

1 **Reduced upwelling of nutrient and carbon-rich water in the subarctic Pacific**
2 **during the Mid-Pleistocene Transition**

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23 Abstract

24 Reduction in atmospheric $p\text{CO}_2$ has been hypothesised as a causal mechanism for the Mid-
25 Pleistocene Transition (MPT), which saw global cooling and increased duration of glacials
26 between 0.6 and 1.2 Ma. Sea ice-modulated high latitude upwelling and ocean-atmospheric CO_2
27 flux is considered a potential mechanism for $p\text{CO}_2$ decline, although there are no long-term
28 nutrient upwelling records from high latitude regions to test this hypothesis. Using nitrogen
29 isotopes and opal mass accumulation rates from 0 to 1.2 Ma, we calculate a continuous high
30 resolution nutrient upwelling index for the Bering Sea and assess possible changes to regional CO_2
31 fluxes and to the relative control of sea ice, sea level and glacial North Pacific Intermediate Water
32 (GNPIW) on deep mixing and nutrient upwelling in the region. We find nutrient upwelling in the
33 Bering Sea correlates with global ice volume and air temperature throughout the study interval.
34 From ~ 1 Ma, and particularly during the 900 ka event, suppressed nutrient upwelling would have
35 lowered oceanic fluxes of CO_2 to the atmosphere supporting a reduction in global $p\text{CO}_2$ during the
36 MPT. This timing is consistent with a pronounced increase in sea ice during the early Pleistocene
37 and restriction of flow through the Bering Strait during glacials after ~ 900 ka, both of which would
38 have acted to suppress upwelling. We suggest that sea-level modulated GNPIW expansion during
39 glacials after 900 ka was the dominant control on subarctic Pacific upwelling strength during the
40 mid-late Pleistocene, while sea ice variability played a secondary role.

41 1. Introduction

42 The Mid-Pleistocene Transition (MPT) occurred between ~ 1.2 and 0.6 Ma when glacial-
43 interglacial cycles in global climate increased from a 41 kyr to a longer quasi-100 kyr periodicity
44 (McClymont et al., 2013). The MPT centres on a step-wise increase in benthic foraminiferal $\delta^{18}\text{O}$
45 at the “900 ka event” (~ 0.9 Ma), characterised by a dramatic increase in continental ice sheet
46 volume and resultant rapid declines in global sea level (~ 50 to 200 m) during post-MPT glacial
47 periods when 100 kyr cyclicity emerges (Lisiecki & Raymo, 2005; Elderfield et al., 2012) together
48 with changes in thermohaline circulation (Schmieder et al., 2000; Sexton & Barker, 2012).
49 Proposed mechanisms for MPT climate evolution include changing land ice-sheet dynamics (Clark
50 & Pollard, 1998; Raymo et al., 2006; Crowley & Hyde, 2008), either controlled by basal erosion
51 or continental ice-sheet instability following expansion of the Antarctic ice sheet (Clark et al.,
52 2006; Pollard & DeConto, 2009). Alternatively, the MPT may represent a tipping point in a long-
53 term decrease in atmospheric $p\text{CO}_2$ (Raymo, 1997; Hönlisch et al., 2009) and/or an alteration in
54 ocean-atmosphere CO_2 exchange (Pena & Goldstein, 2014), particularly from high latitude oceans
55 as a result of increased stratification and/or increased efficiency of the biological pump following
56 altered nutrient/dust supply (McClymont et al., 2008; Martinez-Garcia et al., 2010; Martínez-
57 Garcia et al., 2011; Rodríguez-Sanz et al., 2012; Chalk et al., 2017; Kender et al., 2018). Others
58 have suggested that a shift in the moisture balance and resultant relationship between northern
59 hemispheric sea ice and land ice formation (the “sea ice switch”) following deep ocean cooling
60 could also have been key (Gildor & Tziperman, 2001).

61
62 These hypotheses remain largely untested partly due to a lack of high resolution and long-term
63 palaeoenvironmental data. Despite increasing evidence for changing ocean/atmosphere interaction

64 in the high latitudes and atmospheric teleconnection with lower latitudes following ice-sheet
65 expansion in the mid-late Pleistocene (Marlow et al., 2000; Heslop et al., 2002; Liu & Herbert,
66 2004; McClymont & Rosell-Melé, 2005; McClymont et al., 2008; Sexton & Barker, 2012), it is
67 not clear whether these feedbacks were sufficient to control climate change and cause increased
68 ice volumes and/or decreased atmospheric $p\text{CO}_2$. Modelling and observational evidence is also
69 biased towards the Southern Ocean, a critical region for the growth of land and sea ice, deep water
70 formation and the upwelling of nutrient- and CO_2 -rich waters, fuelling an efficient but variable
71 biological pump that dominates atmospheric CO_2 variability over Quaternary glacial-interglacial
72 cycles (Billups et al., 2018).

73
74 Another key, but comparatively understudied location is the high latitude subarctic Pacific
75 Ocean and the Bering Sea, which is adjacent to the North American Ice Sheets (NAIS) and has
76 been influenced by sea ice since the onset of Northern Hemispheric glaciation (~ 2.6 Ma) (Teraishi
77 et al., 2016; Stroynowski et al., 2017). The Bering Sea, bounded to the north by the Bering Strait
78 which connects the Pacific and Arctic Oceans (Stabeno et al., 1999), is a region of
79 palaeoceanographic importance as nutrient- and carbon-rich North Pacific Deep Water (NPDW)
80 upwells at the Bering shelf. The upwelling and vertical mixing of NPDW, driven by eddies and
81 instabilities in the shelf-adjacent Bering Slope Current (BSC), results in seasonally high photic
82 zone $p\text{CO}_2$ and primary productivity along the Bering slope (Figure 1). Understanding the long-
83 term changes in subarctic Pacific upwelling, in addition to the Southern Ocean, is therefore
84 important to test the hypothesis that high latitude upwelling contributed to a change in atmospheric
85 CO_2 during the MPT.

86
87 Previous research from the Bering slope has shown a strong link between NPDW upwelling at
88 the shelf edge and global atmospheric $p\text{CO}_2$ in the mid-late Pleistocene (0 to 0.85 Ma), with
89 expanded sea ice suggested to modulate deep water upwelling and ocean-atmosphere CO_2
90 exchanges across the wider subarctic Pacific region (Kender et al., 2018; Worne et al., 2019). This
91 process is suggested to result from increased sea ice and restriction of flow through the Bering
92 Strait due to lower sea level during glacials, hereafter referred to as ‘closure of the Bering Strait’,
93 promoting the expansion of dense and macronutrient poor glacial North Pacific Intermediate Water
94 (NPIW) across the subarctic Pacific region. Today, NPIW is widely distributed across the North
95 Pacific Ocean at a water depth between $\sim 300 - 800$ m (Talley, 1993) and is characterised as a
96 salinity minima with a density centred at $26.8 \sigma_\theta$ (Yasuda, 1997). Although NPIW is currently
97 sourced primarily from the Okhotsk Sea, there is evidence that indicates the Bering Sea was a key
98 source of NPIW during past glacials (GNPIW) (Ohkushi et al., 2003; Horikawa et al., 2010) as a
99 result of enhanced brine rejection on the Beringian shelf, following increased sea ice growth since
100 ~ 0.9 Ma (Knudson & Ravelo, 2015b; Kender et al., 2018). Expansion of GNPIW during post-MPT
101 glacials would have prevented NPDW upwelling and causing region-wide isolation of CO_2 in deep
102 waters (Knudson & Ravelo, 2015b; Kender et al., 2018; Worne et al., 2019).

104 However, the short temporal resolution of these existing MPT records from the Bering Sea,
105 and the lack of similar datasets from the early Pleistocene, limit an assessment of the relationship
106 between global climate, atmospheric $p\text{CO}_2$ and subarctic nutrient upwelling, prior to significant
107 glacial sea level decline at 0.9 Ma when the Bering Strait first closed (Kender et al., 2018). Here,
108 we present the first continuous nutrient upwelling index (Worne et al., 2019) from the Bering Sea
109 slope from 1.2 Ma onwards . With this, we aim to determine the long-term evolution of nutrient
110 upwelling and its significance for the wider subarctic Pacific Ocean and the global atmospheric
111 $p\text{CO}_2$ changes hypothesised to control climate cooling during the MPT (Raymo, 1997; Hönisch et
112 al., 2009).

113 2. Materials and methods

114 2.1. Core materials

115 Sediment cores from IODP Site U1343 (57°33.39'N, 175°48.95'W, water depth 1,950 m) were
116 collected during IODP Expedition 323. Situated on a topographic high adjacent to the northern

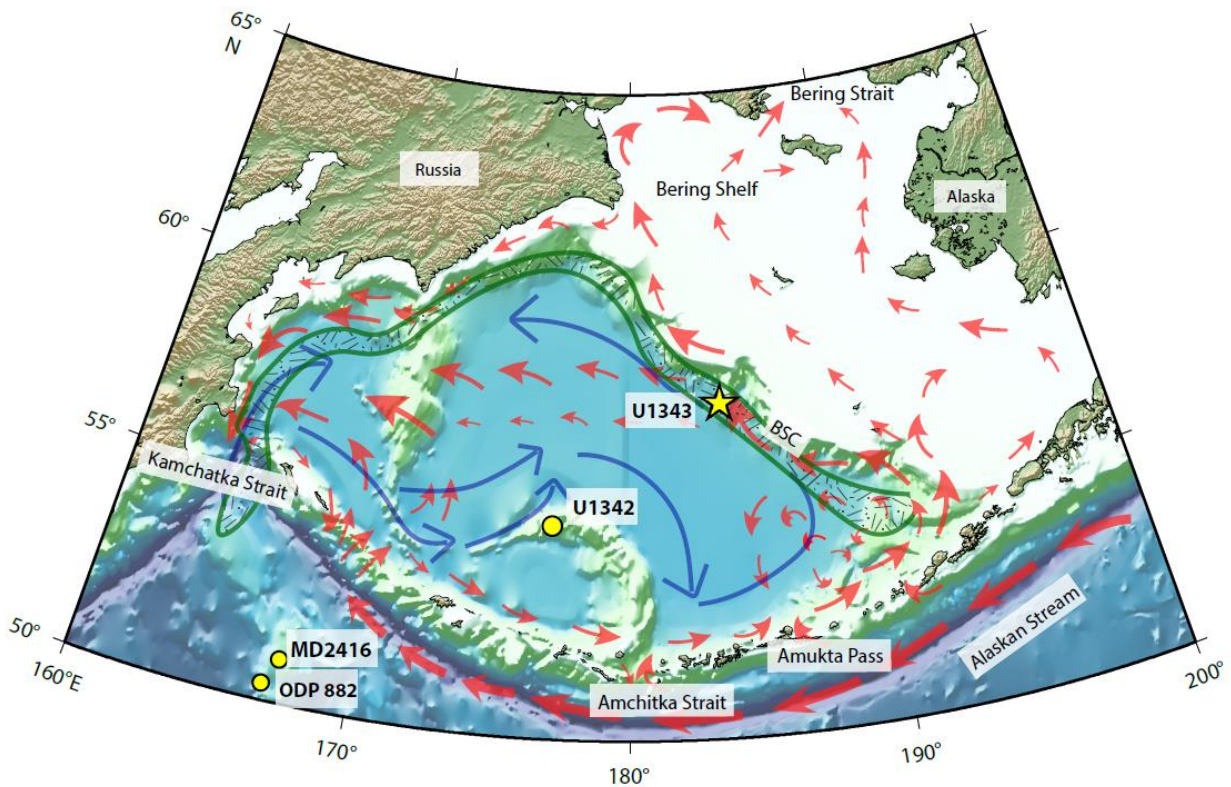


Figure 1 The geographical location and oceanography of the Bering Sea (adapted from Worne et al., (2019)). The white area represents the continental shelf region to the north and the blue represents the Bering Basin. Yellow dots indicate sites of previous important palaeoceanographic study through the Pleistocene including Site ODP 882 and MD2416 from the western subarctic Pacific and IODP Site U1342 from the Southern Bering Sea. Site U1343 (this study) is marked by a yellow star. Surface water circulation is marked by red arrows, which flow in from the Alaskan Stream and through various straits and passes in the Aleutian island arc. Surface water circulates in an anti-clockwise gyre, where turbulence and eddies in the shelf adjacent Bering Slope Current (BSC) causes a high productivity region known as the green belt, represented by the green patterned shape (Springer et al., 1996). Deep water circulation is marked by blue arrows, entering from the lower subarctic Pacific Ocean through the deep western Kamchatka Strait.

117 continental shelf, and proximal to the modern winter sea ice edge, IODP Site U1343 sits in the
118 high productivity green belt region, which is directly influenced by high eddy activity in the shelf-
119 adjacent BSC, which facilitates high rates of nutrient upwelling and stimulates primary
120 productivity (Figure 1). Shelf-slope exchange of upwelled nutrients provides an important source
121 for Bering shelf productivity, while a similar exchange of shelf-derived nutrients to the green belt,
122 particularly iron, may also have an important source for productivity at Site U1343 during periods
123 of low upwelling (Mizobata & Saitoh, 2004; Aguilar-Islas et al., 2007; Worne et al., 2019). Marine
124 sediments at Site U1343 are composed primarily of fine clays and biogenic material, and are
125 characteristically distinct from shelf-transported materials (Takahashi et al., 2011; Aiello &
126 Ravelo, 2012).

127

128 **2.2. Site U1343: updated age model (1.02 – 1.2 Ma)**

129 Good preservation of benthic foraminifera at Site U1343 has allowed construction of a high
130 resolution $\delta^{18}\text{O}$ age model from 0 to 0.85 Ma (1.1 kyr resolution; Worne et al., 2019) and from
131 0.85 to 1.02 Ma (0.22 kyr resolution; Kender et al., 2018). Here we present 48 new benthic $\delta^{18}\text{O}$
132 data points from 1.02 to 1.20 Ma (284.06 – 338.32 m CCSF-A), to extend the age model back to
133 1.2 Ma. Following previous studies at this site, $\sim 100\ \mu\text{g}$ of foraminiferal calcite from four species
134 (*Elphidium batialis*, *Globobulimina auriculata*, *Islandiella norcrossi* and *Uvigerina bifurcate*)
135 were measured for $\delta^{18}\text{O}$, applying species-specific offsets previously defined at Site U1343
136 (Kender et al., 2018) to fit the data to the most commonly occurring species, *E. batialis*. The $\delta^{18}\text{O}$
137 measurements were made using an IsoPrime 100 dual inlet mass spectrometer with a Multicarb
138 device at the National Environmental Isotope Facility, British Geological Survey. Results are
139 calculated relative to the VPDB scale using within-run laboratory standard (KCM, $\delta^{18}\text{O} = -1.73\text{‰}$)
140 that has been calibrated using the international reference material NBS 19 ($\delta^{18}\text{O} = -2.20\text{‰}$). The
141 KCM standard had an analytical reproducibility of $<0.05\text{‰}$ ($\pm 1\sigma$, $n = 94$). We combine all existing
142 records to produce a composite $\delta^{18}\text{O}$ record of 1,825 data points, with an average resolution of
143 0.65 kyr on an updated age model (Figure 2; Supplementary Table 1).

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145 **2.3. Bulk sedimentary $\delta^{15}\text{N}$**

146 Bulk sedimentary $\delta^{15}\text{N}$ was previously published for Site U1343 ($\delta^{15}\text{N}_{\text{U1343}}$) between 0 to 0.85
147 Ma (Kim et al., 2017; Worne et al., 2019) and 0.85 to 1.02 Ma (Kender et al., 2018). Here we
148 present 62 new bulk sediment $\delta^{15}\text{N}_{\text{U1343}}$ data points between 1.02 to 1.20 Ma (284.06 – 338.32 m
149 CCSF-A). These were measured using 50 mg of raw material on a Carlo Erba 1108 elemental
150 analyzer, interfaced to a Thermo Finnigan Delta Plus XP IRMS at the University of California,
151 Santa Cruz, with a precision of 0.15‰ based on duplicates. Stable isotope data were calibrated
152 using Pugel standard (mean $\delta^{15}\text{N} = +5.48\text{‰}$, $\sigma = 0.16$), with additional in-house long term quality
153 controlled through comparison with sediments from IODP Site U1342 in the southern Bering Sea

154 (mean $\delta^{15}\text{N} = +2.89\text{‰}$, $\sigma = 0.19$). We combine all existing records to produce a composite $\delta^{15}\text{N}_{\text{U1343}}$
155 record of 623 data points, with an average resolution of 1.9 kyr on the updated age model.

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157 **2.4. Nutrient upwelling index**

158 The bulk $\delta^{15}\text{N}_{\text{U1343}}$ record in the Bering Sea has been suggested to be influenced by a
159 denitrification signal which propagates from the Eastern Tropical North Pacific (ETNP) (Brunelle
160 et al., 2007). Therefore, we follow previous work (Galbraith et al., 2008; Knudson & Ravelo,
161 2015a; Worne et al., 2019) subtracting North Pacific Ocean $\delta^{15}\text{N}$ records from ODP Site 1012 in
162 the eastern tropical North Pacific Ocean ($\delta^{15}\text{N}_{1012}$), thought to be a site of complete nutrient
163 utilisation as well as being influenced by waters originating from the ETNP denitrification zone
164 (Liu et al., 2005; Galbraith et al., 2008). By constraining for background changes in source water
165 ($\delta^{15}\text{N}_{1012}$), the resultant isotope record ($\delta^{15}\text{N}_{\text{U1343-1012}}$) predominantly reflects changes in nutrient
166 utilisation at the Bering slope (Worne et al., 2019).

167

168 As nutrient utilisation is a product of both the total nutrient supply (predominantly from
169 upwelling along the slope) and biogenic productivity, the opal MAR records from Site U1343
170 (Kim et al., 2014) can be used to further constrain the $\delta^{15}\text{N}_{\text{U1343-1012}}$ record, following the
171 methodology of Worne et al., (2019) in which the opal MAR and $\Delta\delta^{15}\text{N}_{\text{U1343-1012}}$ are normalised:

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$$173 \quad \text{Nutrient Upwelling Index} = \text{Normalised Opal MAR} - \text{Normalised } \Delta\delta^{15}\text{N}_{\text{U1343-1012}} \quad (1)$$

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175 The resultant calculation is termed the nutrient upwelling index (Eq. 1), in which we
176 assume that the upwelling of NPDW was the dominant supply of macronutrients to surface waters
177 at Site U1343, and that rates of nutrient utilisation are controlled by both upwelling strength and
178 the delivery of iron (Fe) from sea ice entrained sources (in addition to contributions from deep
179 water and potential inputs from volcanic sources). Given that the green belt is iron limited
180 (Aguilar-Islas et al., 2007; Takeda, 2011), under a constant rate of nutrient upwelling Fe supply
181 will increase both productivity and nutrient utilisation and will therefore not change the nutrient
182 upwelling index significantly (Worne et al., 2019). Therefore, the resultant “nutrient upwelling
183 index”, is a semi-quantitative measure of nutrient supply, where low (high) values suggest a
184 decrease (increase) in NPDW upwelling strength at the Bering slope.

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186 **3. Results**

187 **3.1. Age model**

188 The extended Site U1343 benthic foraminiferal $\delta^{18}\text{O}_{\text{U1343}}$ record contains 1,825 data points
189 with a mean time step of 0.65 kyr between 0 and 1.2 Ma. The age model was defined by correlating
190 to the LR04 global composite stack (Lisiecki & Raymo, 2005), choosing 30 age-depth tie points
191 at periods of rapid isotopic change (e.g. deglacials) (Figure 2, Supplementary Table 1). Poor linear

192 regression between foraminiferal $\delta^{13}\text{C}$ and raw $\delta^{18}\text{O}$ ($r = 0.43$, $p < 0.01$) shows that diagenetic
193 alteration of foraminiferal shells does not explain the glacial-interglacial variability in the benthic
194 foraminiferal $\delta^{18}\text{O}$ isotope data at Site U1343 (Asahi et al., 2016; Kender et al., 2018; Worne et
195 al., 2019; Detlef et al., 2020).

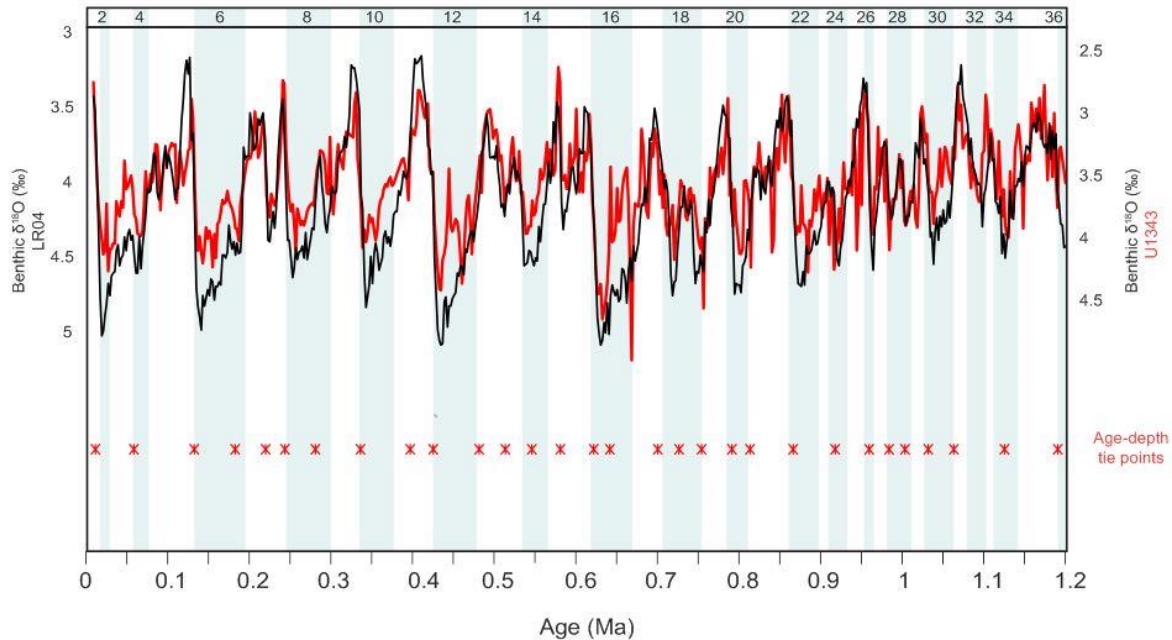


Figure 2 Age Model for Site U1343 from MIS 2 to 36. Benthic foraminiferal $\delta^{18}\text{O}$ results from IODP Site U1343 (red) compared to the LR04 global benthic $\delta^{18}\text{O}$ stack (black) (Lisiecki & Raymo, 2005), with blue bars represent glacial periods. Age-depth tie points used to tune the age model for Site U1343 with the LR04 stack are shown as red crosses (Supplementary Table 1).

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3.2. $\delta^{15}\text{N}_{\text{U1343}}$ and the nutrient upwelling index

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Pre-MPT $\delta^{15}\text{N}_{\text{U1343}}$ results show a higher mean (1.02 to 1.20 Ma; mean = +6.6‰) than during the 900 ka event (~0.85 to 0.95 Ma; mean = +6.0‰) or post-MPT (0 to 0.85 Ma; mean = +5.6‰) (Figure 3A). This is consistent with higher opal MAR during this period, where increased productivity caused a larger proportion of the $\delta^{15}\text{N}$ inferred nutrient pool to be used. The exception to this occurs during MIS 34 when opal MAR is low and $\delta^{15}\text{N}_{\text{U1343}}$ is high, leading to low upwelling index values. Low opal MAR during this glacial is unlikely to be a result of opal dissolution, as silica diagenesis is not prevalent in the cores at Site U1343 (Takahashi et al., 2011), confirmed by good preservation of diatoms down-core (Teraishi et al., 2016). Therefore, low upwelling index results at MIS 34 are most likely the result of increased sea ice and a highly fluctuating sea ice margin during the build up to MPT conditions (Detlef et al., 2018) (see Section 4.2).

There is also glacial-interglacial variability in $\delta^{15}\text{N}_{\text{U1343}}$ with glacials exhibiting significantly lower nutrient utilisation (mean = +5.7‰) than interglacial periods (mean = +5.9‰, $p < 0.05$), co-occurring with higher productivity during warmer periods (Figure 3A). The exception to this occurs at the MIS 31/32 boundary (~1.06 Ma) when nutrient utilisation is notably low, although

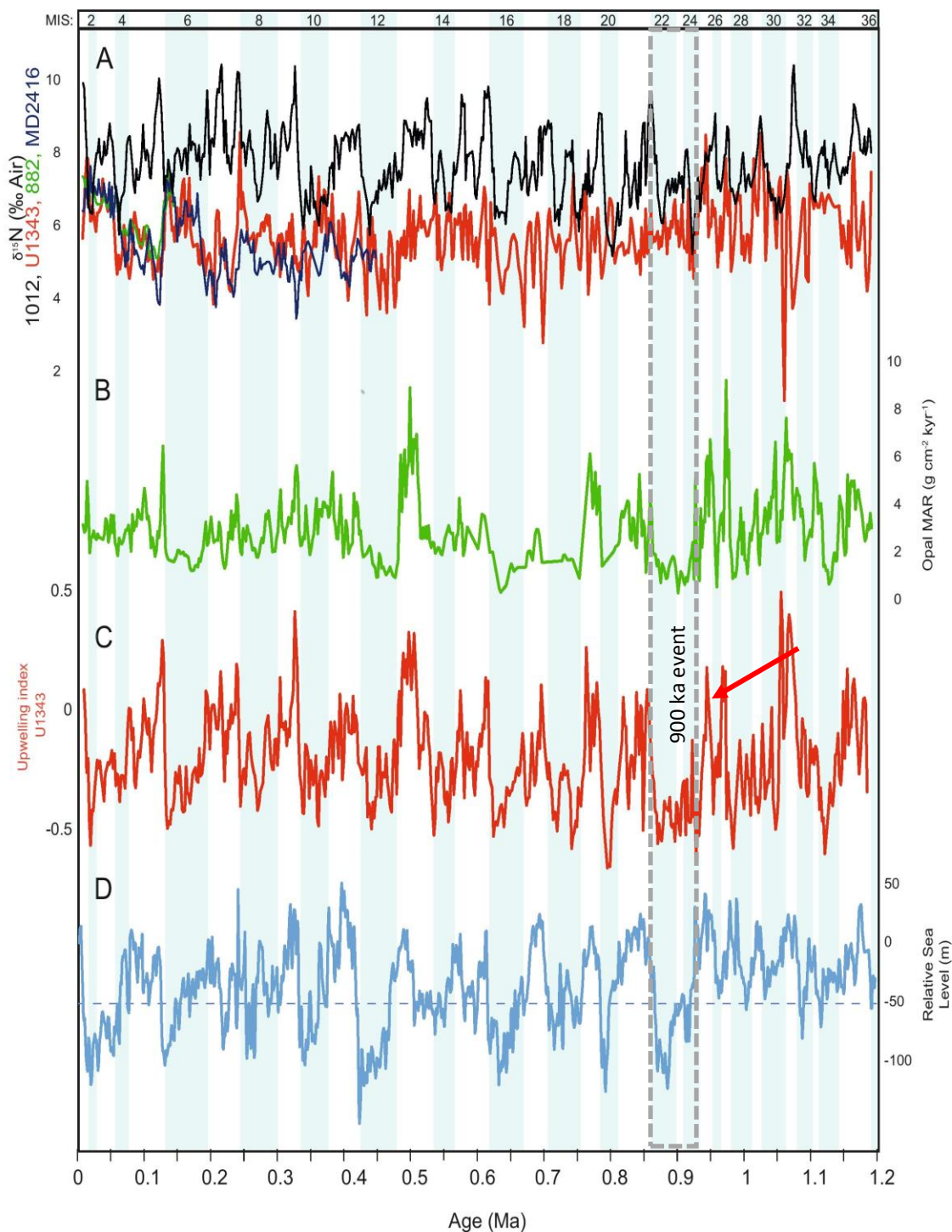


Figure 3 Geochemical proxy results from IODP Site U1343 from MIS 2 to 36. A) Bulk $\delta^{15}\text{N}$ data from IODP Site U1343 compared with deep North Pacific ODP Site 1012 (a site of complete nutrient utilisation) (black) together with records from ODP Site 882 (green) and MD2416 (navy blue) in the subarctic Pacific Ocean. B) Opal mass accumulation rate (MAR) from IODP Site U1343 (Kim et al., 2014). C) Upwelling index between 0 – 1.2 Ma (red) are compared to D) relative sea level estimates from Elderfield et al., (2012), where the dashed line represents a 50 m sea level decline, below which the Bering Strait was likely closed. Blue shaded bars represent glacial periods as defined by the LR04 benthic stack (Lisiecki & Raymo, 2005), with a grey dashed line to represent the 900 ka event.

213 there is no notable change in lithology or biogenic composition of the sediment (Takahashi et al.,
214 2011).

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216 From MIS 33 (~1.12 Ma) the nutrient upwelling index shows a gradual increase, reaching a
217 peak in early glacial MIS 30 (~1.05 Ma), where productivity is high and nutrient utilisation is
218 minimal (Figure 3C). Between MIS 30 and MIS 28 (~1.05 to 0.98 Ma), results show a sharp and
219 continued decrease in nutrient upwelling as colder MPT conditions develop (global composite
220 benthic $\delta^{18}\text{O}$, Figure 2), with interglacial upwelling remaining low during MIS 29 (~1.02 Ma).
221 Despite a recovery in nutrient upwelling strength through MIS 27 – 25 (~0.97 to 0.93 Ma),
222 particularly in interglacials where both productivity (opal MAR) and the rate of nutrient utilisation
223 ($\delta^{15}\text{N}_{\text{U1343}}$) are notably high, a rapid decline in the upwelling index occurs during MIS 24 (~0.91
224 Ma) where productivity is minimal (Figure 3A-C). During the 900 ka event, there is a continued
225 minima in nutrient upwelling index values, particularly through MIS 23 and early MIS 22 (~0.86
226 to 0.91). At the end of glacial MIS 22 there is a gradual increase in nutrient upwelling strength and
227 recovering productivity towards the deglacial peak. From MIS 21 (~0.85 Ma) onwards, nutrient
228 upwelling exhibits strong glacial-interglacial variability, with low upwelling during glacials and
229 high upwelling during interglacials (Worne et al., 2019).

230

231 Although $\delta^{15}\text{N}_{\text{U1343}}$ excursions may also be a result of variable inorganic or terrestrial input,
232 a lack of glacial-interglacial covariation between $\delta^{15}\text{N}_{\text{U1343}}$ and C/N suggests inorganic nitrogen
233 input does not have an overriding control on $\delta^{15}\text{N}_{\text{U1343}}$ (Kim et al., 2017; Worne et al., 2019).
234 Furthermore, low $\delta^{15}\text{N}$ values measured at more distal open ocean subarctic Pacific sites, e.g. Site
235 MD2416, ODP Site 882 (Figure 1) and ODP Site 887, together with diatom-bound $\delta^{15}\text{N}$ values of
236 less than 5‰ at IODP Site U1343 (Kim & Khim, 2016), provides confidence that nutrient
237 utilisation changes rather than terrestrial/inorganic nitrogen input, is the most significant control
238 on Quaternary glacial-interglacial $\delta^{15}\text{N}_{\text{U1343}}$ variability.

239

240 4. Discussion

241 4.1. Nutrient upwelling and glacial-interglacial CO_2 (0.85 – 1.20 Ma)

242 The upwelling index from 0 – 0.85 Ma has been previously shown to correlate with a number
243 of proxy and modelled climate records (Worne et al., 2019), including the LR04 deep ocean $\delta^{18}\text{O}$
244 record (Lisiecki & Raymo, 2005), relative sea level changes (Elderfield et al., 2012), global surface
245 ocean temperatures (Snyder, 2016) and Antarctic air temperatures (Jouzel et al., 2007). In
246 particular, a strong correlation with global benthic $\delta^{18}\text{O}$ and $p\text{CO}_2$ (Lüthi et al., 2008) ($r = 0.60$, p
247 < 0.001), was suggested to indicate a common underlying mechanism between NPDW upwelling
248 in the Bering Sea and global climate changes (Worne et al., 2019). Over the extended 0 – 1.2 Ma
249 interval presented here, a strong correlation is maintained between the upwelling index and relative
250 sea level ($r = -0.49$, $p < 0.001$), surface air temperatures ($r = 0.58$, $p < 0.001$), and particularly the
251 LR04 stack ($r = -0.66$, $p < 0.001$). This is consistent with the hypothesis that subarctic Pacific
252 upwelling was integral to the climate system during the MPT (Kender et al., 2018). Although the

253 age model for the upwelling index was tuned to the LR04 stack, the high resolution of the dataset
254 (2 kyr) and the limited number of tie points used (30; Figure 2, Supplementary Table 1), suggests
255 that the relationship between global ice volume, surface ocean temperature and Bering Sea nutrient
256 upwelling is not an age-model artefact.

257
258 Given the link between upwelling subarctic Pacific Ocean deep water and deglacial
259 atmospheric CO₂ ventilation for the last deglaciation (Rae et al., 2014; Gray et al., 2018),
260 hypotheses that invoke a reduction in atmospheric *p*CO₂ to drive cooling during the MPT (Raymo,
261 1997; Hönlisch et al., 2009) can be partially tested by examining the evolution of subarctic Pacific
262 upwelling in the build up to the MPT. The upwelling index at Site U1343 shows a long-term glacial
263 fall from ~1.1 to 0.9 Ma (arrow in Figure 3C), which is in line with the hypothesis that the supply
264 of subarctic Pacific CO₂ ventilation to the atmosphere decreased during this interval (Kender et al.
265 2018), and is consistent with CO₂ acting as a driver of MPT climate. While there is no continuous
266 *p*CO₂ proxy record through the MPT for direct comparison, δ¹¹B inferred *p*CO₂ reconstruction
267 from ODP Site 990 in the Caribbean Sea (Chalk et al., 2017) and ODP Site 668B in the eastern
268 equatorial Atlantic (Hönlisch et al., 2009), are not inconsistent with the upwelling index during the
269 early Pleistocene (Figure 4B), with higher nutrient upwelling and *p*CO₂ occurring during warmer
270 interglacial periods. Despite an offset between *p*CO₂ and nutrient upwelling minima in MIS 34,
271 the subsequent increase in *p*CO₂ is consistent with increasing nutrient upwelling. Further support
272 for the correlation between nutrient upwelling in the Bering Sea and global *p*CO₂ is found in the
273 predicted *p*CO₂ record from the CYCLOPS carbon cycle model (Chalk et al., 2017) (Figure 4C).
274 The only sustained discrepancy between the two datasets appears during the 900 ka event, when
275 nutrient upwelling remains lower than predicted CYCLOPS *p*CO₂, particularly during late MIS 22
276 (Figure 4C), coincident with a sustained global sea level drop of >50 m (Elderfield et al., 2012;
277 Kender et al., 2018) (Figure 3D). However, as *p*CO₂ records do not exist in high resolution over
278 the MPT, there is a need for more CO₂ proxy data to confirm the nutrient upwelling link with
279 atmospheric *p*CO₂ at that time.

280

281 **4.2. Long-term sea ice controls on Bering Sea nutrient upwelling**

282 Our record demonstrate a consistent relationship between Bering Sea nutrient upwelling and
283 global climate (LR04 benthic stack), with reduced subarctic Pacific upwelling coincident with
284 falling atmospheric CO₂ which has been suggested to have caused MPT cooling (Raymo, 1997;
285 Hönlisch et al., 2009; Pena & Goldstein, 2014) and/or an alteration in ocean-atmosphere CO₂
286 exchange. Although this correlation does not prove that reduced subarctic Pacific upwelling caused
287 the MPT, it does support a common mechanism which links subarctic high latitude upwelling with
288 atmospheric *p*CO₂, which subsequently would have contributed to global climate changes through
289 the MPT (Kender et al., 2018; Worne et al., 2019). Previous studies have proposed expansion of
290 GNPIW across the subarctic Pacific as the linking mechanism to suppress upwelling and regional
291 CO₂ leakage to the atmosphere (Kender et al., 2018; Worne et al., 2019). However, during MIS
292 34, notably low upwelling index values occur prior to 0.9 Ma and are concurrent with higher glacial

293 sea levels (Figure 3C-D) which would not have restricted Bering Strait flow (and hence prevented
294 GNPIW formation). This short-lived period of low productivity and high nutrient utilisation while
295 the Bering Strait was likely open, suggests there was an additional control on nutrient upwelling
296 prior to the 900 ka event, in addition to or instead of GNPIW formation.

297 Glacial-interglacial variability in Bering Sea upwelling index after 0.9 Ma is also suggested
298 to be influenced by sea ice as a secondary control (Worne et al., 2019). Seasonal sea ice cycling
299 plays an active role in controlling total annual primary production (opal MAR) through stabilising
300 the water column and supplying micronutrients, which in turn facilitates a spring melt associated
301 bloom (Aguilar-Islas et al., 2008; Kanematsu et al., 2013). The size of the subsequent
302 summer/autumn bloom is then highly dependent on the degree of post-melt stratification and the
303 availability of remaining nutrients after drawdown in the spring (Hansell et al., 1989), which in
304 turn influences the annual rate of nutrient utilisation ($\delta^{15}\text{N}_{\text{U1343}}$) (Kender et al., 2018; Worne et al.,
305 2019). Diatom evidence from the Bering slope indicates that sea ice began to expand through both
306 glacials and interglacials from at least ~1 Ma (Teraishi et al., 2016; Stroynowski et al., 2017; Detlef
307 et al., 2018), when sea ice seasons became more prominent in the build up to the 900 ka event.
308 Therefore, we suggest that increased seasonal sea ice and greater fluctuations in the location and
309 duration of sea ice margin caused higher frequency variability in nutrient upwelling strength and
310 acted as the dominant control on the upwelling index at the Bering slope prior to the 900 ka event.
311 This is in contrast to conditions after 0.9 Ma, when closure of the Bering Strait and increased sea
312 ice during the 900 ka event caused formation of GNPIW, which became the dominant control on
313 nutrient upwelling. Higher resolution sea ice reconstruction work is required to fully resolve the
314 relationship between deep water upwelling and sea ice dynamics in the early and middle
315 Pleistocene.

316 **4.3. Long-term sea level and GNPIW control on regional subarctic Pacific Ocean** 317 **upwelling**

318 Although sea ice dynamics were likely important for determining primary productivity and
319 nutrient utilisation rates at the Bering slope in the build up to the 900 ka event, this does not
320 preclude the hypothesis that GNPIW had a dominant influence on nutrient upwelling during and/or
321 after the MPT in the subarctic Pacific. For example, Knudson & Ravelo, (2015b) find evidence for
322 GNPIW in the southern Bering Sea (Site U1342; Figure 1) back to at least 1.2 Ma. During the 900
323 ka event, when significant land ice accumulated, sea level declined by more than 50 m and caused
324 probable closure of the Bering Strait (Elderfield et al., 2012; Kender et al., 2018). Diatom evidence
325 also suggests that a prolonged pack ice cover occurred during this peak MPT period (Teraishi et
326 al., 2016; Stroynowski et al., 2017). The coincidence of persistent sea ice cover and Bering Strait
327 closure with suppression of nutrient upwelling through MIS 23 up to the end of MIS 22, supports
328 the idea that GNPIW expansion and enhanced stratification resulted in reduced vertical mixing of
329 nutrient-rich waters across the region (Kender et al., 2018). Therefore, the upwelling index
330 supports the notion that retention of CO_2 in the deep subarctic Pacific, potentially together with
331 changes in the Southern Ocean (Sigman et al., 2010), was an important mechanism in sustaining

332 low subarctic Pacific upwelling, and reducing regional leakage of CO₂ to the atmosphere during
333 the MPT which ultimately promoted longer glacial periods and larger glacial ice sheets due to its
334 cooling effect (Kender et al., 2018).
335

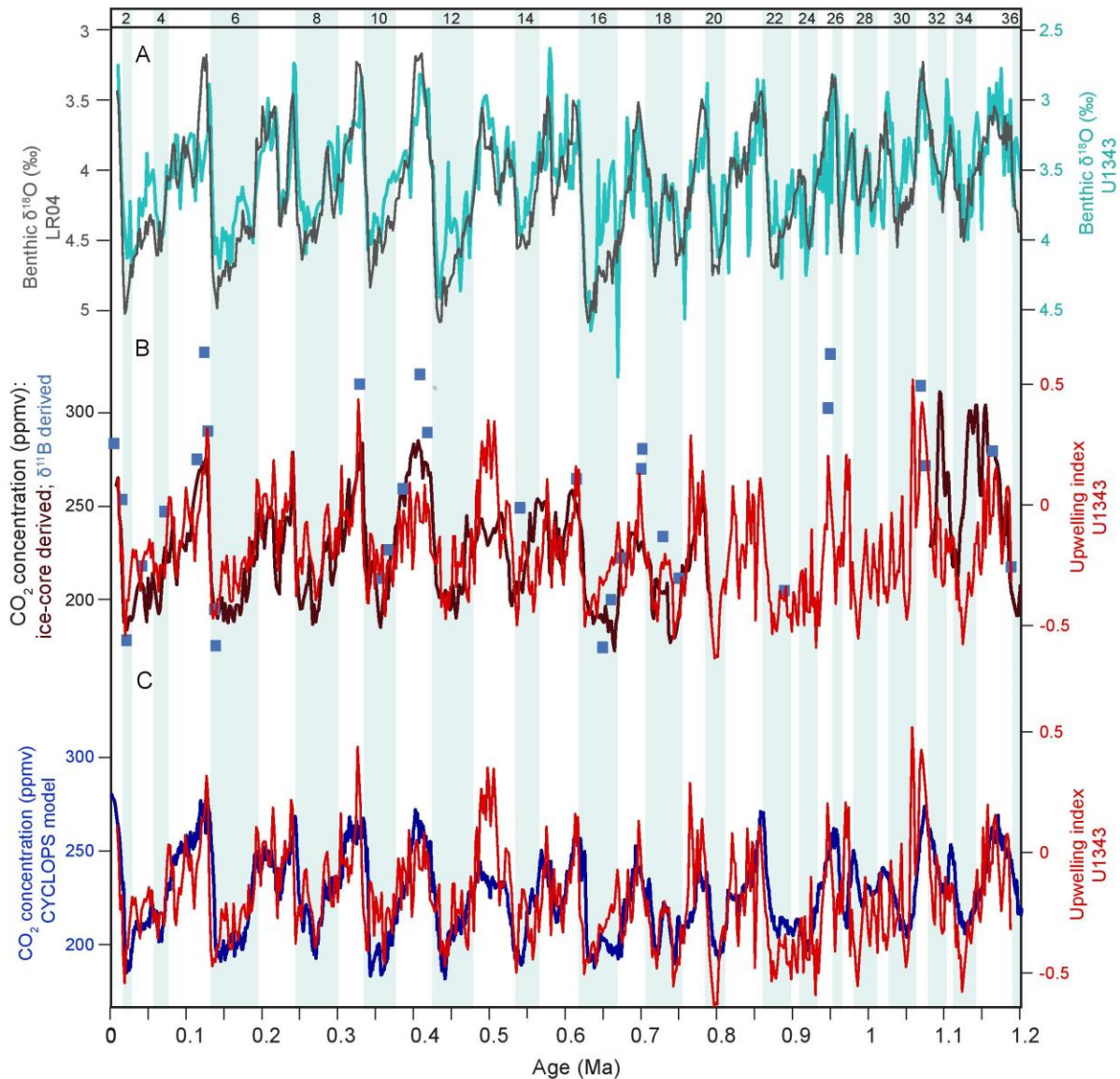


Figure 4 Upwelling index dataset for Site U1343 compared to global climate and pCO₂ reconstructions. A) Benthic foraminifera δ¹⁸O from Site U1343 (red) and the LR04 benthic stack (black). b) Upwelling index between 0 to 1.2 Ma (red) are compared to pCO₂ (black) from the Vostok ice core between 0 to 0.8 Ma (Lüthi et al., 2008), and δ¹¹B between ~1.07 to 1.2 Ma (Chalk et al., 2017). Low resolution boron isotope-derived pCO₂ estimates from Hönisch et al. (2009) are also displayed as light blue squares. C) Comparison of the Bering Sea upwelling index results (red) with modelled atmospheric CO₂ concentrations (dark blue) (Chalk et al., 2017).

336 After the 900 ka event, strong glacial-interglacial variability in the nutrient upwelling index
337 developed, which has been interpreted to reflect continued control of glacially enhanced sea ice
338 and GNPIW formation on nutrient upwelling in the Bering Sea, causing both a reduced

339 summer/autumn bloom season and acting as a physical barrier to deep water upwelling at the
340 Bering Sea slope (Worne et al., 2019). The establishment of clear glacial-interglacial variability in
341 nutrient utilisation ($\delta^{15}\text{N}_{\text{U1343}}$), despite reduced magnitude of opal MAR variability, indicates that
342 the size of the nutrient pool varied, at least partially, independently from primary productivity (and
343 hence seasonality of the sea ice margin) (Figure 3). Indeed, Worne et al., (2019) noted that the
344 correlation between nutrient upwelling and global $p\text{CO}_2$ was particularly strong over the last 0.35
345 Ma. Therefore, we propose that the expansion of GNPIW (reducing the size of the subsurface
346 nutrient pool) would have continued to act as the first-order control on nutrient upwelling after the
347 MPT (Worne et al., 2019), following trends in global climate and $p\text{CO}_2$.

348

349 **5. Conclusions**

350 In summary, we find reduced subarctic nutrient upwelling over the MPT, which would have
351 acted to lower atmospheric $p\text{CO}_2$. We hypothesise that this contributed to global cooling before
352 and during the 900 ka event, possibly alongside changes in other upwelling regions such as the
353 Southern Ocean, by reducing CO_2 . However, existing $p\text{CO}_2$ estimates are of too low resolution to
354 resolve if lower levels coincided with the MPT. During the early Pleistocene, evidence exists for
355 increased Bering Sea sea ice extent, but a highly fluctuating sea ice margin between MIS 28 and
356 24 can account for the high frequency variability in nutrient upwelling found in our records. During
357 the 900 ka event, where our nutrient upwelling index is at its lowest for the whole record (0 to 1.2
358 Ma), accumulation of continental ice sheets and severe sea level decline may have facilitated thick
359 pack ice cover in the Bering Sea. When combined with a closure of the Bering Strait, this likely
360 caused an expansion of a strong GNPIW, layer which suppressed nutrient upwelling at the Bering
361 Slope. Southward propagation of this GNPIW, and reduced regional-scale vertical mixing/deep
362 water ventilation in the subarctic Pacific Ocean, could then have potentially contributed to lower
363 global $p\text{CO}_2$ and ultimately a failure of the interglacial at MIS 23 to result in a full deglacial
364 (Kender et al., 2018)(Kender et al., 2018)(Kender et al., 2018).

365

366 After the 900 ka event, glacial-interglacial coupling in the nutrient upwelling index and climate
367 proxies supports the hypothesis that nutrient upwelling strength in the Bering Sea was controlled
368 by GNPIW formation, modulated by ice sheet growth/sea level decline which followed(Kender et
369 al., 2018) quasi-100 kyr glacial cycles. Given that sea ice volumes remained higher during both
370 glacials and interglacials after the MPT, variability in sea ice seasonality is still considered to have
371 played a role in our upwelling nutrient record. However, continued closure of the Bering Strait in
372 post-MPT glacials may have promoted GNPIW as the dominant mechanism for suppressing
373 nutrient upwelling, causing more prominent glacial-interglacial variability in the nutrient
374 upwelling record. Further model and high resolution CO_2 proxy reconstruction work is needed to
375 better quantify the role of NPIW expansion on the “saw-tooth” shape of post-MPT glacial cycles,
376 as well as the significance of regional changes on global ocean-atmosphere CO_2 exchanges.

377

378 Overall, we surmise that MPT sea ice dynamics controlled nutrient upwelling strength in
379 the Bering Sea and subarctic Pacific via two mechanisms: primarily through GNPIW expansion
380 following sea-level modulated Bering Strait closure from ~ 0.9 Ma, which acted to suppress
381 regional upwelling during glacials as expressed in the LR04 global $\delta^{18}\text{O}$ stack. We also posit that
382 sea ice played a secondary role on the upwelling index through controlling seasonal primary
383 productivity and nutrient utilisation at the Bering slope, which caused higher frequency variability
384 in nutrient upwelling, particularly during sea ice expansion leading up to the 900 ka event.
385

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399 www.pangaea.de, or may be requested from the authors.

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Supplementary Information

Supplementary Table 1 New age-depth tie points for Site U1343, building on Worne et al. (2019).

Depth (CCSF – A) (m)	Age (ka)
0.96	10.15
14.23	57.38
36.72	131.41
48.03	181.46
59.73	219.06
68.72	242.57
79.52	279.96
96.24	335.14
114.56	396.17
119.35	424.39
129.90	480.93
145.02	512.78
152.01	545.32
161.63	580.48
173.39	621.39
174.57	641.03
184.09	700.03
188.27	725.84
191.58	753.63
203.57	790.75
209.04	812.86
227.39	865.95
238.34	917.46
254.16	959.01
266.14	983.50
272.57	1002.99
282.73	1031.59
296.57	1062.96
318.81	1124.99
336.91	1190.47

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