

Lower oceanic $\delta^{13}\text{C}$ during the Last Interglacial Period compared to the Holocene

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Abstract.

The last time in Earth's history when high latitudes were warmer than during pre-industrial times was the last interglacial period (LIG, 129–116 ka BP). Since the LIG is the most recent and best documented interglacial, it can provide insights into climate processes in a warmer world. However, some key features of the LIG are not well constrained, notably the oceanic circulation and the global carbon cycle. Here, we use a new database of LIG benthic $\delta^{13}\text{C}$ to investigate these two aspects. We find that the oceanic mean $\delta^{13}\text{C}$ was $\sim 0.2\text{‰}$ lower during the LIG (here defined as 125–120 ka BP) when compared to the Holocene (7–2 ka BP). A lower terrestrial carbon content at the LIG than during the Holocene could have led to both a lower oceanic $\delta^{13}\text{C}$ and atmospheric $\delta^{13}\text{C}\text{CO}_2$ as observed in paleo-records. However, given the multi-millennial timescale, the lower oceanic $\delta^{13}\text{C}$ most likely reflects a long-term imbalance between weathering and burial of carbon. The $\delta^{13}\text{C}$ distribution in the Atlantic Ocean suggests no significant difference in the latitudinal and depth extent of North Atlantic Deep Water (NADW) between the LIG and the Holocene. Furthermore, the data suggests that the multi-millennial mean NADW transport was similar between these two time periods.

1 Introduction

The most recent and well documented warm time period is the last interglacial period (LIG), which is roughly equivalent to Marine Isotope Stage (MIS) 5e (of PAGES, 2016; Shackleton, 1969). The LIG began at the end of the penultimate deglaciation and ended with the last glacial inception (~ 129 – 116 thousand years before present, ka BP hereafter (Dutton and Lambeck, 2012; Govin et al., 2015; Masson-Delmotte et al., 2013; Menviel et al., 2019)). The LIG was globally warmer than pre-industrial (PI, ~ 1850 – 1900 (IPCC, 2013), Shackleton et al. (2020)), with PI estimated to be $\sim 0.4\text{°C}$ cooler than the peak of the Holocene (10–5 ka BP) (Marcott et al., 2013). Though not an exact analogue for future warming, the LIG may still help shed light on future climates. In particular, we seek to constrain the mean LIG ocean circulation and estimate the global oceanic mean $\delta^{13}\text{C}$.

As greenhouse gas concentrations were comparable to the Holocene, the LIG was most likely relatively warm because of the high boreal summer insolation (Laskar et al., 2004). During the LIG, the atmospheric CO₂ concentration was relatively stable around ~280 p.p.m. (Bereiter et al., 2015; Lüthi et al., 2008), while during the Holocene, CO₂ first decreased by about 8 p.p.m. starting at 11.7 ka BP before increasing by ~17 p.p.m. to 277 p.p.m. at ~2 ka BP (Fig. 1a) (Köhler et al., 2017). CH₄ and N₂O peaked at ~700 p.p.b and ~267 p.p.b, respectively, during both the LIG and the Holocene (Flückiger et al., 2002; Petit et al., 1999; Spahni et al., 2005). Global sea-level was 6–9 m higher at the LIG compared to PI (Dutton et al., 2015; Kopp et al., 2009), thus indicating significant ice-mass loss from both Antarctica and Greenland.

Strong polar warming is supported by terrestrial and marine temperature reconstructions. A global analysis of sea surface temperature (SST) records suggests that the mean surface ocean was 0.5 ± 0.3 °C warmer during the LIG compared to 1870–1889 (Hoffman et al., 2017), similar to another global estimate which suggests SSTs were 0.7 ± 0.6 °C higher during the LIG compared to the late Holocene (McKay et al., 2011). However, there were differences in the timing of these SST peaks in different regions compared to the 1870–1889 mean: North Atlantic SSTs peaked at $+0.6 \pm 0.5$ °C at 125 ka BP (e.g. Fig. 1b) and Southern Hemisphere extratropical SSTs peaked at $+1.1 \pm 0.5$ °C at 129 ka BP (Hoffman et al., 2017). On land, proxy records from mid to high latitudes indicate higher temperatures during the LIG compared to PI, particularly in North America (Anderson et al., 2014; Axford et al., 2011; Montero-Serrano et al., 2011). Similarly, the EPICA DOME C record suggests that the highest Antarctic temperatures from the last 800 ka occurred during the LIG (Masson-Delmotte et al., 2010) (Fig. 1c).

Polar warming was also associated with significant changes in vegetation. Pollen records suggest a contraction of tundra and an expansion of boreal forests across the Arctic (CAPE, 2006), in Russia (Tarasov et al., 2005), and in North America (Govin et al., 2015; Muhs et al., 2001; de Vernal and Hillaire-Marcel, 2008). The few Saharan records suggest a green Sahara period during the LIG (Drake et al., 2011; Larrasoana et al., 2013), consistent with a stronger West African monsoon (Otto-Bliesner et al., 2020). Although these reconstructions indicate changes in vegetation distribution during the LIG, the total amount of carbon stored on land remains poorly constrained.

Recent numerical experiments of the LIG as part of the Paleomodel Intercomparison Project Phase 4 (PMIP4) simulate significant warming over Alaska and Siberia in boreal summer, with mean annual temperature anomalies of close to zero, which is in good agreement with the proxy record (Otto-Bliesner et al., 2020). Despite this and other recent data compilations and modelling efforts (including Bakker et al. (2013)), there are many open questions remaining about the LIG. In particular, stronger constraints are needed on the extent of Greenland and Antarctic ice sheets, on ocean circulation and the global carbon cycle, including CaCO₃ accumulation in shallow waters, and peat and permafrost carbon storage (Brovkin et al., 2016).

It is important to constrain the state of the Atlantic Meridional Overturning Circulation (AMOC) at the LIG given its significant role in modulating climate. Seven coupled climate models integrated with transient 130–115 ka BP boundary conditions simulate different AMOC trends, with some models producing a strengthening of the AMOC while others simulate a weakening during the LIG (Bakker et al., 2013). Paleoproxy records suggest equally strong and deep North Atlantic Deep Water (NADW) during the LIG and the Holocene (e.g. Böhm et al., 2015; Lototskaya and Ganssen, 1999), with a possible southward expansion of the Arctic front related to changes in the strength of the subpolar gyre (Mokeddem et al., 2014), and AMOC

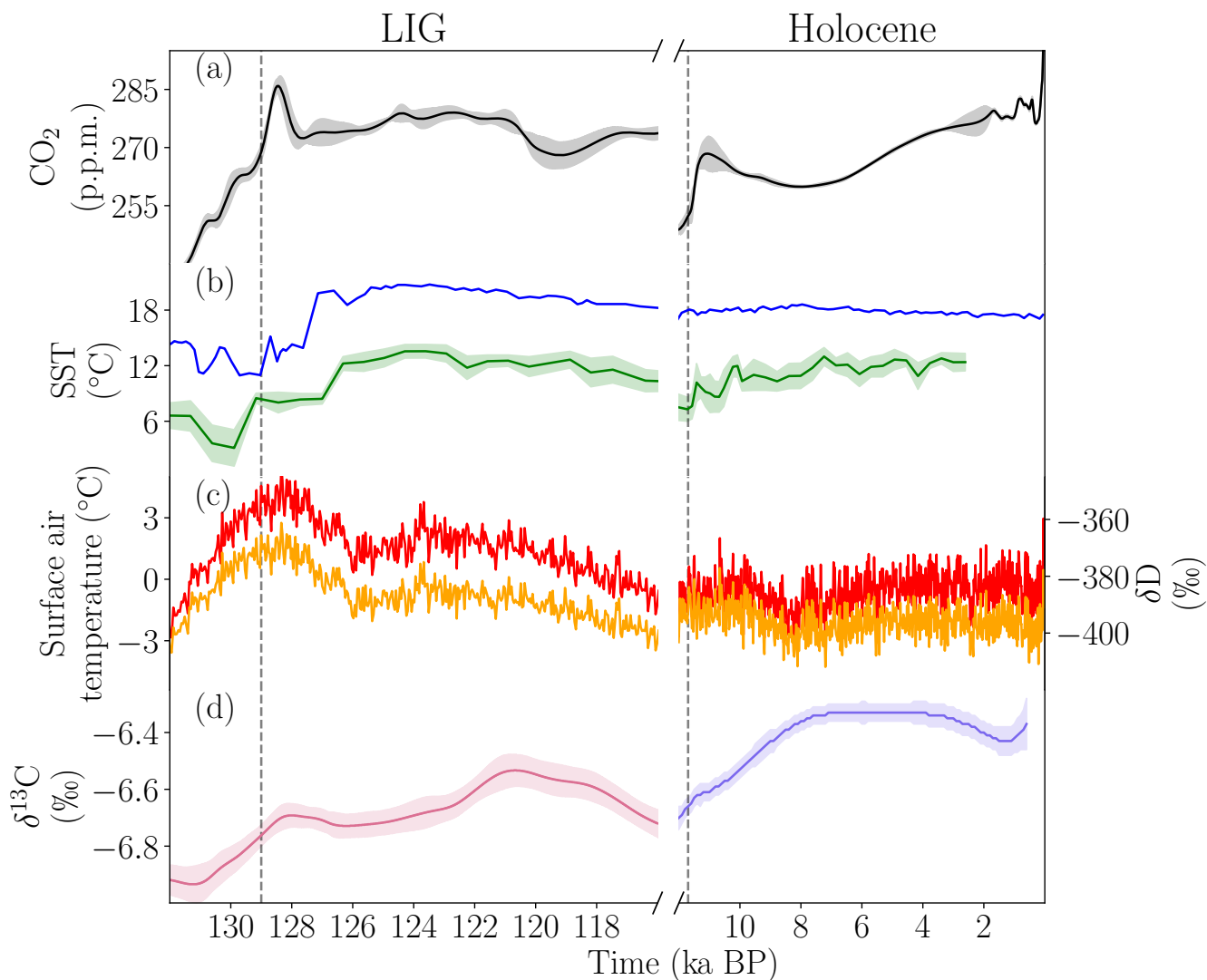


Figure 1. LIG and Holocene timeseries of a) CO₂ stack smoothed with a spline based on the age model AICC2012 (Köhler et al., 2017), b) sea surface temperatures (SSTs) determined from alkenones and aligned with oxygen isotopes from the Iberian Margin (MD01-2444, blue, Martrat et al. (2007b)) and the North Atlantic (GIK23414-6, green, Candy and Alonso-Garcia (2018)), c) EPICA Dome C ice core (EDC96) deuterium measurements (orange) and estimated surface air temperature anomaly relative to the mean of the last 1 ka (red, Bazin et al. (2013); Jouzel et al. (2007)) on the AICC2012 time scale and d) spline of atmospheric $\delta^{13}\text{C}$ from EPICA Dome C and the Talos Dome ice cores (Holocene, Eggleston et al. (2016)) and Monte Carlo average of three Antarctic ice cores atmospheric $\delta^{13}\text{C}$ (LIG, Schneider et al. (2013)) both based on the age model AICC2012. Shading around the lines indicates 1σ . Vertical grey shading indicates the periods of analysis in this paper. Grey vertical dotted lines indicate the commencement of the LIG and Holocene.

weakening during a few multi centennial-scale events between 127 and 115 ka BP (e.g. Galaasen et al., 2014b; Helmens et al., 2015; Lehman et al., 2002; Mokeddem et al., 2014; Oppo et al., 2006; Rowe et al., 2019; Tzedakis et al., 2018).

Stable carbon isotopes are a powerful tool for investigating ocean circulation (e.g. Curry and Oppo, 2005; Eide et al., 2017) and the global carbon cycle (e.g. Menviel et al., 2017; Peterson et al., 2014). Since the largest carbon isotope fractionation occurs during photosynthesis, organic matter is enriched in ^{12}C (low $\delta^{13}\text{C}$), while atmospheric CO_2 and surface water dissolved inorganic carbon (DIC) become enriched in ^{13}C (high $\delta^{13}\text{C}$). Organic matter on land includes the terrestrial biosphere, as well as carbon stored in soils, such as in peats and permafrosts. Different photosynthetic pathways (which differentiate C3 and C4 plants) fractionate carbon differently, producing typical signatures of about -37 to -20 ‰ for C3 plants (Kohn, 2010) and around -13 ‰ for C4 plants (Basu et al., 2015), though these values vary with a number of factors including precipitation, atmospheric CO_2 concentration and $\delta^{13}\text{C}$, light, nutrient availability, and plant species (Cernusak et al., 2013; Diefendorf et al., 2010; Diefendorf and Freimuth, 2017; Farquhar, 1983; Farquhar et al., 1989; Keller et al., 2017; Leavitt, 1992; Schubert and Jahren, 2012). In the ocean, phytoplankton using the C3 photosynthetic pathway are found to have fractionation during photosynthesis that depends on the concentration of dissolved CO_2 . Thus, atmospheric $\delta^{13}\text{C}$ during the LIG (Fig. 1d) is influenced by the cycling of organic carbon within the ocean, changes in the amount of carbon stored in vegetation and soils, temperature-dependent air-sea flux fractionation (Lynch-Stieglitz et al., 1995; Zhang et al., 1995), and, on longer time scales, by interactions with the lithosphere (Tschumi et al., 2011). The mean surface DIC is enriched by ~ 8.5 ‰ compared to the atmosphere due to fractionation during air-sea gas exchange (Menviel et al., 2015; Schmittner et al., 2013).

NADW is characterised by low nutrients and high $\delta^{13}\text{C}$ as a result of a high nutrient and carbon utilisation by marine biota and fractionation during air-sea gas exchange in the northern North Atlantic. Along its path through the Atlantic basin interior, organic matter remineralisation and mixing with southern source waters lowers $\delta^{13}\text{C}$, with $\delta^{13}\text{C}$ values of ~ 0.5 ‰ in the deep Southern Ocean.

The tight relationship between the water masses' apparent oxygen utilisation, nutrient content and $\delta^{13}\text{C}$ allows $\delta^{13}\text{C}$ to be used as a water mass ventilation tracer (e.g. Boyle and Keigwin, 1987; Curry and Oppo, 2005; Duplessy et al., 1988; Eide et al., 2017). The $\delta^{13}\text{C}$ of benthic foraminifera shells, particularly of the species *Cibicides wuellerstorfi*, has been found to reliably represent the $\delta^{13}\text{C}$ signature of DIC (Belanger et al., 1981; Duplessy et al., 1984; Zahn et al., 1986) and has therefore been used to better constrain the extent of different water masses. Mass balances of $\delta^{13}\text{C}$ between the atmosphere, ocean and land have been previously used to constrain changes in terrestrial carbon between the Last Glacial Maximum (~ 20 ka BP) and Holocene (e.g. Peterson et al., 2014). However, on longer time scales, exchanges with the lithosphere including volcanic outgassing (Hasenclever et al., 2017; Huybers and Langmuir, 2009), CaCO_3 burial in sediments and weathering, release of carbon from methane clathrates, and the net burial of organic carbon also influence the global mean $\delta^{13}\text{C}$. It has been estimated that the amount of carbon both entering and exiting the lithosphere due to weathering and burial of organic carbon fluxes could be from 0.274 to 0.344 Gt C yr^{-1} (Schneider et al., 2013), though these vary through time (Hoogakker et al., 2006). Over timescales greater than 10 ka, the influence of weathering and burial of carbon might dominate the $\delta^{13}\text{C}$ signal (Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2020), so a mass balance cannot be accurately applied to evaluate terrestrial carbon changes between the LIG and Holocene.

Here, we present a new compilation of benthic $\delta^{13}\text{C}$ from *Cibicides wuellerstorfi* spanning the 130–118 ka BP time period. We use this data to compare the $\delta^{13}\text{C}$ signal of the LIG with that of the Holocene and to determine the difference in average ocean $\delta^{13}\text{C}$ between the two time periods. We then investigate the AMOC during the LIG with our new benthic $\delta^{13}\text{C}$ database. Finally, we qualitatively explore the role of the various processes affecting the $\delta^{13}\text{C}$ difference between the LIG and the
95 Holocene.

2 Database and methods

2.1 Database

We present a new compilation of benthic $\delta^{13}\text{C}$ covering the periods 130–118 ka BP and 8–2 ka BP. From these two sets of data, we select data pertaining to the LIG and compare it to data from the Holocene. Our database only includes measurements on
100 *Cibicides wuellerstorfi* as no significant fractionation between the calcite shells and the surrounding DIC has been measured in this species (Belanger et al., 1981; Duplessy et al., 1984; Zahn et al., 1986).

Our compilation is predominantly based on Lisiecki and Stern (2016) (53 cores), but includes 14 cores described in Oliver et al. (2010), as well as a few other records (CH69-K09 (Labeyrie et al., 2017), MD03-2664 (Galaasen et al., 2014a), MD95-2042 (Martrat et al., 2007a), ODP 1063 (Deaney et al., 2017), and U1304 (Hodell and Channell, 2016)). The full core lists are
105 provided in Tables 1 and 2 for the LIG and the Holocene, respectively.

2.2 Age models

Due to the lack of absolute age markers, such as tephra layers, the LIG age models mostly rely on alignment strategies that tie each record to a well-dated reference record. The age model tie-points used in this study are taken from the original age model publications. The reference records (LS16, Lisiecki and Stern (2016)) consist of eight regional stacks (one for the
110 intermediate and one for the deep ocean for each the North Atlantic, South Atlantic, Pacific and Indian Oceans) of benthic $\delta^{18}\text{O}$ that were dated through alignment with other climatic archives such as ice-rafted debris records, synthetic ice core records and speleothems. The use of regional stacks, rather than a single global stack, improved stratigraphic alignment targets and provided more robust age models. The estimated age model uncertainty (2σ) for this group of cores is 2 ka. Please refer to Lisiecki and Stern (2016) for further details. Oliver et al. (2010) defined their age tie points assuming that sea level minima
115 and benthic $\delta^{18}\text{O}$ maxima are synchronous. The benthic $\delta^{18}\text{O}$ records were aligned with each other and then tied to the Dome Fuji chronology (based on O_2/N_2) (Kawamura et al., 2007). Please refer to Shackleton et al. (2000) and Oliver et al. (2010) for an extensive method description. The age model uncertainty on this group of cores is estimated to range from 1 to 2.5 ka.

The published age models for the additional cores were determined using similar alignment techniques: SSTs were correlated to the NGRIP Greenland ice core for CH69-K09 and MD95-2042 (Govin et al., 2012). The age model for MD03-2664 was
120 determined by correlating MD03-2664 $\delta^{18}\text{O}$ with previously dated MD95-2042 $\delta^{18}\text{O}$ (Galaasen et al., 2014b). ODP 1063 and U1304 $\delta^{18}\text{O}$ were originally aligned to the LR04 stack (Lisiecki and Raymo, 2005). In order to align all the records, adjustments

Table 1. List of cores for the last interglacial period (LIG). Provided is the core name ('Core'), latitude (Lat, °), longitude (Lon, °), depth (Dep, m), the region and the reference. Regions: NEA: northeast Atlantic, NWA: northwest Atlantic, SWA: southwest Atlantic, SEA: southeast Atlantic, SA: south Atlantic, NP: north Pacific, SP: south Pacific, I: Indian. Reference abbreviations: BW96: Bickert and Wefer (1996), CL82: Curry and Lohmann (1982), dA03: de Abreu et al. (2003), KJ8994: Keigwin and Jones (1989, 1994), KS02: Keigwin and Schlegel (2002), L99: Labeyrie et al. (1999), MB99: Mackensen and Bickert (1999), OH00: Oppo and Horowitz (2000), SH84: Shackleton and Hall (1984), SS0405: Skinner and Shackleton (2004, 2005), VH02: Venz and Hodell (2002), V99: Venz et al. (1999), ZM1011: Zarriss and Mackensen (2010, 2011).

Core	Lat	Lon	Dep (m)	Region	Reference	Core	Lat	Lon	Dep (m)	Region	Reference
ODP758	5.38	90.36	2,935	I	Chen et al. (1995)	SU90-39	52.5	-22	3,955	NEA	Cortijo (2003)
RC12-339	9.13	90.03	3,010	I	Members (2006)	ODP983	60.4	-23.64	1,984	NEA	McIntyre et al. (1999)
GEOB3004-1	14.61	52.92	1,803	I	Schmiedl and Mackensen (2006)	SU90-03	40.05	-32	2,475	NEA	Chapman and Shackleton (1999)
MD01-2378	-13.08	121.79	1,783	I	Holbourn et al. (2005)	U1308	49.88	-24.24	3,883	NEA	Hodell et al. (2008)
Y69-71	0.1	-95.65	2,740	NP	Lyle et al. (2002)	ODP980	55.49	-14.7	2,168	NEA	McManus et al. (1999); Oppo et al. (1998)
ODP677	1.2	-83.73	3,450	NP	SH84, Shackleton et al. (1990)	ODP982	57.51	-15.85	1,134	NEA	Jansen et al. (1996), V99, VH02
ODP849	0.18	-110.52	3,839	NP	Shackleton et al. (1990)	EW9209-1JPC	5.91	-44.2	4,056	NWA	Curry and Oppo (1997)
V24-109	0.43	158.8	2,367	NP	Duplessy et al. (1984)	GEOB4403-2	6.13	-43.44	4,503	NWA	Bickert and Mackensen (2003)
Y69-106	2.98	-86.55	2,870	NP	Lyle et al. (2002); Pisias and Mix (1997)	ODP1063	33.68	-57.62	4,584	NWA	Deaney et al. (2017)
ODP807A	3.61	156.63	2,804	NP	Zhang et al. (2007)	CH69-K9	41.75	-47.35	4,100	NWA	L99, Waelbroeck et al. (2001)
GIK17961-2	8.51	112.33	1,795	NP	Wang et al. (1999)	SU90-11	44.07	-40.02	3,645	NWA	Julien et al. (2006); Labeyrie et al. (1995)
MD97-2151	8.73	109.87	1,598	NP	Lee et al. (1999); Wei et al. (2006)	U1304	53.06	-33.53	3,065	NWA	Hodell and Channell (2016)
ODP1143	9.36	113.29	2,772	NP	Cheng et al. (2004)	V27-20	54.0	-46.2	3,510	NWA	Ruddiman and Members (1982)
V28-304	28.53	134.13	2,942	NP	Duplessy et al. (1984)	MD03_2664	57.44	-48.61	3,442	NWA	Galaasen et al. (2014a)
V32-128	36.47	177.17	3,623	NP	Duplessy et al. (1984)	ODP925	4.2	-43.49	3,040	NWA	Bickert et al. (1997)
PS2495	-41.28	-14.49	3,134	SA	Mackensen et al. (2001)	ODP926	3.72	-42.91	3,598	NWA	Curry et al. (1995)
ODP1089	-40.94	9.89	4,621	SA	Hodell et al. (2001)	ODP928	5.46	-43.75	4,012	NWA	Bickert et al. (1997)
PS2082	-43.22	11.74	4,610	SA	McCorkle and Holder (2001)	V28-127	11.65	-80.13	3,237	NWA	Oppo and Fairbanks (1987)
MD06-3018	-23	166.15	2,470	SP	Russon et al. (2009)	KNR140-37JPC	31.41	-75.26	3,000	NWA	Curry and Oppo (2005), KS02
RC13-110	-0.1	-95.65	3,231	SP	Mix et al. (1991)	GEOB3801-6	-29.51	-8.31	4,546	SEA	Bickert and Mackensen (2003)
ODP846	-3.1	-90.82	3,296	SP	Shackleton et al. (1995)	GEOB1214	-24.69	7.24	3,210	SEA	BW96
V19-27	-0.47	-82.07	1,373	SP	Mix et al. (1991)	GEOB1211	-24.48	7.53	4,084	SEA	BW96
GEOB1101	1.66	-10.98	4,588	NEA	BW96	GEOB1710	-23.43	11.7	2,987	SEA	Schmiedl and Mackensen (1997)
GIK13519-1	5.67	-19.85	2,862	NEA	Zahn et al. (1986)	GEOB1034	-21.74	5.42	3,772	SEA	BW96
GIK16402	14.42	-20.54	4,202	NEA	Sarnthein et al. (1994)	GEOB1035	-21.59	5.03	4,453	SEA	BW96
GIK12392-1	25.17	-16.85	2,573	NEA	Shackleton (1977); Zahn et al. (1986)	GEOB1028-5	-20.1	9.19	2,209	SEA	Bickert and Mackensen (2003)
GIK16004	29.98	-10.65	1,512	NEA	Sarnthein et al. (1994)	V22-174	-10.07	-12.82	2,630	SEA	Shackleton (1977)
GEOB4216	30.63	-12.4	2,324	NEA	Freudenthal et al. (2002)	GEOB1112	-5.78	-10.75	3,125	SEA	BW96, MB99
GIK15669	34.89	-7.82	2,022	NEA	Sarnthein et al. (1994)	GEOB1115	-3.56	-12.56	2,945	SEA	BW96, MB99
GIK15612-2	44.36	-26.54	3,050	NEA	Sarnthein et al. (1994)	GEOB1041	-3.48	-7.6	4,033	SEA	BW96, MB99
NO79-28	45.63	-22.75	3,625	NEA	Duplessy (1996)	GIK16867	-2.2	5.1	3,891	SEA	Sarnthein et al. (1994)
GIK23416-4	51.57	-20.0	3,616	NEA	Sarnthein et al. (1994)	GEOB1105	-1.67	-12.43	3,225	SEA	BW96, MB99
NEAP18K	52.77	-30.35	3,275	NEA	Chapman and Shackleton (1999)	GIK16772-1	-1.34	-11.97	3,911	SEA	Sarnthein (2003)
GIK23415-9	53.18	-19.15	2,472	NEA	CL82, Sarnthein et al. (1994)	V29-135	-19.7	8.88	2,675	SEA	Sarnthein et al. (1994)
GIK23414-9	53.54	-20.29	2,196	NEA	Sarnthein et al. (1994)	RC13-228	-22.33	11.2	3,204	SEA	Bickert and Mackensen (2003)
CH73-139	54.63	-16.35	2,209	NEA	Curry et al. (1988); Sarnthein et al. (1994)	ODP1087	-31.46	15.31	1,372	SEA	Lynch-Stiegitz et al. (2006)
GIK17049-6	55.26	-26.73	3,331	NEA	Sarnthein et al. (1994)	MD96-2080	-36.27	19.48	2,488	SEA	Rau et al. (2002)
V28-56	68.03	-6.12	2,941	NEA	Ruddiman and Members (1982)	GEOB2109-1	-27.91	-45.88	2,504	SWA	Vidal et al. (1999)
ODP984	61	-24	1,650	NEA	Raymo et al. (2004)	V22-38	-9.55	-34.25	3,797	SWA	Ruddiman and Members (1982)
V29-202	61	-21	2,658	NEA	Oppo and Lehman (1995)	GEOB1117	-3.82	-14.9	3,984	SWA	BW96, MB99
ODP664	0.11	-23.23	3,806	NEA	Raymo et al. (1997)	GEOB1118	-3.56	-16.43	4,675	SWA	BW96, MB99

to the age models of cores from Oliver et al. (2010) and the five additional cores (CH69-K09, MD95-2042, MD03-2664, ODP 1063 and U1304) were made by aligning the $\delta^{18}\text{O}$ minima during the LIG to the corresponding $\delta^{18}\text{O}$ minima of the nearest LS16 stack. The $\delta^{18}\text{O}$ data before and after the alignment is given in Fig. S1.

125 The Holocene age models are based on planktonic foraminifera radiocarbon dates (Stern and Lisiecki, 2014; Waelbroeck et al., 2001), which have been converted into calendar ages using IntCal13 and using reservoir ages based on modern observations (Key et al., 2004), which are assumed to have remained fairly stable across the Holocene. The age uncertainty associated with these Holocene radiocarbon-based age models is generally less than 0.5 ka. However, it is important to note that Holocene age models from Oliver et al. (2010) were derived using the same method as their LIG age models, leading to larger age uncer-
130 tainties of about 1–2.5 ka for this set of Holocene records (4 cores). The tie points were used to derive a full age-depth model assuming a constant sedimentation rate between tie-points (i.e. linear interpolation).

2.3 Spatial coverage

The spatial distribution of the database for the Holocene and the LIG is shown in Fig. 2 and the depth distribution in each ocean basin is shown in Fig. 3. There is more data in the Atlantic Ocean (65 LIG, 118 Holocene) than in the Pacific (15 LIG, 19
 135 Holocene) and Indian (3 LIG, 7 Holocene) Oceans. We used this database to determine 1) if there is a significant difference in the average ocean $\delta^{13}\text{C}$ signal at the LIG compared to the Holocene, and 2) if ocean circulation patterns were comparable. Due to the sparsity of data in the Indian and Pacific Oceans, our investigation is primarily focused on the Atlantic. Additionally, the temporal uncertainties (~ 2 ka) do not permit an investigation of centennial-scale events, and therefore we restrict our analysis to mean LIG and Holocene conditions.

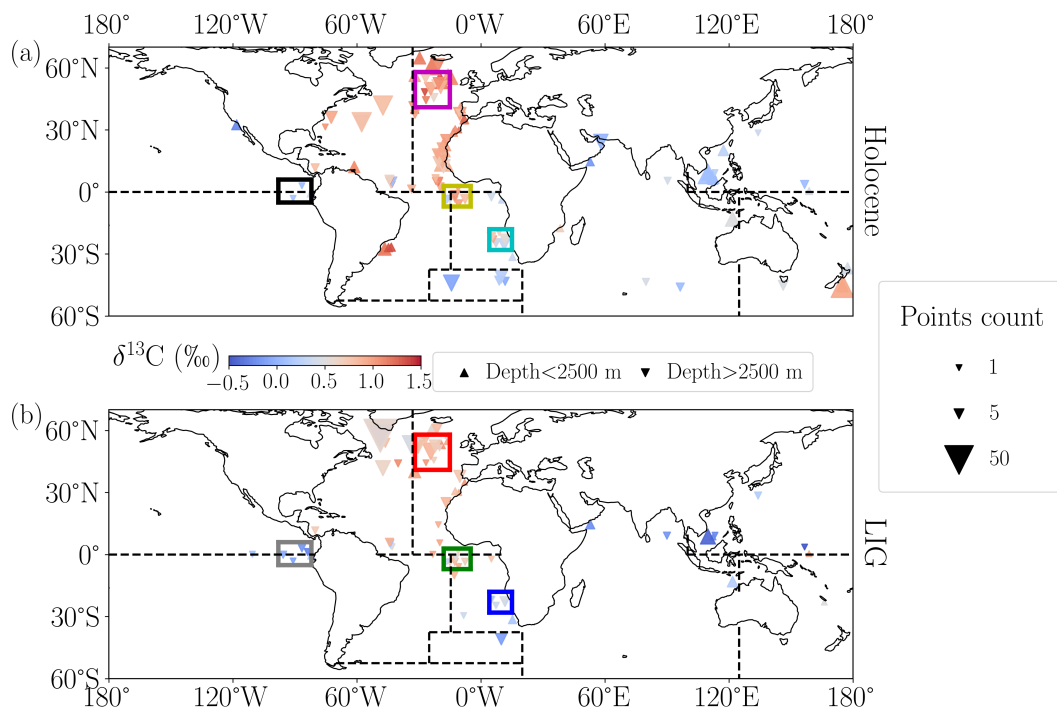


Figure 2. Global distribution of benthic foraminifera $\delta^{13}\text{C}$ covering the periods studied here: the Holocene (7–2 ka BP) (a) and LIG (125–120 ka BP) (b). Symbol size indicates the number of values per core, colour indicates average $\delta^{13}\text{C}$, and the triangle direction indicates the proxy depth (upward-pointing triangle: between 1,000 and 2,500 m depth, downward-pointing triangle: deeper than 2,500 m). Four specific regions used in Sect. 3.1 are outlined: eastern equatorial Pacific (black, grey), equatorial Atlantic (yellow, green), southeast Atlantic (cyan, blue), and northeast Atlantic (magenta, red). Regional boundaries used to calculate the global volume-weighted mean $\delta^{13}\text{C}$ (Sect. 3.2) are indicated by dotted black lines as defined in Peterson et al. (2014).

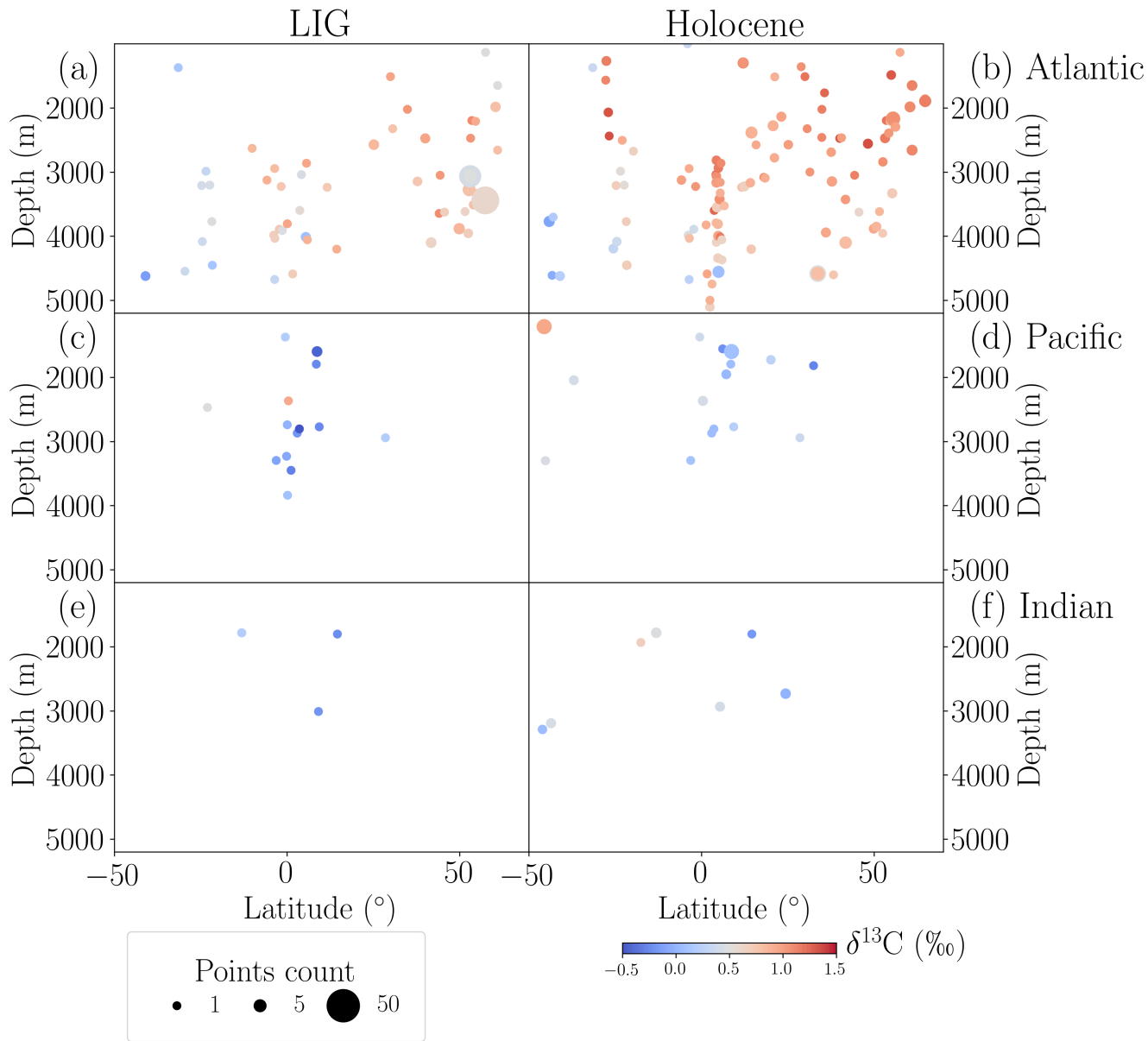


Figure 3. Zonal distribution of benthic foraminifera $\delta^{13}\text{C}$ (‰) during the LIG (125–120 ka BP; a, c, e) and the Holocene (7–2 ka BP; b, d, f) in the Atlantic Ocean (a, b), Pacific Ocean (c, d) and Indian Ocean (e, f). Symbol size indicates the number of measurements per core and colour indicates average $\delta^{13}\text{C}$.

The $\delta^{13}\text{C}$ signal varies significantly regionally and with depth. The highest average $\delta^{13}\text{C}$ values are associated with NADW and are generally found at depths between $\sim 1,500$ and $3,000$ m in the North Atlantic, with organic matter remineralisation and mixing with southern source waters leading to a $\delta^{13}\text{C}$ decrease along the NADW path. The lowest $\delta^{13}\text{C}$ values are in the deep south Atlantic ($>4,000$ m) because the Antarctic Bottom Water (AABW) end member is much lower than its NADW counterpart. Since the Indian and Pacific Oceans are mostly ventilated from southern-sourced water masses, $\delta^{13}\text{C}$ generally decreases northward in these two basins.

Since the number of cores is not consistent across the two time periods, and given the high regional variability observed in $\delta^{13}\text{C}$, it is not possible to simply average all available data to determine the global mean $\delta^{13}\text{C}$. Furthermore, the spatial heterogeneity of the data density adds to the complexity of the problem. To address these points, we first analyse differences between the LIG and Holocene records for pre-defined small regions with high data density. We then calculate regional volume-weighted $\delta^{13}\text{C}$ means for larger regions from which we estimate the global LIG-Holocene anomaly.

3.1 Regional reconstruction of $\delta^{13}\text{C}$

We define regions with high densities of cores to reconstruct regional mean $\delta^{13}\text{C}$ (Fig. 2). These regions need to be small enough to assume reasonably small spatial variability in the $\delta^{13}\text{C}$ signal and yet still have enough data to establish a reliable statistical difference between the two time periods.

Based on these requirements, four regions are selected: the northeast Atlantic, the equatorial Atlantic, a region off the Namibian Coast (southeast Atlantic), and a region around the Galapagos Islands (eastern equatorial Pacific). The boundaries of each region are defined in Table 3.

We then define the time periods within the LIG and the Holocene to perform our analyses. For the Holocene, as most of the available data is dated prior to 2 ka BP, we define the end of our Holocene time period as 2 ka BP. To capture as much of the Holocene data as possible, we include data back to 7 ka BP, ensuring that we do not include instability associated with the 8.2 kiloyear event (Alley and Ágústsdóttir, 2005; Thomas et al., 2007). This provides a time span of 5 ka of data that we will consider for our analysis of the Holocene.

For the LIG, we seek to avoid data associated with the end of the penultimate deglaciation, which is characterised by a benthic $\delta^{13}\text{C}$ increase in the Atlantic until ~ 128 ka BP (Govin et al. (2015); Menviel et al. (2019); Oliver et al. (2010), Fig. 4). In addition, a millennial-scale event has been identified in the North Atlantic between ~ 127 and 126 ka BP (Galaasen et al., 2014b; Tzedakis et al., 2018). Considering the typical dating uncertainties associated with the LIG data (2 ka), we thus decide to start our LIG time period at 125 ka BP. To ensure that the two time periods are of same length (5 ka BP), we define the LIG period for our analysis to be 125–120 ka BP. We note that our definition should also avoid data associated with the glacial inception (Govin et al., 2015; of PAGES, 2016). We verify that the LIG time period has sufficient data across the selected four regions, noting that the highest density of data falls within the 125–120 ka BP time period—particularly in the equatorial Atlantic and southeast Atlantic (Fig. 4b, c).

Table 3. Regional summary of $\delta^{13}\text{C}$ below 2,500 m depth for the LIG (125–120 ka BP) and Holocene (7–2 ka BP) using a single value per core for each time slice. Shown are the non-volume-weighted means ($\delta^{13}\text{C}$, ‰), standard deviations (σ , ‰), and counts (N) for both time periods, along with the time period regional anomalies ($\Delta\delta^{13}\text{C}$, ‰), propagated standard deviations for the anomaly (σ , ‰), and p-values from two-sample t-tests between the two time periods.

Region	Latitude	Longitude	Holocene			LIG			LIG-Holocene		
			$\delta^{13}\text{C}$ (‰)	σ (‰)	N	$\delta^{13}\text{C}$ (‰)	σ (‰)	N	$\Delta\delta^{13}\text{C}$ (‰)	σ (‰)	P value
Northeast Atlantic	41N-58N	32E-15E	0.89	0.21	34	0.76	0.11	23	-0.13	0.12	0.0096
Equatorial Atlantic	7S-3N	18E-5E	0.79	0.32	22	0.62	0.23	14	-0.17	0.20	0.1110
Southeast Atlantic	28S-18S	4W-15W	0.55	0.22	27	0.40	0.11	12	-0.15	0.12	0.0361
Equatorial Pacific	5S-6N	98E-82E	0.09	0.05	4	-0.11	0.10	8	-0.20	0.06	0.0056

We round the data to the nearest 1 ka, find an average per 1 ka, and refer to this as a time slice. We consider the LIG-Holocene anomaly across these two time periods for the four regions selected, and consider qualitatively the influence of changes in the average depth in which the proxies were recorded, as indicated by the direction of the black triangles in Fig. 4.

The average $\delta^{13}\text{C}$ anomaly between the LIG and Holocene periods for cores deeper than 2,500 m is consistent across the different regions despite their geographic separation, suggesting a significantly lower $\delta^{13}\text{C}$ during the LIG than the Holocene, with differences ranging from -0.13 ‰ in the northeast Atlantic to -0.20 ‰ in the equatorial Pacific (Table 3). The statistical significance between the two time periods is established using a two-tailed t-test on data of one mean value per core and spans the entire time slices (125–120 ka BP and 7–2 ka BP). The t-test shows that there is a statistically significant difference everywhere except in the equatorial Atlantic, with confidence intervals varying from 0.13 in the equatorial Atlantic to 0.04 in the northeast Atlantic. When using a single tail t-test instead, the difference becomes significant in the equatorial Atlantic, giving a new p-value of 0.02. Fig. 4 suggests that the difficulty in determining significance in this region for cores deeper than 2,500 m might be due to a singular outlier measurement in the equatorial Atlantic; a value of -0.23 ‰ from GeoB1118 at ~3.5 ka BP. If this value is excluded, then an anomaly of -0.22 with a p-value less than 0.005 is observed.

We also compare the distribution of $\delta^{13}\text{C}$ for cores deeper than 2,500 m for three overlapping periods within the LIG (early LIG: 128–123 ka BP; LIG: 125–120 ka BP; late LIG: 123–118 ka BP). The results for the four regions are shown in Fig. 5. The statistical characteristics do not show much variation between the LIG and late LIG $\delta^{13}\text{C}$ distributions. In the equatorial Pacific, the difference between the early LIG and the Holocene is smaller than between the LIG and Holocene, but this is countered with a larger difference in the equatorial Atlantic between early LIG and Holocene. The spread in the data is generally larger during the Holocene than during the other time periods which might be due to the greater number of measurements during the Holocene. The spread of data during the early LIG is slightly larger than during the LIG and late LIG in the equatorial and southeast Atlantic. The equatorial Atlantic is the only region which displays significantly more points with lower $\delta^{13}\text{C}$ during the early LIG. Overall, these distributions do not suggest that the LIG-Holocene anomalies that we have determined would be significantly impacted by slight variations in the selected time window. We perform an analysis of variance (ANOVA) on each region and post hoc tests on the data. We find that the Holocene data is significantly different from the three LIG periods in the northeast Atlantic, the southeast Atlantic and the equatorial Pacific, while the three periods within the LIG are not significantly different from each other for any of the regions.

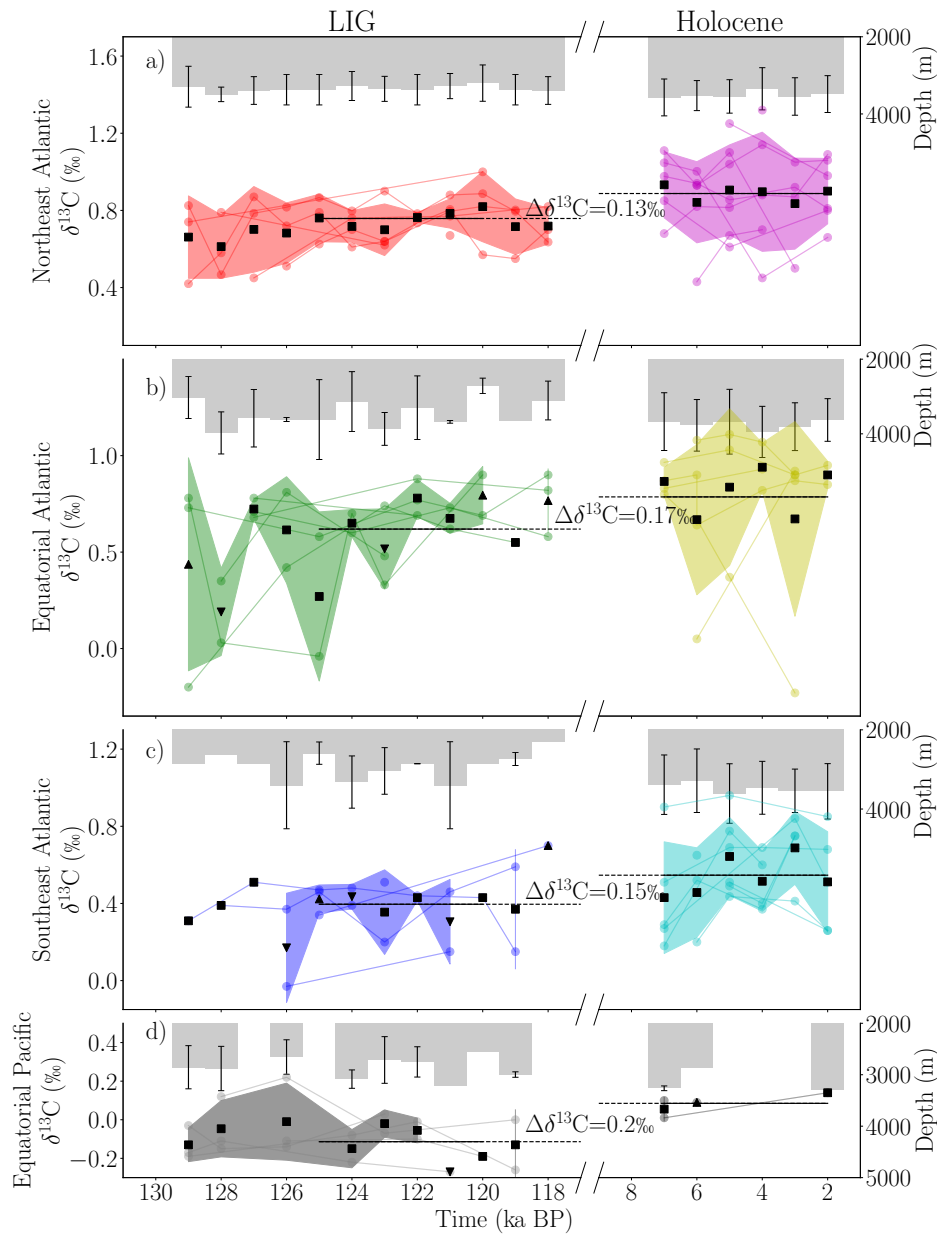


Figure 4. Benthic foraminifera $\delta^{13}\text{C}$ (left y-axis, ‰) during the LIG (left) and Holocene (right) for four defined regions; northeast Atlantic (a), equatorial Atlantic (b), southeast Atlantic (c), and eastern equatorial Pacific (d). Data is presented in discrete time slices spanning 1 ka. Only cores deeper than 2,500 m are shown. Circular, coloured points connected by lines show each average $\delta^{13}\text{C}$ value per core per time slice. Black symbols represent $\delta^{13}\text{C}$ averages per slice. Each slice has a corresponding averaged depth (right y-axis, m), with 1 standard deviation on either side shown in the bars. Slices with an average depth within ± 300 m of the mean core depth of all slices are represented with a square point. Slices with an average depth shallower than 300 m less than the mean are shown with an upward triangle, and deeper than 300 m more than the mean are shown with a downward triangle. Shading shows 1 standard deviation on either side of the mean for slices where more than 1 point exists.

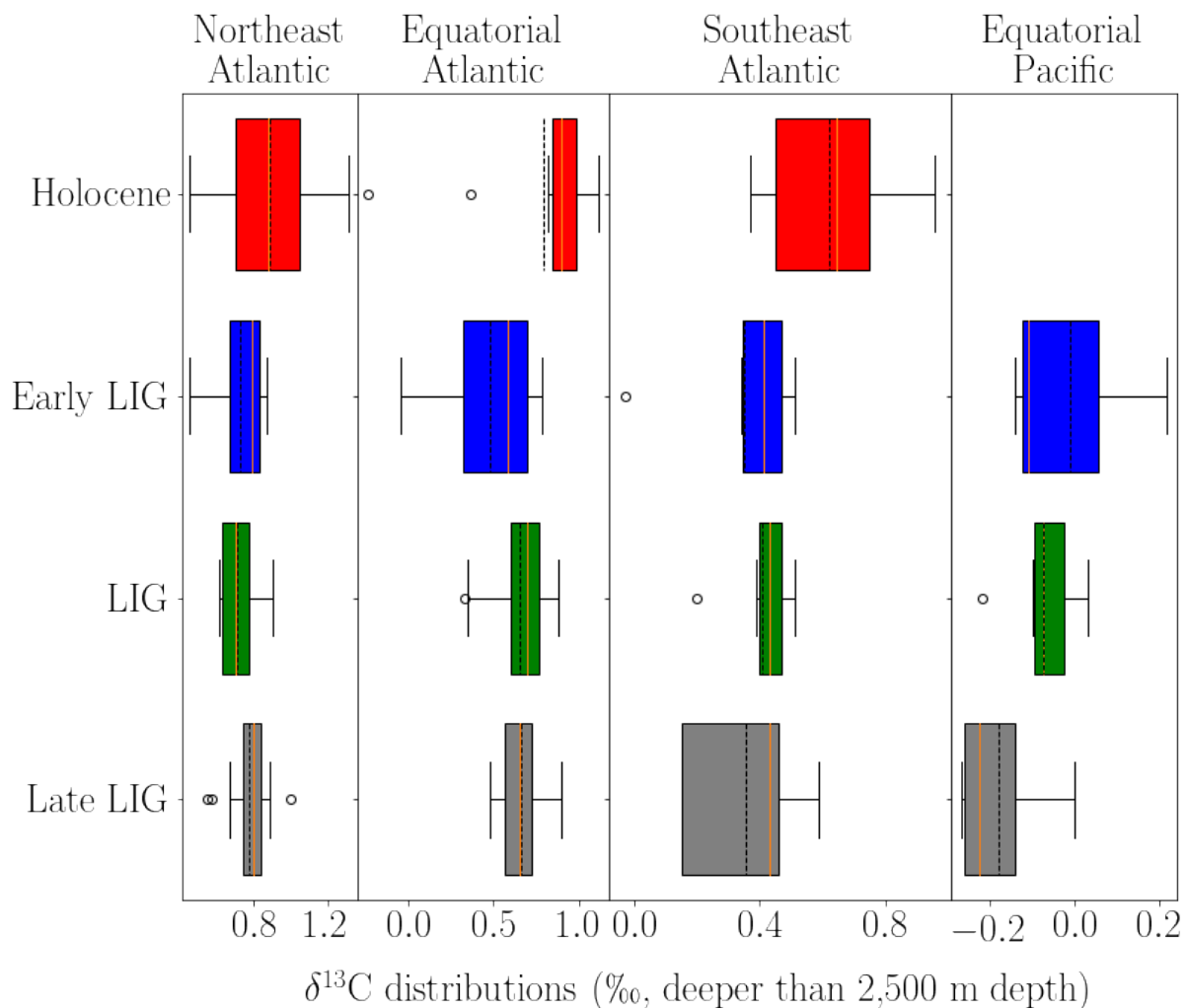


Figure 5. Distributions of $\delta^{13}\text{C}$ for all core measurements deeper than 2,500 m during the Holocene (7–2 ka BP, red), the early LIG (128–123 ka BP), the LIG (125–120 ka BP), and the late LIG (123–118 ka BP) across four regions (equatorial Pacific, equatorial Atlantic, southeast Atlantic, northeast Atlantic). Lower end of the box indicates quartile 1 (Q1) and the upper end indicates quartile 3 (Q3). Orange vertical lines show the median and dotted vertical lines show the mean. The whiskers indicate the lower and upper fences of the data calculated as $Q1 - 1.5 \cdot (Q3 - Q1)$ and $Q3 + 1.5 \cdot (Q3 - Q1)$, respectively, and the clear circles are outliers.

Table 4. Regional breakdown of $\delta^{13}\text{C}$ data for all depths during the Holocene (7–2 ka BP) and LIG (125–120 ka BP) averaged across the 1 ka time slices. For each region: the average number of data points (labelled as ‘Points’) and cores per time slice (labelled as ‘Cores’), the average standard deviation of $\delta^{13}\text{C}$ per time slices (‰), the mean depth (m) across time slices, and the standard deviation of depth (m) between time slices (σ_{depth}). NEA: northeast Atlantic, NWA: northwest Atlantic, SA: south Atlantic, SEA: southeast Atlantic, SWA: southwest Atlantic, I: Indian, NP: north Pacific, SP: south Pacific.

Area	Holocene						LIG					
	$\delta^{13}\text{C}$ (‰)	Points	Cores	$\sigma_{\delta^{13}\text{C}}$ (‰)	Mean depth (m)	σ_{depth} (m)	$\delta^{13}\text{C}$ (‰)	Points	Cores	$\sigma_{\delta^{13}\text{C}}$ (‰)	Mean depth (m)	σ_{depth} (m)
NEA	0.94	73	47	0.19	2853	944	0.76	32	22	0.21	2746	789
NWA	0.81	28	13	0.27	3698	867	0.64	41	9	0.27	3679	455
SA	0.08	6	4	0.18	4103	429	-0.14	3	2	0.11	4533	120
SEA	0.63	13	12	0.26	3306	787	0.55	14	14	0.23	3163	799
SWA	0.96	6	4	0.32	2302	929	0.51	2	2	0.12	4156	172
I	0.23	6	4	0.26	2287	529	0.06	4	4	0.19	2347	581
NP	0.03	14	7	0.20	2015	448	-0.10	9	8	0.24	2815	673
SP	0.45	12	5	0.30	2285	924	0.06	3	3	0.15	2724	709

3.2 Volume-weighted regional $\delta^{13}\text{C}$

200 The second approach we use to further constrain the LIG-Holocene $\delta^{13}\text{C}$ anomaly is to estimate the volume-weighted regional $\delta^{13}\text{C}$. We define our regional boundaries based on the regions described in Peterson et al. (2014), however we only include the regions where there is enough data to justify an analysis. For all the data in each of these regions, we calculate a mean value by taking the direct averages of all data. We divide the ocean basins into eight regions (Table 4, shown in Fig. 2) and calculate the volume-weighted averages $\delta^{13}\text{C}$ for each of these regions. Since the Atlantic and Pacific Oceans have more data than the
205 Indian Ocean, there is greater confidence in the $\delta^{13}\text{C}$ estimates for these regions. These regional averages are then used to calculate a global volume-weighted $\delta^{13}\text{C}$.

Results for the Atlantic and Pacific Oceans are given in Fig. 6, and show a mean LIG-Holocene anomaly of -0.21 ‰ and -0.27 ‰ respectively, slightly higher than the range of estimates for the four regions selected in Sect. 3.1. There is a higher offset estimated in this definition of the southwest Atlantic (-0.45 ‰) than in Sect. 3.1, however there are only 4 cores available
210 in this region during the Holocene and 2 during the LIG.

The estimated LIG-Holocene anomaly in the south Pacific is relatively high at -0.39 ‰, giving a relatively large Pacific anomaly estimate of -0.27 ‰. This could be due in part to the deeper location of the LIG cores compared to the mean of the Holocene cores (439 m difference, Table 4). There is less confidence in the estimate of the Pacific volume-weighted mean since the proxy data is sparse, and the majority of cores are from the eastern equatorial Pacific as shown in Fig. 2. We also note
215 that the average depths of cores from the Pacific Ocean (LIG: 2,711 m, Holocene: 2,131 m) and Indian Ocean (LIG: 2,383 m, Holocene: 2,303 m) are shallower than that of the Atlantic Ocean (LIG: 3,531 m, Holocene: 3,157 m; Fig. 3). However, as the vertical gradient below 2,000 m depth in the Pacific Ocean is small (e.g. Eide et al., 2017), this might not significantly impact our results.

There is a small positive trend in the average Atlantic $\delta^{13}\text{C}$ from 125 ka BP, reaching a maximum value at 118 ka BP (Fig.
220 6). The average core depth over the 125–120 ka BP time period does not suggest that a change in the mean depth could explain

this variation. Fitting a linear regression over this period indicates an increase in $\delta^{13}\text{C}$ of 0.03‰ ka^{-1} in the Atlantic, with a p-value of 0.01 and an R^2 of 0.85 (Fig. 4a). For the Pacific, there is a $\sim 0.13\text{‰}$ increase in $\delta^{13}\text{C}$ between 7 and 5 ka BP, which could be associated with the early Holocene terrestrial regrowth (Menviel and Joos, 2012).

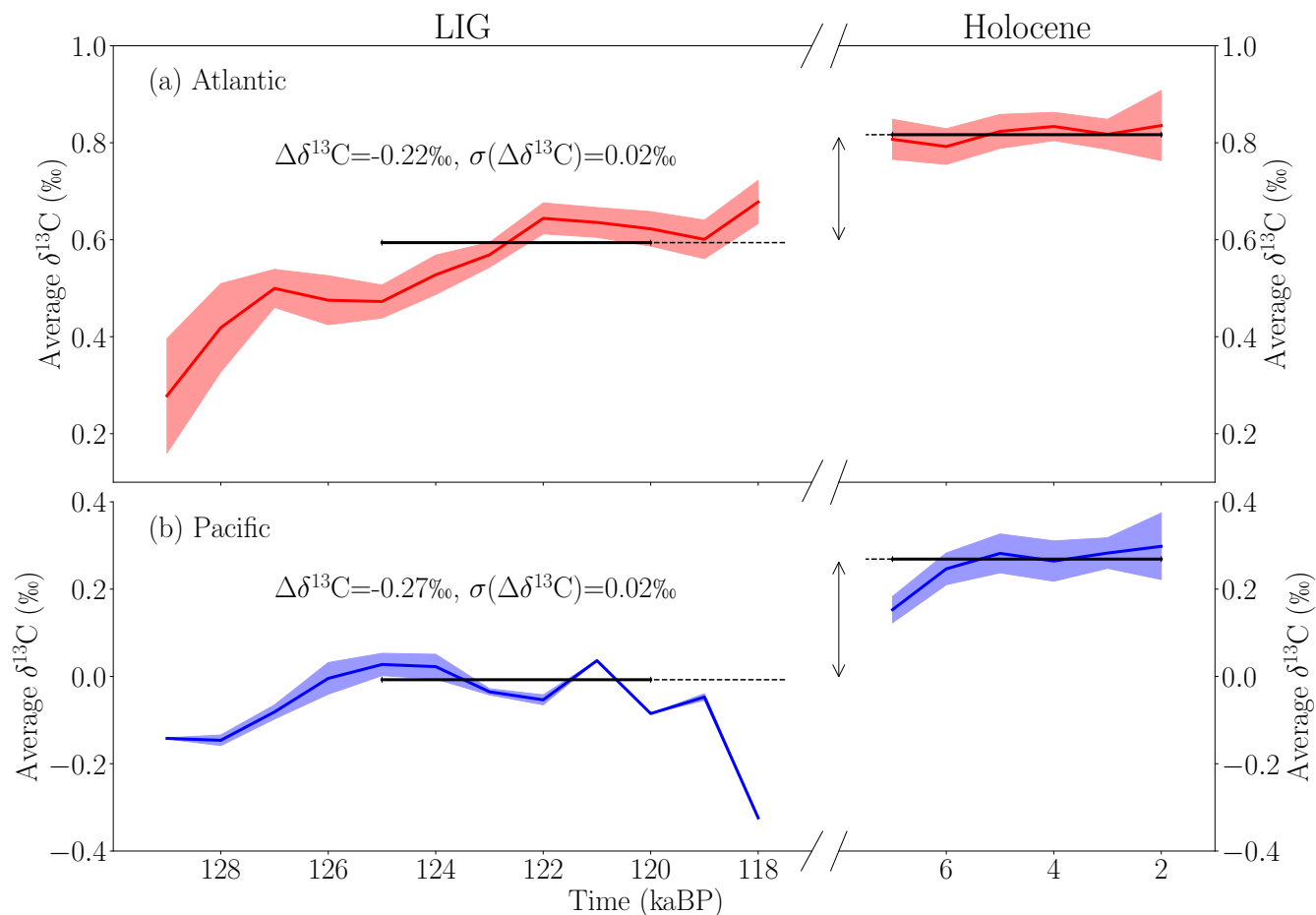


Figure 6. Comparison of volume-weighted $\delta^{13}\text{C}$ for the Atlantic (red) and Pacific (blue) for the LIG and Holocene, calculated using the regions from Peterson et al. (2014) from data covering all depths. Solid coloured lines indicate the mean volume-weighted $\delta^{13}\text{C}$, and the shading indicates the volume-weighted sum of square deviations from the mean. The horizontal bars indicate the mean of the stable period determined from the regional analysis as defined in Sect. 3.1 (LIG: 125–120 ka BP, Holocene: 7–2 ka BP), with the $\Delta\delta^{13}\text{C}$ indicating the mean anomaly between these two average and the standard deviation ($\sigma(\delta^{13}\text{C})$, ‰).

For the Indian Ocean, we only include four cores, as these are the only ones spanning both the LIG and Holocene. An LIG anomaly of -0.13‰ in the Indian Ocean compared to the Holocene is therefore associated with higher uncertainties. The whole ocean mean LIG $\delta^{13}\text{C}$ anomaly is -0.25‰ , but it is associated with higher uncertainties than each region anomaly.

Both the regional analysis of our new database and our volume-weighted estimate indicate that the global mean $\delta^{13}\text{C}$ was about 0.2 ‰ lower during the LIG than during the Holocene. We further test the robustness of this result in the next section.

3.3 Reconstruction of the LIG Atlantic Meridional Overturning Circulation

230 In this section, we analyse the spatial $\delta^{13}\text{C}$ distribution in the Atlantic Ocean to assess potential changes in the penetration depth and southward expansion of NADW during the LIG, defined here as 125–120 ka BP, with respect to the Holocene. A change in NADW might influence our estimate of the mean $\delta^{13}\text{C}$, given that most of the available data is localised in the Atlantic Ocean.

We use simple statistical regression models to reconstruct NADW and AABW separately with a quadratic-with-depth and
235 linear-with-latitude equation following the method of Bengtson et al. (2019). For consistency, the regression algorithm only includes records from cores that span both the LIG and Holocene and uses a weighted least squares approach, where the weighting equals the number of samples per core. The modelled region is defined between 40° S and 60° N as this is the region where we can expect to find both the NADW and AABW $\delta^{13}\text{C}$ signals.

The results are shown in Fig. 7. We test the robustness of our statistical model using the jackknifing technique. We systemati-
240 cally exclude each individual core from the database one at a time, fit the parameters using this modified database, and compare the model prediction against the core which was excluded. This produces small variations in the average mean response of the statistical models (the standard deviations were 0.01 ‰ for both the LIG and Holocene, respectively).

We calculate end-member values based on proxies located near the water mass sources. These are taken as 0.79 ‰ and
245 1.02 ‰ for NADW for the LIG and Holocene, respectively, and -0.09 ‰ and 0.23 ‰ for AABW for the LIG and Holocene, respectively. The end-member values are calculated as the average of cores shallower than 3,000 m but deeper than 1,000 m and located between 50° N and 70° N for NADW. The NADW end-member cores have an average depth of 2,043 m and a standard deviation of 478 m during the LIG. For the AABW end-member, the only eligible core is ODP1089, which is at ~41° S and 4,621 m.

The mean volume-weighted $\delta^{13}\text{C}$ for the Atlantic Ocean between 40° S and 60° N based on this interpolation is 0.53 ‰ for
250 the LIG and 0.70 ‰ for the Holocene (Fig. 7). This suggests a 0.17 ‰ lower Atlantic $\delta^{13}\text{C}$ at the LIG than the Holocene. Our statistical reconstruction points to a very similar NADW depth (~2,600 m) for both time periods (Fig. 7). The NADW depth is defined here as the depth of maximum $\delta^{13}\text{C}$ in the North Atlantic.

We also investigate the meridional gradient in $\delta^{13}\text{C}$ in the Atlantic Ocean to determine whether the NADW southward
255 penetration, transport and remineralisation rates were significantly different during the LIG compared to the Holocene. We only consider cores that are located between depths of 1,000 and 3,000 m in order to stay within the main pathway of NADW (Fig. 8a). Though there is significant scatter, in accordance with our previous findings, a moving average through the Holocene and the LIG data shows that LIG $\delta^{13}\text{C}$ is typically lower than the Holocene counterparts. However, the meridional $\delta^{13}\text{C}$ statistical model gradients are not very different for the LIG (0.0036 ‰ °latitude⁻¹) and the Holocene (0.0030 ‰ °latitude⁻¹) (Fig. 8a), suggesting a similar southward penetration of NADW.

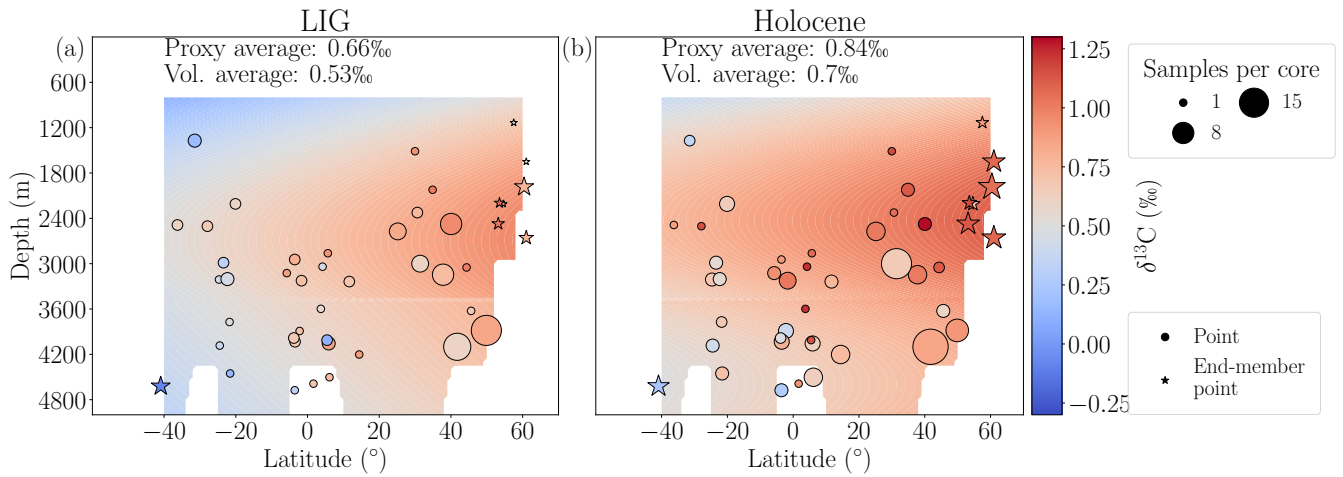


Figure 7. Reconstructed Atlantic $\delta^{13}\text{C}$ (‰) meridional section during the LIG (125–120 ka BP) and Holocene (7–2 ka BP). The circular points represent the proxy data, showing the average $\delta^{13}\text{C}$ with colour and the number of points per core with size. The stars represent the proxy data which make up the end-members. Background shading shows the reconstructed $\delta^{13}\text{C}$ using a quadratic statistical regression of the proxy data following the method described in Bengtson et al. (2019).

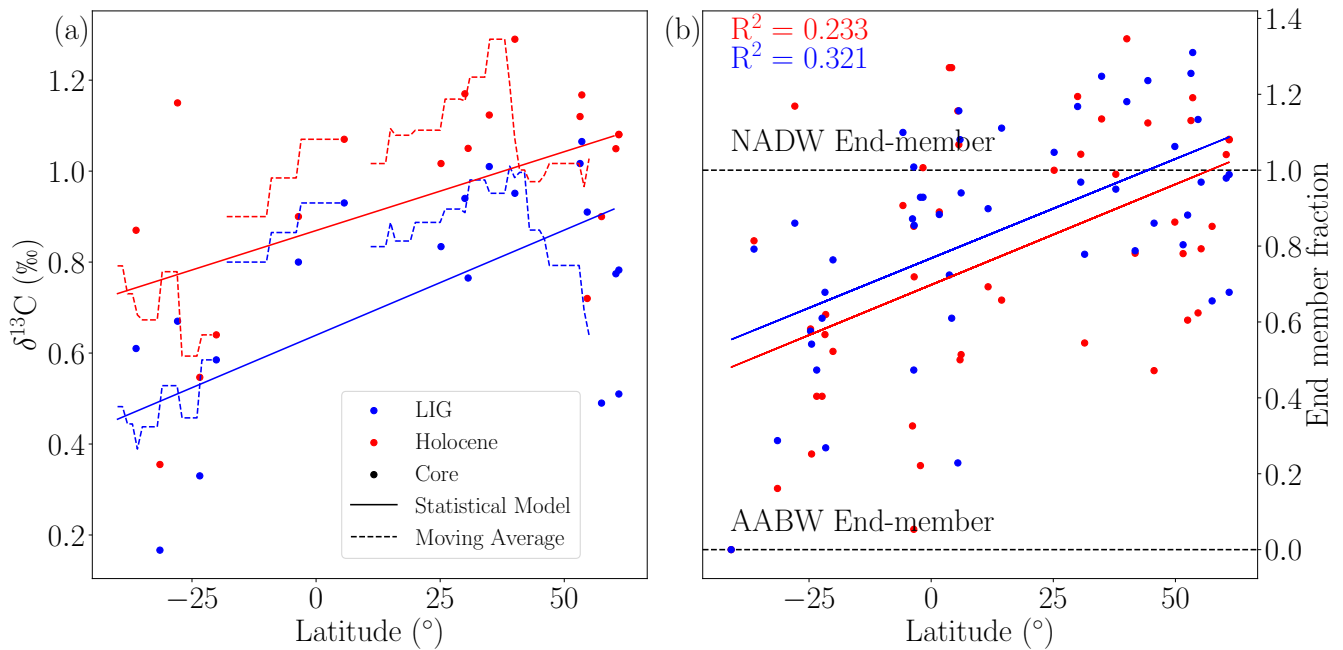


Figure 8. The meridional gradient of the Atlantic Ocean benthic $\delta^{13}\text{C}$ (‰). a) Holocene (red) and LIG (blue) $\delta^{13}\text{C}$ for each core (points) between 1,000 m and 3,000 m. Dotted lines are the moving averages of the cores. Solid lines indicate the results of our statistical model at 2,000 m. b) Average $\delta^{13}\text{C}$ for each record deeper than 1,000 m as a proportion of the end-members. A value of one indicates the NADW end-member and a value of zero the AABW end-member. Solid lines show the linear regressions of the records.

260 Using $\delta^{13}\text{C}$ of the end-members for NADW and AABW, we use a simple binary mixing model for all cores deeper than 1,000 m to estimate changes in NADW penetration (Fig. 8b). The LIG and Holocene $\delta^{13}\text{C}$ slopes in the Atlantic are similar, indicating similar southward penetration of NADW during both time periods. This suggests that the differences in $\delta^{13}\text{C}$ between the two time periods is most likely due to change in end-member values, while the mean Atlantic oceanic circulation was likely similar.

265 Based on our analysis, there appears to be no significant difference in the mean time-averaged AMOC between the LIG and the Holocene. Negative LIG-Holocene anomalies are found for each of the smaller regions selected (northeast Atlantic, equatorial Atlantic, southeast Atlantic, and eastern equatorial Pacific), with statistical significance seen in all regions except the equatorial Atlantic, where an unusual low $\delta^{13}\text{C}$ value in one core is responsible for narrowing the difference between the two period means. Additionally, our volume-weighted mean $\delta^{13}\text{C}$ estimates have similar anomalies in the Atlantic and Pacific Oceans (-0.21 ‰ and -0.27 ‰ respectively, Fig. 6).

270 4 Discussion

One of the goals of our study is to assess the mean change in oceanic $\delta^{13}\text{C}$ between the LIG and the Holocene. Given the uncertainties in the chronologies, avoiding data that pertains to deglaciation, and capturing the same length of time during the LIG and the Holocene, we chose the periods 125 to 120 ka BP for the LIG and 7 to 2 ka BP for the Holocene. Using a similar geographical distribution of data points for both periods, we find that the oceanic $\delta^{13}\text{C}$ was ~ 0.2 ‰ lower during the LIG than 275 the Holocene.

Our analysis of the $\delta^{13}\text{C}$ signal suggests consistent LIG-Holocene $\delta^{13}\text{C}$ anomalies in different regions of the Atlantic basins, as well as in the Pacific and Indian Oceans, even if there are significant uncertainties with the later due to fewer available records. The $\delta^{13}\text{C}$ distribution in the Atlantic Ocean suggests that there was no significant mean change in the southward penetration or depth of NADW during the LIG (125–120 ka BP) compared to the Holocene (7–2 ka BP). A statistical reconstruction 280 of the early LIG (128–123 ka BP) $\delta^{13}\text{C}$ compared to our 125–120 ka BP reconstruction does not reveal a significant difference in either the NADW core depth or NADW extent as indicated by the meridional $\delta^{13}\text{C}$ gradients (Fig. S2). The volume weighted average $\delta^{13}\text{C}$ during the early LIG is 0.06 ‰ lighter than during the LIG period considered here (125–120 ka BP). Since both time slices (128–123 ka BP and 125–120 ka BP) are 5 ka averages and include dating uncertainties of ~ 2 ka, it is not possible to resolve potential centennial-scale oceanic circulation changes (e.g. Galaasen et al., 2014b; Tzedakis et al., 2018).

285 Explanations for the 0.2 ‰ lower $\delta^{13}\text{C}$ anomaly in the ocean may include a redistribution between the ocean-atmosphere system. Such a redistribution can result from a change in end-member values (Fig. 8). As fractionation during air-sea gas exchange is temperature dependent, globally higher SSTs at the LIG could lead to a lower oceanic $\delta^{13}\text{C}$. However, the effect of this is likely small (Brovkin et al., 2002) and would also lead to a higher atmospheric $\delta^{13}\text{C}$ at the LIG, which is inconsistent with Antarctic ice core measurements that suggest an anomaly of -0.3 ‰ (Schneider et al., 2013). Lower nutrient utilisation in 290 the North Atlantic would decrease surface ocean $\delta^{13}\text{C}$ and thus the $\delta^{13}\text{C}$ end-members. However, this would also imply that less organic carbon would be remineralised at depth. Therefore, it is unlikely that the lower average oceanic mean $\delta^{13}\text{C}$ results from a change in end-members through lower surface ocean nutrient utilisation. Currently, there is still a lack of constraints on

nutrient utilisation in these end-member regions during the LIG compared to the Holocene. Therefore, the lower $\delta^{13}\text{C}$ in the ocean-atmosphere system cannot be explained by a simple redistribution of $\delta^{13}\text{C}$ between the atmosphere and the ocean.

295 An alternative explanation for the anomaly is a change in the terrestrial carbon storage, which has a typical signature of approximately -37 to -20 ‰ for C3 derived plant material (Kohn, 2010) and -13 ‰ for C4 derived plant material (Basu et al., 2015). The total land carbon content at the LIG is poorly constrained. Proxies generally suggest extensive vegetation during the LIG compared to the Holocene (CAPE, 2006; Govin et al., 2015; Larrasoana et al., 2013; Muhs et al., 2001; Tarasov et al., 2005; de Vernal and Hillaire-Marcel, 2008), which would imply a greater land carbon store. However, other terrestrial carbon
300 stores including peatlands and permafrost may also have differed during the LIG compared to the Holocene. With an estimated ~ 550 Gt C stored in peats today (mean $\delta^{13}\text{C} \sim -28$ ‰, Dioumaeva et al. (2002); Novák et al. (1999)) and $\sim 1,000$ Gt C in the active layer in permafrost, which may have been partially thawed during the LIG (Reyes et al., 2010; Schuur et al., 2015; Stapel et al., 2018), less carbon stored in peat and permafrost at the LIG could have led to a lower total land carbon store compared to the Holocene. However, it is not possible to infer this total land carbon change from the oceanic and atmospheric
305 $\delta^{13}\text{C}$ anomalies because it cannot be assumed that the mass of carbon and ^{13}C is preserved within the ocean-atmosphere-land biosphere system on glacial-interglacial timescales. There is indeed continuous exchange of carbon and ^{13}C between the lithosphere and the coupled ocean, atmosphere and land biosphere carbon reservoirs. Isotopic perturbations associated with changes in the terrestrial biosphere are communicated to the burial fluxes of organic carbon and CaCO_3 and are therefore attenuated on multi-millennial time scales (Jeltsch-Thömmes et al., 2019; Jeltsch-Thömmes and Joos, 2020). Nevertheless,
310 when hypothetically neglecting any exchange with the lithosphere, we find that the change in terrestrial carbon needed to explain the difference in $\delta^{13}\text{C}$ would be in the order of 310 ± 44 Gt C less during the LIG than the Holocene (Text S1).

In addition, due to the warmer conditions at the LIG than during the Holocene, there could have been a release of methane clathrates which would have added isotopically light carbon ($\delta^{13}\text{C}$: ~ -47 ‰) to the ocean-atmosphere system. However, available evidence suggests that geological CH_4 sources are rather small (Bock et al., 2017; Dyonisius et al., 2020; Hmiel
315 et al., 2020; Saunois et al., 2020) making this explanation unlikely, although we cannot completely exclude the possibility that the geological CH_4 source was larger at the LIG than the Holocene. Similarly, since $\delta^{13}\text{CO}_2$ from volcanic outgassing has a similar value to atmospheric $\delta^{13}\text{CO}_2$ (Brovkin et al., 2016) and modelling suggests volcanic outgassing likely only had a minor impact on $\delta^{13}\text{CO}_2$ (Roth and Joos, 2012), it is unlikely that volcanic outgassing of CO_2 played a significant role in influencing the mean oceanic $\delta^{13}\text{C}$.

320 While changes in terrestrial carbon could have impacted the oceanic $\delta^{13}\text{C}$ at the LIG, the LIG-Holocene differences in the isotopic signal of both the atmosphere and ocean were most likely due to a long-term imbalance between the isotopic fluxes to and from the lithosphere, including the net burial (or redissolution) of organic carbon and CaCO_3 in deep-sea sediments, and changes in shallow water sedimentation and coral reef formation (Jeltsch-Thömmes and Joos, 2020).

5 Conclusions

325 We present a new compilation of benthic $\delta^{13}\text{C}$ from 130 to 115 ka BP covering the LIG. Over this time period, benthic $\delta^{13}\text{C}$ generally display a maximum value at ~ 121 ka BP (± 2 ka), in phase with the maximum atmospheric $\delta^{13}\text{CO}_2$ (LIG value of -6.5 ‰ at ~ 120 ka BP). As there are significant chronological uncertainties associated with LIG records, we analyse data between 125 and 120 ka BP to avoid data associated with millennial-scale events and the deglaciation. We compare this LIG benthic $\delta^{13}\text{C}$ data to a similar database covering the Holocene (7–2 ka BP). We find that during these specific time periods, 330 LIG oceanic $\delta^{13}\text{C}$ was about 0.2 ‰ lower than during the Holocene. This anomaly is consistent across different regions in the Atlantic Ocean. Even though there are less records available, benthic $\delta^{13}\text{C}$ data from the Pacific Ocean also support an anomaly of about 0.2 ‰.

An analysis of $\delta^{13}\text{C}$ gradients across the Atlantic Ocean suggests that there were no significant changes in mean, long-term ocean circulation between the two intervals. While reduced high northern latitude peat and permafrost caused by higher 335 temperatures at the LIG than during the Holocene (Otto-Bliesner et al., 2020) could have lead to a lower atmospheric and oceanic $\delta^{13}\text{C}$, the most likely explanation for the lower LIG oceanic $\delta^{13}\text{C}$ is a long term imbalance in the weathering and burial of carbon. Additional studies are required to further constrain the LIG carbon balance.

Data availability. The data is published on Research Data Australia at DOI <https://doi.org/10.26190/5efe841541f3b>.

Author contributions. SAB, LCM, and KJM designed the research. CDP and LEL provided significant portions of the $\delta^{13}\text{C}$ data. SAB, 340 LCM, KJM, and LM analysed the data and developed the methodology. FJ assisted in the interpretation of the results. SAB prepared the manuscript with contributions from all co-authors.

Competing interests. The authors declare that they have no conflict of interest.

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