margins of continents (western coasts of 77 78 modern North America, South America, Africa, and Australia) (Capone and Hutchins, 2013). 79 While these upwelling zones represent a minor percentage of ocean area, they are responsible for 80 a major portion of marine primary productivity. Estimates suggest that half the ocean 81 biogeochemical flux of N is derived from continental margins occupying only 20% of world ocean (Walsh, 1991). Nutrient upwelling along these margins is driven by Ekman Transport, 82 which is limited to the upper few hundred meters of the ocean surface (e.g. Huyer, 1983; Currie, 83 1992; Smith, 1995). Typically the ocean's nutricline is coincident with the thermocline, both of 84 which lie above the base of upwelling, such that upwelling transports these nutrient-rich waters 85 86 to the photic zone, driving primary productivity. Models and data related to modern climate warming suggest that increasing ocean temperature is depressing the thermocline/nutricline, and 87

there are concerns that if they are depressed below the base of upwelling that this may greatly reduce nutrient transport to the photic zone, and consequently primary productivity (Kamykowski and Zentara, 1986; Behrenfeld et al., 2006; Doney et al., 2012; Moore et al., 2018). In contrast, some studies suggest global warming would intensify upwelling through increased wind shear (Bakun, 1990). While these models suggest a direct link between ocean temperatures and nutrient delivery to the photic zone, the net impact on primary productivity under hothouse Earth conditions remains uncertain.

Examination of the nitrogen isotope records provides a means to assess the degree of 95 nutrient stress in ancient marine environments. Heterotrophic denitrification and/or anaerobic 96 ammonia oxidation are the principal mechanism for loss of ocean nitrogen, returning to the 97 atmosphere as N_2 (Ward et al., 2009). Regions of significant denitrification (i.e., the reduction of 98 NO_3/NO_2 to N_2) leave subsurface waters highly enriched in ¹⁵N. In contrast, atmospheric 99 nitrogen fixation produces organic matter relatively depleted in ¹⁵N, with δ^{15} N values close to 100 101 that of the atmosphere (0‰). As such, the $\delta^{15}N$ of organic matter (OM) in modern oceans is highly variable, but relatable to biogeochemical processes of different marine environments 102 (Somes et al., 2010). The rates of N₂ fixation are closely associated with, both geographically 103 104 and temporally, marine nitrogen removal, implying a close coupling of nitrogen fixation to nitrogen-deficient water in denitrification zones (Deutsch et al., 2007). Thus, in any single 105 106 location, when N supply from anoxic deep waters to the photic zone is reduced, diazotrophs 107 increase N fixation (Carpenter et al., 1997), producing biomass with significantly reduced values of δ^{15} N in the particulate OM sediment record. With this, changes in the balance between 108 109 denitrification and nitrogen fixation through time can be tracked.

The geological record of N isotopes can provide key insight into changes in the paleomarine N cycle. Modern settings demonstrate that there is little diagenetic alternation of δ^{15} N in sedimentary OM (Altabet et al., 1999a; Altabet et al., 1999b), and post depositional temperature changes also have limited effect on sedimentary δ^{15} N (Ader et al., 1998). Thus, stable isotopes of nitrogen provide an effective tracer of nutrient stress, as the balance between denitrification and nitrogen fixation controls the abundance and isotopic composition of nitrate in local marine environments (Ganeshram et al., 2000).

The closure of the Uralian ocean, during final consolidation of Pangea, was associated with 117 development of a nutrient-rich upwelling margin along northern Pangea since at least the 118 Sakmarian (Stemmerik and Worsley, 1995; Beauchamp and Baud, 2002; Reid et al., 2007; 119 Beauchamp and Grasby, 2012; Blomeier et al., 2013). By the Late Permian, coastal upwelling 120 zones along the northern margin of Pangea were major regions of marine primary productivity 121 (Beauchamp and Baud, 2002). However, several studies have shown that immediately following 122 the LPE, upwelling of nutrient-rich waters was greatly reduced across northern and western 123 Pangea, leading to nutrient-limited conditions, enhanced nitrogen fixation, and reduced 124 bioproductivity (Beauchamp and Baud, 2002; Knies et al., 2013; Schoepfer et al., 2013; Grasby 125 126 et al., 2015). Climate models also suggest reduced mid-latitude upwelling of nutrient-rich waters under Early Triassic hothouse conditions occurred due to decreased wind-stress-driven Ekman 127 transport (Kidder and Worsley, 2004; Winguth et al., 2015). Nutrient trapping due to deepened 128 129 thermocline/nutricline during Early Triassic hothouse conditions has also been suggested (Grasby et al., 2016b). It is important to recognize that available observations cannot discern 130 between reduced physical upwelling of water, as compared to reduced nutrient transport, in a 131 132 system where upwelling is maintained or even enhanced. For example, a depressed

thermocline/nutricline would limit nutrient transport to the photic zone even if upwelling was 133 intensified, effectively trapping nutrients below the base of upwelling (Grasby et al., 2016b). 134 Along with decreased nutrient delivery to the photic zone, Early Triassic 135 greenhouse/hothouse conditions are thought to increase denitrification related to increased 136 anoxia, that also drives increased N fixation to maintain a Redfield balance (N/P = 14) with 137 138 phosphorus over longer timescales (Tyrrell, 1999; Kidder and Worsley, 2010), even though N fixation is an overall more energetically costly process in comparison to assimilation of pre-139 existing fixed N (Brandes et al., 2007). A rise in sea surface temperature would also intensify 140 141 thermal stratification of the ocean, expand N-limited subtropical gyres (Sarmiento et al., 1998), as well as deepen the thermocline (and nutricline), further limiting nutrient resupply to the photic 142 zone (Kamykowski and Zentara, 1986; Behrenfeld et al., 2006). How this affects marine 143 productivity depends partly on the degree to which diazotrophs offset net N loss (Saltzman, 144 2005). Data from the Sverdrup Basin suggests that initial nutrient limitation at the LPE (Knies et 145 146 al., 2013) was the start of an even larger trend towards more nutrient restricted conditions throughout the entire Early Triassic that stressed primary production (Grasby et al., 2016b), as 147 marked by a progressive decrease of δ^{15} N values through the Griesbachian/Dienerian towards 148 values of atmospheric nitrogen ($\delta^{15}N \approx 0\%$) and concurrent drops in TOC and bioproductivity 149 proxies. 150

151 STUDY AREA AND PALEO-ENVIRONMENTAL SETTING

The Festningen section, located at Kapp Starostin, Spitsbergen (Fig. 1), provides a near
continuous exposure of Carboniferous to Cenozoic strata along a low sea-cliff from Kapp
Starostin to Festningsdodden, including the thickest known development of Lower Triassic
marine stratigraphy on the island. Located in the eastern part of the West Spitsbergen Fold and

Thrust Belt, the Festningen section is part of the steeply inclined short-limb of a kilometer-scale
east-vergent fold structure (Maher and Craddock, 1988; Dallmann et al., 1993; CASE-Team,
2001). An igneous sill (dating from the Cretaceous 124.7 Ma) (Corfu et al., 2013) intrudes the
sedimentary section near the basal Triassic contact but has limited and local thermal effect
(Grasby et al., 2015).

The upper 40 m of the Kapp Starostin Formation is characterized by Lopingian (Upper 161 Permian) spiculitic chert (Blomeier et al., 2013), considered equivalent to the Black Stripe and 162 Lindström formations of the Sverdrup Basin (Beauchamp et al., 2009; Bond et al., 2015). These 163 cherts are in sharp contact with overlying Lower to Middle Triassic shale, siltstone and minor 164 sandstone (Mørk et al., 1982) equivalent to the Blind Fiord Formation of the Sverdrup Basin 165 (Embry, 1989). The contact between the Kapp Starostin and Vardebukta formations coincides 166 with the Latest Permian Extinction, and the basal ~6-7 m of the Vardebukta Formation is latest 167 Permian in age (Wignall et al., 1998; Grasby et al., 2015). 168

169 The Lower Triassic succession at Festningen is divided into the shale and siltstone

170 dominated Vardebukta (uppermost Changhsingian, Griesbachian and Dienerian) and

171 Tvillingdodden (Smithian/Spathian) formations (Embry, 1989; Wignall et al., 1998; Grasby et

al., 2016a; Wignall et al., 2016). The sediments were deposited in a distal shelf setting (Wignall

et al., 1998; Stemmerik and Worsley, 2005; Blomeier et al., 2013) at estimated paleolatitudes of

¹⁷⁴ ~40 to 45° N (Golonka and Ford, 2000; Scotese, 2004; Hounslow et al., 2007). Early work on the

175 Triassic sequence at Festningen showed onset of ocean anoxia following the LPE (Wignall et al.,

176 1998). Further work demonstrated that this anoxia was the culmination of progressive

environmental deterioration, initiated with ocean acidification, loading of toxic metals, and final

onset of anoxia (Grasby et al., 2015). Mercury records also show anomalies at the LPE as well as

later Smithian extinction events, likely associated with Siberian Trap eruptions (Grasby et al.,
2016a). In addition, the Lower Triassic record at Festningen shows changes in bioturbation,
paleoecology, pyrite framboid content and trace metal concentrations that demonstrate anoxic
phases alternated with intervals of better ventilation (Wignall et al., 2016). Through Early
Triassic time, only the Dienerian and early Smithian had oxygenation sufficient for supporting a
diverse benthic community. Anisian strata (Middle Triassic) are represented by phosphatic
organic-rich shales of the Botneheia Formation (Krajewski, 2008).

The Paleozoic–Mesozoic transition along northwest Pangea was marked by a change from 186 very low rates of biosiliceous sediment accumulation during the Late Permian to rapid rates of 187 188 clastic sedimentation throughout the Early and Middle Triassic (Embry and Beauchamp, 2008; Beauchamp and Grasby, 2012). Deteriorating environmental conditions during the Late Permian, 189 interpreted as resulting from the shoaling of the calcite lysocline and establishment of 190 increasingly acidic conditions in response to global warming, inhibited the production and 191 192 preservation of biogenic benthic carbonates in a vast area from Western Canada (Schoepfer et al., 2013) to the Canadian (Beauchamp et al., 2009) and Norwegian (Bond et al., 2015) Arctic. 193 Slowly-producing siliceous sponges were the only organisms that could thrive in such a hostile 194 195 environment, resulting in significant condensation and preservation of their spiculitic remains as biogenic chert (Beauchamp and Grasby, 2012). The subsequent encroachment of anoxic waters 196 onto the shallow shelves further contributed to the near-complete eradication of carbonate-197 198 secreting benthic organisms (Grasby and Beauchamp, 2009). However, organic productivity in the upper part of the water column remained high as shown by increasing TOC up to the LPE 199 200 horizon, which reflects enhanced preservation of organic matter in uppermost Permian sediments 201 due to the establishment of anoxic conditions on the sea floor, not an increase in organic

productivity near the sea surface (Grasby and Beauchamp, 2009). A major shift in sedimentary
regime occurred across the LPE as large volumes of terrigenous clastic material were shed onto
northwestern Pangea shelves and basins throughout the Early and Middle Triassic. While the
change in sedimentation rates and style across the LPE might have affected the absolute
concentration of certain elements, elemental and isotopic ratios should have remained unaffected
by these changes.

208 METHODS

209 Samples were collected at the Festningen Section, located at N78°5.72'; E13°49.424' (relative to NAD83). Field sampling was conducted relative to the Kapp Starostin/Vardebukta formation 210 211 contact that represents the LPE horizon, whereby samples are recorded in metres above (positive) and below (negative) the top of the last chert bed that defines the top of the Kapp 212 Starostin Formation. Sample spacing varied, from 20 cm within 1 to 2 m of the formation contact 213 to higher spacing of 50 cm for the rest of the section sampled. Weathered surfaces were removed 214 215 and then samples were collected from an isolated layer no greater than 2 cm thick. These same samples have been subject of previous studies (Bond et al., 2015; Grasby 216 al., 2016a; Wignall et al., 2016), and previously published data are indicated where relevant. We 217 used the previously published organic carbon isotope record to sub-sample for N isotope 218 219 analyses, such that the selected sample subset would accurately reproduce the full carbon isotope trend through time. From this, 98 samples were selected for N isotope analyses (approximately 220 every 3rd sample). Analytical results are provided in Table 1. 221

In the laboratory, any remaining weathered surfaces were removed and fresh samples were powdered by agate mortar and pestle. Total N and δ^{15} N were analysed by using an elemental analyser connected to an isotope ratio mass spectrometer (EA-IRMS). Approximately 20% of the

samples were analyzed in duplicate with a mean standard deviation of 0.16‰. Results are reported as standard δ -values in per mil (‰ vs. air). The reference material used during analysis of the samples (IA-R001 wheat flour, Iso-Analytical Ltd.) had a δ^{15} N value of 2.55‰ versus air and contained 1.88% N (w/w). Control samples were analysed to check the accuracy of the measurements, with precision better than ±0.2‰.

230 **RESULTS**

The Festningen section records significant changes in global biogeochemical cycles that 231 occurred through Late Permian to Middle Triassic time as expressed by variation in $\delta^{13}C_{org}$. We 232 use this record, to place into context new data presented here; including nutrient (N and P), stable 233 isotope (δ^{15} N), and element enrichment factors for bioproductivity proxies for (Ba, Ni, Cu). 234 235 Previous work has shown that the organic carbon isotope record at Festningen can be readily correlated with that of the Smithian stratotype (Fig. 3) and other sections in the Sverdrup Basin, 236 237 as well as inorganic carbon isotope records from the Tethys Ocean (Grasby et al., 2015; Grasby et al., 2016a; Wignall et al., 2016). The Festningen $\delta^{13}C_{org}$ record (Fig. 4a) shows a significant 238 10‰ negative shift at the LPE boundary, followed by progressive recovery through 239 Griesbachian/Dienerian time, returning to close to pre-extinction values in the lower Smithian. 240 There is then a progressive drop through the Smithian to lows of $\sim -33\%$, below the 241 Smithian/Spathian boundary, coincident with a significant late Smithian anoxic event (Grasby et 242 al., 2013; Wignall et al., 2015). Above this δ^{13} Corg values fluctuate through the Spathian and 243 finally stabilize in the Anisian. 244 The total organic carbon (TOC) values prior to the Capitanian Crises are generally low (< 245 ~ 0.5%), then increase in the uppermost Permian (Fig. 4b). TOC values drop at the LPE and then 246

briefly increase in the basal Griesbachian up to values of 1.0%, before dropping to values < 0.1%

248	through to the end of the Smithian. The TOC values then increase up to 1.0% in the Spathian
249	before declining again. At the onset of the Anisian the TOC values show a significant
250	progressive increase to values up to 3% in the Middle Triassic Botneheia Formation.
251 252	δ ¹⁵ N data
253	The nitrogen isotope record at Festningen shows initial high $\delta^{15}N$ values (> 8‰) prior to the
254	Capitanian Crises of Bond et al. (2015), and then a drop to values of ~ 6‰ through the latest
255	Permian (Fig. 4c). At the LPE event δ^{15} N values fall again to ~3‰ in the lower Griesbachian.
256	Through the remainder of the Lower Triassic $\delta^{15}N$ values continued to decline down to values of
257	~ 1‰ near the top of the Spathian. The δ^{15} N values then showed a positive shift, increasing to
258	~2‰ in the Anisian.

N and P data

The concentrations of N and P in sediments vary from 0.015 to 0.18% and 0.001 to 0.53% 260 261 respectively. For N, concentrations are low at the base of the section and show an increasing 262 trend about the level corresponding with the Capitanian Crises through to the lower Griesbachian to $\sim 0.12\%$ (Fig. 4d). Values are then low (< 0.50%) throughout the remainder of the Lower 263 264 Triassic but increase in the Middle Triassic to the highest values observed in the section (0.18%). Through this time period P shows different trends, remaining low through the Permian (0.03%)265 and then showing a general increasing trend through the Griesbachian/Dienerian. The P values 266 then remained relatively stable at $\sim 0.1\%$ through the rest of the Lower Triassic with the 267 exception of a brief increase to >0.2% in the Smithian. P values are highest in the Anisian 268 Botneheia Formation (>0.25%) which is characterized by abundance of phosphate nodules. 269 While our data in Figure 4e shows relatively high P in the Middle Triassic, this represents only 270 271 values measured in shales and does not account for the presence of these P nodules. Estimates

from equivalent units indicate that bulk rock P content (P in shales and nodules) can be up to 10 x these concentrations (Grasby et al., 2016b). The N/P ratio is highest in the Upper Permian (2 to 5) and then drops significantly through the Griesbachian to values < 1 (Fig. 4f). The N/P ratio stays low throughout the Lower Triassic and increases to ~ 1 in the Middle Triassic, but could be up to an order of magnitude lower when accounting for P in phosphate nodules. In general, trends in the N/P closely corresponds to changes in TOC through the Lower Triassic but this relationship breaks down in the Middle Triassic.

279 Paleoproductivity proxies

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Trace metals that act as micronutrients can be used as proxies for paleoproductivity (Tribovillard 281 et al., 2006). To counter potential dilution affects related to changes in sedimentation rates, these 282 are best examined as element enrichment factors (EF), defined as deviations of Al normalised 283 284 samples (to account for potential terrestrial input) from average shale values, taken here as Post Archean Average Shale values (PAAS) (Wedepohl, 1995). Whereby EF > 1, calculated as EF =285 (X_{sample}/Al_{sample})/(X_{PAAS}/Al_{PAAS}), are thought to indicate high primary productivity. As no single 286 productivity proxy is completely reliable, we calculated these for Ba, Ni and Cu as plotted in 287 Figure 4g. Enrichment factors for Ba and Ni are high (>1) through the Permian and then all show 288 a significant drop to values <<1 immediately following the LPE, with a brief recovery followed 289 by a shift to values near 1 through most of the Early Triassic. In contrast, Cu EFs remain low 290 though most of the section. There is a brief return to high EF in the Spathian consistent with 291 higher TOC values at that time. Following this EF return to values close to 1 and then shift to 292 higher values (>1) in the Anisian. These trends are also illustrated by comparing average EF 293 values for Ba and Ni during the Late Permian (1.17, 1.46 respectively), 50 m above the 294 extinction horizon (0.58, 0.99) and the remainder of the Early Triassic (0.88, 1.12). 295

296 **DISCUSSION**

297 Early Triassic Nitrogen limitation

The Festningen section records significant fluctuations in $\delta^{13}C_{org}$ that are consistent with

inorganic records from Tethyan sections as well as the $\delta^{13}C_{org}$ record from the Smithian 299 stratotype in the Sverdrup Basin (Fig. 3). This demonstrates that Festningen records open marine 300 conditions, with geochemical records that reflect global signals of perturbations to the carbon 301 pool. The >8‰ Late Permian δ^{15} N values at Festningen are consistent with significant water-302 column denitrification occurring in continental margin upwelling zones that leaves subsurface 303 waters highly enriched in ¹⁵N (Knies et al., 2013). These results are similar to those of other 304 305 studies showing that the broader margin of northern and western Pangea was a regional zone of upwelling in Late Permian time (Beauchamp and Baud, 2002; Kidder and Worsley, 2004; Knies 306 et al., 2013; Schoepfer et al., 2013; Grasby et al., 2016b) (Fig. 2a). The δ^{15} N record of 307 Festningen then shows a ~3% decline in δ^{15} N values across the LPE, that we interpret to reflect 308 a decline of nutrient delivery to the photic zone, and as a consequence greater reliance on 309 atmospheric N fixation to support primary productivity. This is consistent with broader regional 310 drops in δ^{15} N values observed at the LPE across northern and western Pangea, including the 311 Sverdrup and Western Canada basins (Knies et al., 2013; Schoepfer et al., 2013; Grasby et al., 312 2016b). In contrast to this regional trend, the East Greenland Fiskegrav section had lower overall 313 314 δ^{15} N values prior to the LPE, and does not show any significant change across the extinction event (Mettam et al., 2017). This likely reflects the highly restricted nature of the East Greenland 315 Basin, which was separated from wider Panthalassa ocean circulation during Late Permian time 316 317 (Mettam et al., 2017; Roberts et al., 2018). East Greenland was thus not affected by regional 318 upwelling prior to the LPE, nor changes to N delivery after the extinction. Instead it more likely 319 reflects a depositional environment that was isolated from overall changes in the global ocean.

520 This is also seen as a distinctly different carbon isotope record in East Orechand v
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Barrera et al., 2015), as compared to both northern Pangea and other global records.

On a more global scale, a drop in δ^{15} N across the LPE occurs in most studied sections, and 322 can be even more significant elsewhere than northern Pangea (Fig. 5). Numerous Tethyan 323 sections from China show a significant drop in δ^{15} N values to zero or less right after the LPE 324 (Cao et al., 2009; Luo et al., 2011; Saitoh et al., 2014; Xiang et al., 2016). A lesser, but still 325 noticeable, δ^{15} N drop across the LPE is also recorded in the Peri-gondwanan sections at Guryul 326 327 (Algeo et al., 2007) and the western Tethyan Bulla section (Jia et al., 2012). It is instructive to compare these sections, as NW Pangea shows the most enriched $\delta^{15}N$ values prior to the 328 329 extinction, consistent with previous research that indicated this region of the Panthalassa Ocean was a dominant upwelling zone with strong nutrient recycling (Beauchamp and Baud, 2002; 330 331 Knies et al., 2013; Schoepfer et al., 2013; Grasby et al., 2015). To do this we used the two time markers of the LPE and Permian/Triassic boundary to stretch different records in order to allow 332 comparison of N isotope trends across Pangea as seen in Figure 5. The very rapid and significant 333 negative shifts across the LPE in the Tethys, to δ^{15} N values consistent with a nutrient-limited 334 system supported by N₂ fixation, suggest more severe nutrient limitations in the Tethys than 335 northern Pangea. This can be explained by model results that show the Tethys Sea was strongly 336 stratified at the LPE due to limited connection with the larger Panthalassa Ocean (Kiehl and 337 Shields, 2005). In contrast, the only ~3‰ drop in δ^{15} N values across the LPE in sections from 338 northern Pangea suggests that while stressed, the region still maintained relatively high nutrient 339 levels in the immediate aftermath of the LPE. 340

The growing prevalence of atmospherically fixed nitrogen immediately following the LPE
 is supported by the widespread evidence for cyanobacteria blooms, including diazotrophs, during

the Early Triassic, as documented by biomarker data in sections globally (Grice et al., 2005; Xie
et al., 2005; Hays et al., 2007; Xie et al., 2007; Hays et al., 2012). This is consistent with
eukaryotic algae being more vulnerable to extinction in a N-limited ocean than prokaryotic
photoautotrophs, whereby primary producers capable of nitrogen fixation would be favoured
(Anbar and Knoll, 2004; Knoll et al., 2007). Thermal stress of the Early Triassic ocean would
also decrease microbial diversity (Sharp et al., 2014) that might have further limited primary
productivity.

Most previous studies of the δ^{15} N record have just focused on the LPE itself, making it 350 351 difficult to examine the Early Triassic record on a global basis. However, for northern Pangea we show that the Festningen δ^{15} N record is very similar to the Smith Creek record of the Sverdrup 352 Basin (Grasby et al., 2016b). Namely, the initial negative shift in δ^{15} N values at the LPE 353 boundary at Festningen was just the start of a longer term progressive decline. At Festningen The 354 negative δ^{15} N shift was characterised by a further ~ 4‰ decline in δ^{15} N through the 355 Griesbachian. The δ^{15} N values then remained low (~1-2‰) through the Smithian and Spathian. 356 We interpret this to indicate ongoing development of nutrient stress with a N cycle dominated by 357 diazotrophs fixating atmospheric N₂ through the entire Early Triassic. In contrast to the Tethys 358 region, where nutrient limitation developed very rapidly, the disruption of the N cycle along 359 northern Pangea appears to be characterised by longer-term progressive development of nutrient 360 361 limitation through the Griesbachian/Dienerian.

Early Triassic N-limited conditions at Festningen appear to have also directly affected primary productivity, as observed by the very low TOC levels despite recurrent anoxia (Grasby et al., 2013; Wignall et al., 2016) that would have otherwise enhanced preservation of organic matter in a productive margin. Through the Early Triassic TOC also closely tracks the N/P ratio,

with lower TOC values corresponding to drop in N/P (Fig. 4), further supporting that N-366 limitation directly affected primary productivity. Drawdown of bio-essential micronutrients 367 related to Early Triassic anoxia may have placed even further stress on productivity at this time 368 (Grasby and Beauchamp, 2009). The EFs for primary productivity proxies Ba and Ni track each 369 other and show values that are consistent with a productive upwelling setting prior to the LPE, 370 371 that can shift to values <1 (indicating low productivity) through the Early Triassic. The EFs for Cu are low throughout the section and may not reflect changes in bioproductivity. Overall, we 372 373 interpret these results to suggest that stable isotope evidence for Early Triassic N-limited 374 conditions is also manifest as reduced primary production along the northern margin of Pangea, characterised by the overall organic-lean shales. This is also seen in the organic-lean Lower 375 Triassic Vega-Phroso Member shales and subsurface equivalents in NE British Columbia, that 376 have apparently high TOC due to secondary oil migration (Riediger et al., 1990; Riediger, 1997). 377

378 Middle Triassic return to productive margins

Following the Early Triassic accumulation of organic lean shales at Festningen, there was a 379 significant switch in the Middle Triassic to deposition of black organic-rich phosphatic shales 380 that are indicative of a change to a highly productive margin. This switch from organic lean to 381 organic-rich conditions is coincident with the end of the Early Triassic hothouse and return to 382 normal marine temperatures (Sun et al., 2012). This was a significant event as the black shale 383 deposited at Festningen is represented by the Botneheia Formation which forms a key source 384 rock of the Barents Sea oil fields (Krajewski, 2008). This is also correlative with the 385 development of other major black shale source rocks of Middle Triassic age, including the 386 Murray Harbour Formation of the Sverdrup Basin (Grasby et al., 2016b), the Shublik Formation 387 388 of Alaska (Parrish et al., 2001) and Doig Phosphate zone of western Canada (Riediger, 1997). Similar Middle Triassic black shales are also found in the western Tethys (Bernasconi and Riva, 389

1993), suggesting that cooling oceans led to an increase of primary productivity and associated
 drawdown and sequestration of atmospheric CO₂.

Similar to the Sverdrup Basin, the δ^{15} N values of Festningen still remained low through 392 the Middle Triassic. While we interpret the low $\delta^{15}N$ values of the Early Triassic to reflect 393 nutrient-stressed conditions leading to a productivity crisis, these N isotope values can only be 394 interpreted in the broader context of the shale geochemistry. In contrast to the organic lean Early 395 Triassic shales, the widespread formation of Middle Triassic source rocks requires a different 396 interpretation of the N isotope data. We argue that the low δ^{15} N values still represent N-limited 397 conditions, but in the sense that it reflects a shift to low N/P waters (as implied by abundant P 398 nodules) at that time. Thus, similar to Grasby et al. (2016b), the formation of Middle Triassic 399 organic rich source rocks is related to renewed upwelling of P-rich waters that had been trapped 400 by a deepened thermocline below the zone of upwelling through Early Triassic time – setting off 401 a phosphate bomb that drove high productivity and in turn draw down of atmospheric CO₂. 402 Although N_2 fixation has a high energy demand, when nutrient N concentrations are low relative 403 to nutrient P (i.e. N/P << Redfield ratio) diazotrophs can outcompete non-N₂ fixing algae 404 (Tyrrell, 1999). Thus a large flux of low N/P waters to the photic zone would have fueled 405 atmospheric nitrogen fixation to provide sufficient nutrient N supply to drive the observed 406 increased primary productivity (Grasby et al., 2016b), while still maintaining low δ^{15} N values 407 due to N-limited conditions (relative to P). This interpretation is similar to Cretaceous Ocean 408 Anoxic Events (OAEs), whereby atmospheric N₂ fixation was the dominant source of N, along 409 with remineralised P, driving high bioproductivity and organic carbon burial (Kuypers et al., 410 2004). 411

412 Global Implications

Various indirect lines of argument have been used to suggest significantly reduced primary 413 productivity following the LPE, including significantly reduced fossil abundance (Twitchett et 414 al., 2001; Payne, 2005; Twitchett, 2007), reductions in body size in many fossil groups, 415 including conodonts (Luo et al., 2008), sponges (Liu et al., 2013), brachiopods (He et al., 2007; 416 He et al., 2010) and molluscs (Twitchett, 2007). In addition, the negative excursion in marine 417 carbonate δ^{13} C profiles (Rampino and Caldeira, 2005) has been used to argue for reduced 418 419 primary production, although other models such as volcanic emissions can also explain this (Payne and Kump, 2007). Shen et al. (2014) also show proxies for primary productivity in south 420 China are consistent with decreased productivity across the LPE. Retallack (2004) also made the 421 422 interesting observation that most Lower Triassic sections show much lower TOC levels than underlying Late Permian or overlying Middle Triassic rocks in the same sequence. Similarly, the 423 scarcity of organic-rich shale from Lower Triassic shelf sections has been noted by the global 424 search for petroleum source rocks (Tissot, 1979; Klemme and Ulmishek, 1991). Given evidence 425 for global anoxia, that would favour organic preservation, the scarcity of organic-rich shales 426 during the Early Triassic is consistent with overall reduced global primary productivity during 427 that time. 428

In contrast to the above, increased primary productivity after the LPE has been favoured by several authors. Carbon isotope data, such as positive excursions in marine carbonate δ^{13} C profiles, have also been used to argue for increased productivity in at least parts of the Early Triassic (Suzuki et al., 1998; Horacek et al., 2007a). As well, enhanced carbon-isotope depth gradients in Lower Triassic limestone of the Tethys have been suggested to reflect increased primary productivity (Meyer et al., 2011). However, Song et al. (2013) used similar data to make the opposite argument, for reduced productivity in the immediate aftermath of the LPE.

Development of organic-rich mudstones in deep water Panthalassa sections (Kakuwa, 1996; 436 Suzuki et al., 1998; Sashida et al., 2000; Takemura et al., 2004) immediately following the LPE 437 suggests potential for enhanced mid-Panthalassa productivity, at least during the Griesbachian; 438 after which deposition switches back to organic lean conditions. Shen et al. (2015) also argued 439 for increased primary productivity from the late Changhsingian to the Griesbachian in most 440 441 regions of the globe, including northern Pangea, based on geochemical proxies. Their study, however, is largely restricted to the absolute latest Permian (post LPE) or earliest Triassic 442 (Griesbachian) and does not provide insight into overall trends in the Early Triassic. 443 Most of the debate though has been based on observations of Tethyan sections. More 444 relevant to study of changes of marine primary productivity in the aftermath of the LPE is to 445 focus on the marine records of those areas affected by upwelling, i.e. the northern and western 446 margins of Pangea. To obtain a broader northern Pangea perspective, we compare here the 447 geochemical record from Spitsbergen and the Sverdrup Basin, with data plotted as a function of 448 time rather than stratigraphic thickness (Fig. 6). For Figure 6 we have excluded the basal portion 449 of the Festningen section as correlative data is not available. This figure shows consistent trends 450 from Late Permian through to Middle Triassic along the northern margin of Pangea. The region 451 452 was characterised by significant upwelling in the Late Permian (Beauchamp and Baud, 2002; Knies et al., 2013; Schoepfer et al., 2013; Grasby et al., 2015; Grasby et al., 2016b), with a shift 453 to nutrient reduced conditions at the LPE. There is then an overall trend to greater nutrient stress 454 through the Early Triassic, albeit with some diachroneity. For instance, the shift to lower $\delta^{15}N$ 455 values was earlier at Festningen (initiated in the Griesbachian) as compared to Smith Creek that 456 did not reach lower values until the early Dienerian. As well, minimum δ^{15} N values at 457 458 Festningen are ~ 2‰ higher than that recorded in the Smith Creek section of the Sverdrup Basin, suggesting nutrient limitation may have been slightly greater in the Sverdrup Basin. Overall though, our data demonstrate a significant shift occurred in northern Pangea, from N supply related to water-column denitrification occurring in continental margin upwelling zones prior to the LPE, to N supply related to atmospheric N fixation in the aftermath. This change is coincident with the shift from Late Permian greenhouse to Early Triassic hothouse conditions demonstrated by conodont δ^{18} O data (Sun et al., 2012).

Our observations of nutrient limitations in upwelling zones is consistent with the HEAT 465 model of Kidder and Worsley (2010), whereby global warming drives increased ocean anoxia, 466 467 that in turn leads to enhanced denitrification and anaerobic ammonium oxidation, favouring atmospheric N₂ fixation by diazotrophs. As this is a more energy intensive process as well as Fe 468 limited, overall net primary productivity would be reduced. Our results also directly support 469 predictions of weakened trade winds in response to Early Triassic global warming, and a 470 coincident decline in Ekman transport of nutrients to the photic zone and primary productivity 471 (Winguth et al., 2015). As such, our data for northern Pangea are consistent with hothouse Earth 472 conditions creating extremely stressed marine environments that limited biodiversity and overall 473 bioproductivity. Our model is similar to concerns expressed for modern global warming leading 474 to deep ocean nutrient trapping and drastic decline in shallow water biological productivity of the 475 ocean (Kamykowski and Zentara, 1986; Bopp et al., 2001; Sarmiento et al., 2004; Behrenfeld et 476 al., 2006; Cermeño et al., 2008; Doney et al., 2012; Moore et al., 2018). 477

During the time of the single super continent Pangea, eastern boundary currents would have been limited to the Panthalassa Ocean (Fig. 2a), suggesting that upwelling zones and associated primary productivity would have been restricted to an even smaller extent of world oceans than today – largely along the western and northern margin of Pangea, but also possibly

in the Tethys as zones of equatorial upwelling (Kidder and Worsley, 2004; Grasby et al., 2016b). 482 While decline in nutrient upwelling in northern Pangea appears to have placed direct stress on 483 local marine ecosystems, significantly reducing primary productivity across northern Pangea, 484 broader global trends remain to be determined. Similar detailed studies of nutrient stress through 485 the Early Triassic in Tethyan sections are required. However, given the disproportionate role that 486 487 upwelling zones have on net biologic productivity, reduced upwelling along northern Pangea would likely have had global impacts, and contributed to overall marine stress and prolonged 488 biotic recovery during the Early Triassic hothouse. A significant decline in marine productivity 489 490 could also have had larger global effects, as shown by Winguth et al. (2015) who demonstrated that it could alter global climate (Andreae, 2007) and sustain hothouse conditions. 491

Intriguingly, N_2 fixation is also suggested to have provided sufficient nutrient N to drive the carbon pump to effectively reduce atmospheric CO₂ levels during the mid-Cretaceous greenhouse (Kuypers et al., 1999; Kuypers et al., 2004). The Anisian is marked by a similar widespread deposition of black shales driven by atmospheric N_2 fixation marking the end of the Early Triassic Hothouse. We suggest then that renewed upwelling of P-rich waters along with atmospheric N_2 fixation may have played a similar major role in driving the carbon pump to reduce the detrimental effects of Early Triassic global warming.

Our results can also provide some insight into global carbon budgets. Despite numerous attempts to explain significant shifts in carbonate isotope values through the Early Triassic, there is no consistent view on overall drivers. Our work is similar to that of Grasby et al. (2013) who showed organic carbon isotope records of northern Pangea are consistent with the inorganic records of the Neo-Tethys and Tethys regions (Fig. 7), supporting an external driver for negative carbon excursions such as eruption of the Siberian Traps (e.g. Payne and Kump, 2007). More

relevant is that our results from Festningen, as well as the Sverdrup Basin (Grasby et al., 2016b), 505 indicate that the large carbon isotope excursions through the Early Triassic are not related to 506 changes in nutrient levels as shown by the Nitrogen isotope records (Figs. 6, 7). These results 507 suggest some degree of decoupling of the carbon cycle from nutrient levels, whereby low 508 productivity and carbon burial in the Early Triassic occurred as nutrients were trapped in the 509 510 deep ocean by a depressed thermocline (Grasby et al., 2016b), and primary productivity was limited by low rates of N-fixation. If correct, this lends further support to an external driver such 511 as volcanism for the large carbon isotope excursions observed through the Early Triassic. 512

513 CONCLUSIONS

Geochemical records from the Festningen section on Spitsbergen provide new insight into the 514 515 evolution of the ocean nutrient levels and bioproductivity from Late Permian through to Middle Triassic time. Our results show that under Early Triassic Hothouse conditions there was a 516 progressive decrease in nutrient levels, whereby nutrient-N became restricted and dominantly 517 518 sourced from atmospheric N₂ fixation. This nutrient stress appears to have also reduced primary 519 productivity, yet shows no relationship to major swings in the global C isotope record through 520 Early Triassic time. These patterns are observed across the margin of northern Pangea, which at that time in Earth history should have been a major zone of bioproductivity in world oceans, 521 522 such that nutrient stress in this region would have had global impact, and may have played a significant role in the delayed recovery of life following the Latest Permian mass extinction. The 523 apparent decoupling of decreased N-nutrient levels along with bioproductivity from the carbon 524 isotope record supports an external driver such as volcanic emissions to explain major swings in 525 526 δ^{13} C through the Early Triassic. These conditions were ameliorated in the Middle Triassic as

marked by return of highly productive margins across northern Pangea, which werecoincident
with final cooling of world oceans, radiation of life, and return of normal marine ecosystems.

529 Our findings may also provide insight into concerns over the impact of modern climate 530 warming as both increased wind shear, driving increased upwelling, as well as deepening of the

⁵³¹ nutricline are predicted. These two impacts would have opposing effects on marine productivity.

532 Our study suggests that in the Early Triassic the deepening of the nutricline offset any increased

533 physical upwelling such that warming oceans saw a net decline in primary productivity. Our

results are consistent with predicted impacts of global warming on modern marine

bioproductivity (e.g. Moore et al., 2018), although while those models suggest millennial

timescale impacts, our results indicate productivity was impacted for millions of years following

537 the LPE.

538

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540

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862 FIGURE CAPTIONS

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Figure 1. Map showing Svalbard and the location of the Festningen section near the entrance of

865 Isfjorden on the island of Spitsbergen.

- Figure 2. Palaeogeographic maps showing the study area in Late Permian time, including (A)
- reconstruction of Pangea (after Scotese, 2004) showing likely patterns of Coriolis affect driven
- ocean circulation, forming eastern boundary currents in the Panthalassa Ocean along the western
- 870 margins of Pangea. (B) Paleogeographic map showing relative locations of sections from
- 871 Spitsbergen and the Sverdrup Basin during Early Triassic time, as well as location relative to
- 872 Pangea (inset box).
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874 Figure 3. Chemostratigraphic correlation of organic carbon records from Late Permian through to Middle Triassic time of the Festningen section (this study) with that from sections in the 875 Sverdrup Basin, Arctic Canada (Grasby et al., 2016a). LPE=Latest Permian Extinction level, 876 Grie. = Griesbachian. 877

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Figure 4. Plots of geochemical data for Festningen. (A) δ^{13} C of organic carbon, red dots indicate 879 sub-samples selected for $\delta^{15}N$ measurement. (B) Total organic carbon (TOC). (C) $\delta^{15}N$ of N in 880 organics, (D) total N in sediments. (E) total P in sediments. (F) ratio of N/P in sediments. (G) 881 plots of element enrichment factors (EF) for Ba, Ni, and Cu. LPE = Latest Permian Extinction 882 level, Tri. = Triassic, Bot. = Botneheia, Fm = Formation. 883

Figure 5. Comparison of δ^{15} N records from global sections, after Saitoh et al. (2014). P/T =

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Permian Triassic Boundary, LPE = Latest Permian Extinction. Data are derived from Festningen 886 (this study), Arctic Canada (Knies et al., 2013), Opal Creek (Schoepfer et al., 2013), Guryul 887 Ravine (Algeo et al., 2007), Bulla (Jia et al., 2012), Zuodeng and Taiping (Luo et al., 2011) 888 Meishan (Cao et al., 2009), Chaotian (Saitoh et al., 2014). Temporal control to compare data was 889 provided by stretching individual sections such that the two time points, P/T = Permian Triassic890 Boundary and LPE = Latest Permian Extinction level are at the same vertical scale. 891 892 Figure 6. Comparison of Early Triassic trends across NW Pangea from sections at Smith Creek 893 (Grasby et al., 2016b) and Festningen (this study). The basal portion of the Festningen section 894 has been excluded as correlative data is not available. Data are shown for $\delta^{15}N$, $\delta^{13}C$ of organic

carbon, and total organic carbon (TOC). Plots are shown relative to time by stretching data plots 896

897	of individual sub-stage boundaries. Sedimentary gaps, changes in biodiversity, and ocean
898	temperature are from Chen and Benton (2012), Grasby et al. (2016b), and Sun et al. (2012). Pr. =
899	Permian, Ch = Changhsingian, Gr. = Griesbachian, Di.= Dienerian, Sm. = Smithian, TOC= total
900	organic carbon.
901	Figure 7. Plot of inorganic carbon isotope records through the Early Triassic from the Neotethys
902	Zal section (Horacek et al., 2007b) and Tethys Nanpanjiang section (Sun et al., 2012), as well as
903	the organic carbon Boreal records from Smith Creek (Grasby et al., 2013), and Festningen
904	(Grasby et al. 2016a) showing similarity of global trends in carbon isotope from both inorganic
905	and organic carbon pools. The trends in N isotope values from Smith Creek (Grasby et al. 2016b)
906	and Festningen (this study) are largely decoupled from changes to the global carbon pool. Gries.
907	= Griesbachian, Dien. = Dienerian.