Enhanced ocean-atmosphere carbon partitioning via the carbonate counter pump during the last deglacial

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Several synergistic mechanisms were likely involved in the last deglacial atmospheric $pCO_2$ rise. Leading hypotheses invoke a release of deep-ocean carbon through enhanced convection in the Southern Ocean (SO) and concomitant decreased efficiency of the global soft-tissue pump (STP). However, the temporal evolution of both the STP and the carbonate counter pump (CCP) remains unclear, thus preventing the evaluation of their contributions to the $pCO_2$ rise. Here we present sedimentary coccolith records combined with export production reconstructions from the Subantarctic Pacific to document the leverage the SO biological carbon pump (BCP) has imposed on deglacial $pCO_2$. Our data suggest a weakening of BCP during the phases of carbon outgassing, due in part to an increased CCP along with higher surface ocean fertility and elevated [CO$_2$aq]. We propose that reduced BCP efficiency combined with enhanced SO ventilation played a major role in propelling the Earth out of the last ice age.
The Southern Ocean (SO) is a key part of the global overturning circulation as it witnesses the outcropping of carbon- and nutrient-rich Circumpolar Deep Water (CDW) in the Antarctic Zone (AZ), as a result of wind-driven (Ekman) upwelling\(^1\). A portion of these upwelled waters flow southwards to feed the abyssal circuit to form Antarctic Bottom Water (AABW), while the remainder flows to the North to feed Subantarctic Surface Waters (SSW) that mix with warm subtropical waters to form Antarctic Intermediate Waters (AAIW) and Subantarctic Mode Waters (SAMW), the mid-depth oceanic tropical waters to form Antarctic Intermediate Waters (AAIW) Subantarctic Surface Waters (SSW) that mix with warm sub-

water (AABW), while the remainder of this mixed ocean water supplies nutrients to the low-latitude thermocline\(^1,2\). The STP, that is the net downward flux of carbon associated with oceanic matter export, counteracts carbon evasion to the atmosphere, as a fraction of the photosynthetic biomass that fixes dissolved inorganic carbon (DIC) in the sunlit ocean is exported and remineralized in the ocean interior. However, owing to iron (Fe) limitation on phytoplankton growth\(^14\), the pre-industrial SO STP was unable to fully compensate the CO\(_2\) outgassing and this area represented one of the main oceanic sources of natural CO\(_2\) to the atmosphere\(^1\).

During the last ice age, the deep circuit was probably more isolated from the atmosphere due to increased sea-ice coverage\(^6\) and increased stratification\(^7,8\). Meanwhile, the STP, fueled by enhanced deposition of Fe-bearing dust that favored a more complete macronutrient uptake by phytoplankton, might have been more efficient\(^9,10\). Therefore, reduced rates of vertical exchange combined with a more efficient STP promoted the storage of CO\(_2\) in the ocean abyss, thereby contributing to lowering atmospheric CO\(_2\)\(^12\).\(^{11}\)

The collapse of vertical \(\Delta^{14}C\) and \(\delta^{13}C\) gradients in the SO suggests that more vigorous deep and mid-depth circulations would have reconnected the deep carbon reservoir to the surface during Heinrich Stadial 1 (HS1, 17.5–14.7 kyr BP) and the Younger Dryas (YD, 12.8–11.5 kyr BP), thus promoting the transfer of respired carbon to the surface ocean and the atmosphere\(^13,14\). These observations have been corroborated by sedimentary geochemical data suggesting that surface waters of the Subantarctic Atlantic and the Eastern Equatorial Pacific (EEP), which derive from water upwelled in the SO, became a substantial circuit that supplies nutrients to the low-latitude thermocline\(^1,2\). and Subantarctic Mode Waters (SAMW), the mid-depth oceanic tropical waters to form Antarctic Intermediate Waters (AAIW) Subantarctic Surface Waters (SSW) that mix with warm sub-

Water (AABW), while the remainder

\(^{1}\) This single-celled phytoplankton group has unique effects on the marine carbon cycle\(^24\). The production of particulate inorganic carbon (PIC) by calcifying plankton in the sunlit ocean and its contribution of the CCP, despite its fundamental role in the marine carbon cycle\(^24\). The production of particulate inorganic carbon (PIC) by calcifying plankton in the sunlit ocean and its eventual dissolution in the subsurface engenders a surface-to-depth alkalinity gradient, causing CO\(_2\) to be released back to the atmosphere\(^24\). As such, the CCP acts to partially offset the air-sea partitioning of carbon associated with the STP.

Therefore, it is crucial to overcome these important shortcomings by focusing on the production pattern of specific phytoplankton groups from a broad range of locations within the SAZ and evaluating their impact on the carbon cycle. Coccolithophores are relevant for addressing this outstanding issue. Here, we explore the deglacial calcification pattern of coccolithophores, particularly the Noelaerhabdaceae family, in a well-dated sediment core\(^13\), retrieved from the Chilean margin (MD07-3088; 46.1°S, 75.7°W, 1536 m water depth), at the transition of AAIW and the Pacific deep water (PDW)\(^2\) (Fig. 1 and Methods). This site is located within the Antarctic Circumpolar Current (ACC) under the direct influence of the northward transport of nutrient-rich SSW\(^2\) and relatively far from the main dust sources today, but likely also in the past\(^22\). As such, this core represents a suitable archive to document the deglacial rise in atmospheric CO\(_2\) at a decadal timescale. Our study highlights that changes in biological export production in high southern latitudes operated synergistically with physical mechanisms thereby enhancing the transfer of carbon from the ocean to the atmosphere during the last deglaciation. The reinvigoration of the SO vertical mixing contributed to the release of respired carbon and regenerated nutrients to the SAZ that promoted planktonic calcification, thereby increasing the CCP, and concomitantly weakening the BCP.

**Results and discussion**

Increase in SSW fertility and [CO\(_2\)_aq] during SO upwelling. In Fig. 2, we present coccolith abundance and mass (Fig. 2a, c, d, i) from sediment core MD07-3088 (Methods) that are compared to \(\Delta^{14}C\) and \(\delta^{13}C\) reconstructions from the same core\(^4\) (Fig. 2f, g), coccolith abundances from the SE Pacific\(^29\) (ODP 1233, Fig. 2b; Methods and Supplementary Fig. 1), biogenic opal flux from the South Atlantic\(^30\) (TN057-13-4PC, Fig. 2h), \(^{61}B\)-based \(\Delta\text{PCO}_2\) from the EEP\(^15\) (ODP 1238, Fig. 2j; Methods; Supplementary Fig. 1), and local summer SST estimates\(^14,31\) (Fig. 2e), to better understand their relationships to productivity and ocean circulation patterns on a regional scale (Figs. 1 and 2). Coccolithophore calcification patterns are not affected by diagenetic alteration, with no evidence of coccolith dissolution (Methods and Supplementary Fig. 2). Noelaerhabdaceae coccolith abundance features three distinct deglacial peaks (18.6–18.2, 17.7–16.2, 11.5 kyr BP), thus promoting the transfer of respired carbon to the surface ocean and the atmosphere during the last deglaciation. The reinvasion of the SO vertical mixing contributed to the release of respired carbon and regenerated nutrients to the SAZ that promoted planktonic calcification, thereby increasing the CCP, and concomitantly weakening the BCP.

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West Antarctic Ice Sheet Divide ice core56 (WDC, 79.5°S, 112.1°W, 1766 m above sea level) and the YD (Fig. 2a). Within Subantarctic ecosystems located typically modulated by the supply of dissolved phosphate (PO43−) away from the main dust sources, phytoplankton growth is plotted with the Ocean Data View (ODV) software68 with WOA0969. Solid black lines represent the Subtropical (STF), Subantarctic (SAF), Polar (PF) and SAF and the STF respectively.

4PC30 (53.2°S, 5.1°E, 2850 m), and sites ODP 123329 (41.0°S, 74.4°W, 838 m) and 123815 (1.5°S, 82.5°W, 2203 m). The solid white square highlights the Subantarctic Circumpolar Current (SACCF) Fronts70. The Polar Frontal and Subantarctic Zones are the regions between the PF and SAF, and between the SAZ29 as well as opal fluxes in the AZ at sites influenced by similar processes30. This suggests that the inferred changes in productivity were neither limited to a specific phytoplankton group nor a specific area, but rather highlight a regional sensitivity of phytoplankton growth to ocean circulation and nutrient supply from below.

The second outstanding feature of the micropalaeontological records relates to the ~50% distinct increases in the mean Noëlaerhabdaceae coccolith mass (Fig. 2i), coincident with changes in coccolith area associated to changes in cell sizes27,28,42 and as with increasing surface water δ13C values in the EEP15 (Fig. 2j; Methods; Supplementary Fig. 1). Numerous studies related coccolith mass to the degree of coccolith calcification in Pleistocene and recent sediments39–41. Indeed, variations in coccolith mass can, under some circumstances, reflect variations in the thickness of an individual coccolith, and therefore relates to the calcite quota of a given cell27. However, changes in coccolith mass may additionally be driven by changes in coccolith area associated to changes in cell sizes27,28,42 and as such coccolith mass must be size-normalized to represent the calcite quota of a given cell27.
the Noëlaerhabdaceae family\textsuperscript{43} (Supplementary Fig. 2). We find that changes in coccolith mass typically reflect changes in coccolith thickness (Fig. 3), suggesting that they document changes in the coccosphere calcite quota. Our assumptions are further corroborated by the clear positive relationship that exists between coccolith mass and the size normalized thickness index “SN”\textsuperscript{27,44} (Methods) ($r^2 = 0.73$) as well as the coccolith aspect ratio “AR”\textsuperscript{28} (Methods) ($r^2 = 0.63$) (Fig. 3), which both document the degree of Noëlaerhabdaceae coccolith calcification.

Batch culture experiments provided conflicting responses related to coccolithophore calcification rates with studies reporting both depressed\textsuperscript{45,46} or elevated\textsuperscript{47} calcification under high [CO$_2$\textsubscript{aq}]. However, in the geological record—when general selection for growth strategies\textsuperscript{48} and phenotypic plasticity naturally occurred and regulated the carbon acquisition within the cell\textsuperscript{48}—more heavily calcified coccoliths were systematically associated with increased atmospheric pCO$_2$\textsuperscript{27,28,49,50}. Indeed, high pCO$_2$ favors intracellular competitive reallocation of dissolved bicarbonate (HCO$_3^-$) from the site of photosynthesis (chloroplast) to the site of calcification (coccolith vesicle)\textsuperscript{68}. Such processes may be relevant in coastal ecosystems such as the Chilean margin, where highly calcified _E. huxleyi_ morphotypes thrive under low-pH sea-surface conditions\textsuperscript{49}. Therefore, it is most likely that more heavily calcified coccoliths reported from site MD07-3088 at times when the upwelling of CO$_2$-rich deep waters increased, reflect increasing surface [CO$_2$\textsubscript{aq}] and highlight the equatorward advection of SSW together with AAIW/SAMW, thus supporting the mechanisms behind upper-ocean acidification previously documented in the SAZ and the EEP during these time intervals\textsuperscript{15}. The 50% increase in Noëlaerhabdaceae mass observed both during HS1 and YD occurred at times of ~2–3 µmol/L rises in SSW [CO$_2$\textsubscript{aq}] in the SAZ\textsuperscript{15}, which is in the exact same order of magnitude than the coccolith mass and [CO$_2$\textsubscript{aq}] increases (50%, ~3 µmol/L respectively) previously documented for the penultimate deglaciation within the southernmost Pacific\textsuperscript{28}. We cannot exclude that increased temperatures during major upwelling phases (~+4 °C during HS1, and ~+3 °C during YD\textsuperscript{14,31}) may have partially contributed in promoting coccolith production and calcification\textsuperscript{51,52}, but warming was not always in phase with the coccolith patterns, and may thus be of secondary importance (Fig. 2).

**Reduced BCP due to increased CCP during SO upwelling.** Sedimentary bromine (Br) and calcium (Ca) have been shown to be associated with biogenic organic carbon and carbonate in marine sediment records, respectively. Br is primarily associated with marine organic matter\textsuperscript{52} as it is directly involved in the marine biological cycle and in non-biological reactions in the water-column that implicate marine organic matter\textsuperscript{53}. Calcium may be of detrital, biogenic or diagenetic origin. At site MD07-3088, the organic origin of Br is clear as testifying by the overall excellent linear correlation with discrete TOC measurements ($r^2 = 0.87$; Supplementary Fig. 3) as well as with the δ$^{13}$C and C/
Fig. 3 Noëlaerhabdaceae coccolith morphometrics, and their response to excepted [CO2aq] at site MD07-3088 over the last deglaciation. a-d Relationships between coccolith mass (pg) and coccolith area (a), thickness (b), as well as coccolith aspect ratio (ARL) (c) and SN thickness (d) (Methods section). e-i Coccolith morphometric changes during the deglaciation: e mass (pg), f area (μm²), g thickness (μm), h-i SN27 and ARL28 indices (Methods section). Coccolith mass show no relationship with coccolith area, but clear positive relationships with size normalized coccolith mass indices ARL and SN which indicates that the mass of coccoliths typically increases in proportion with their thickness. Therefore, changes in coccolith mass document changes in the degree of coccolith calcification (i.e. PIC/POC ratio). Obviously, the Noëlaerhabdaceae coccolith mass increases observed during enhanced SO upwelling associated with higher sea surface fertility conditions (yellow shading), document increased coccosphere calcite quota in response to SSW [CO2aq] rises during HSI and YD.

![Graphs](image_url)

N values of bulk organic matter (ranging from −24.9 to 20.05% and from 7.6 to 11.5, respectively) that cluster well within the typical ranges for well-preserved marine organic components (Supplementary Fig. 4). The sediment mostly receives carbonate-free terrigenous material sourced from metamorphic and plutonic rocks of the Andes that contain negligible amounts of calcium-bearing minerals (plagioclases), while Ca and Ca/Ti report excellent correlations with CaCO3 (r² = 0.75 and 0.73, respectively; Supplementary Fig. 3) thus excluding any Ca of terrigenous origin. As for other sites from the Chilean margin located well above the lysocline (Methods), it is thus reasonable to consider that Ca is primarily associated with biogenic carbonates, and more particularly planktonic calcifiers. Indeed, bulk-sediment carbonate content fluctuations mimic those observed for the CaCO3 produced by coccolithophores and planktonic foraminifera (Fig. 4, Supplementary Fig. 3; Methods). We suggest that, in our core, POC:PIC ratio changes in the sediments likely reflect changes in the C rain ratio (POC:PIC) (Methods). Therefore, the downcore Br/Ca ratio is used to provide an estimate of the strength of the STP relative to the CCP, which serves as a robust tool to reconstruct decadal changes in the BCP efficiency (Fig. 4d). This record depicts highest values during the Late Glacial (19.6–17.7 ka), the Antarctic Cold Reversal (ACR; 14.1–12.0 ka) and the Mid Holocene (8.6–3.0 ka). On the other hand, significant reductions in Br/Ca are observed at times intense SO upwelling prevailed, particularly during HSI and the YD. These transient declines are mainly driven by changes in CaCO3 export during HSI since the TOC record is characterized by increasing values during this specific time interval (Supplementary Fig. 3), while both increasing CaCO3 and relatively high yet decreasing TOC values might be associated during the YD. Furthermore, they match the pronounced peaks in surface ocean fertility (Fig. 2a–d) as well as coccolith and planktonic foraminifera abundances and masses that are well expressed by 3-fold to 10-fold and up to 20-fold increases in the overall amount of burial CaCO3 produced by coccolithophores and planktonic foraminifera respectively, and coincide with prominent rises in atmospheric pCO2 (Fig. 4). This increase in the CCP, associated with rising macronutrient availability and thus, enhanced fertility in the SAZ, is comparable to the 6–10 folds increase in deep-ocean PIC fluxes previously documented for naturally iron-fertilized sites from the Polar Frontal Zone compared to non-fertilized ones. In both cases, increased fertility is linked to a rise of about one order of magnitude of the PIC flux, thus confirming the important role of CCP in mediating the reduction of deep-ocean CO2 storage. The impact of changing POC:PIC ratio (1/p) on pCO2 is shown in Fig. 5 for HSI and the ACR, in cases for which 10 to 50% of the exported POC is preserved in the sediments (Methods). In all cases, primary production decreased sea surface [CO2aq], as 1/p is higher than the critical value of 0.54 for which the CCP would completely counteract the STP. Nevertheless,

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during HS1, the efficiency of the BCP was reduced compared to the ACR owing to lower POC:PIC ratios. The SAZ thus became a net source of CO₂ during HS1 and the YD, due to enhanced SO upwelling of aged, CO₂-enriched deep waters and a concomitant weakening of the BCP. Indeed, the increase in calcite production by coccolithophores and planktonic foraminifera caused a decrease in surface-ocean alkalinity (ALK) (or in other words, an increase in pCO₂(aq)), thus promoting the net outgassing of carbon from the ocean interior to the atmosphere (Fig. 5). In such a scenario, the CCP would have contributed to weaken the marine BCP, with significant impact on atmospheric pCO₂ since the very beginning of the last deglaciation. The STP was not efficient enough to offset the carbon release during the last deglaciation, in part due to the contribution of the CCP. Increased planktonic calcification in the SAZ has the potential to effectively amount to a reduction of the overall POC:PIC rain ratio in the SO (Fig. 5), with significant impacts on the net flux of CO₂ from the ocean to the atmosphere.

Our study reveals the intrinsic link between BCP strength and changes in Southern Ocean circulation in coordinating the
partitioning of carbon between the ocean interior and the atmosphere during the last glacial termination. As such, much more attention should be brought to the response of calcifying plankton at other sites within the Southern Ocean but also in low latitudes, to better quantify their relative contribution in the past global pCO2 budget.

Methods

Material and site description. The CALYPSO core MD07-3088 was retrieved during the IMAGES PACHIDERME (MD 159) expedition by the French R/V Marion Dufresne during the IMAGES PACHIDERME (MD 159) expedition by the French R/V Marion Dufresne off Southern Chile (46°04' S; 075°41' W), at a water depth of 1536 m, i.e., well above the modern lysocline (around 3700 m) (Fig. 1). The site is 14C ka) was characterized by a lower difference between planktonic and benthic in order to obtain a robust common stratigraphic framework. Hence, we more attention should be brought to the response of calcifying plankton at other sites within the Southern Ocean but also in low latitudes, to better quantify their relative contribution in the past global pCO2 budget.

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would simultaneously impact all coccolith morphotypes, without any discrimination between morphotypes.

Foraminifera abundance and mass data. Planktonic foraminifera assemblages were determined at the LSCE (Laboratoire des Sciences du Climat et de l’Environnement) counting at least 300 specimens per sample. From three different depths (570, 950, and 990 cm), we weighted 30 individuals from the most abundant species (Neo globocaudina pachyderma (sinistral and dextral coiling), Globigerina bulloides, Globorotalia inflata, Tuborotalobula quinqueloba and Globigerinella glutinata) for different sizes (>450 µm, 315–450 µm, 250–315 µm, 150–250 µm) to determine their mean weight. For this core, we obtained mean weights of: 7±2 µg for N. pachyderma, T. quinqueloba, and G. glutinata, 18±5 µg for G. bulloides, and 19±5 µg for G. inflata. For Globigerinella cales, Globigerinella fuscomaculata, G. ruber, Globigerinoides hexagonus (representing <2% in all samples), Neogloboquadrina dutertrei and Huestigerina digitata (representing <0.5% in all samples), we assumed a mean weight similar to G. bulloides. At last, for Globorotalia truncatulinoides, Globorotalia crassaformis, and Globorotalia hirsuta, we assumed a mean weight similar to G. inflata. From the assemblage and the mean weight of the different species, we estimated the planktonic foraminifera calcite mass for each sample. 

\[
\text{CaCO}_3^{\text{pl, foramin, mass}} = \frac{N \times 205}{M} \times \sum (m_i \times X_i) 
\]

where N is the total amount of determined foraminifera (≥300), split is the number of split done before establishing a planktonic assemblage, M is the total dry mass of the sample (mg), \(m_i\) the weight of the species i (mg), and X_i the percentage of the species in the sample. This approach is a first order estimate of the foraminifera mass percentage as it does not fully take into account smaller species often <150 µm (such as G. aurita and partly T. quinqueloba) and juveniles. Besides, for 16 depths (covering LGM, HS1, ACR, YD and the Holocene), we weighted 6 to 60 specimens of G. bulloides (the most abundant) from different size ranges (150–200, 200–250, 250–315, 315–355, 355–400, and 400–450 µm) in order to statistically characterize potential weight changes within a narrow size range. Mean weights for the different size classes decrease of about 20% from LGM to Holocene, and of about 17 and 18% during HS1 and YD respectively. If similar weight decreases are observed within the other planktonic species, the magnitude of the changes in the overall weight (~20%) would not be sufficient enough to significantly change the estimated planktonic foraminifera mass flux. Indeed, because of the drastic increases within the planktonic foraminifera abundance during these time intervals (more than one order of magnitude), fluctuations in the planktonic foraminifera weights would imply changes in the flux of planktonic foraminifera calcite mass that remain within the error bars.

Total CaCO₃ and organic carbon analyses. Total CaCO₃ was determined at GEOPS laboratory using the vacuum-gasometric technique with a precision better than ±2%. 100 mg (±5) of crushed-dried sediments react with a few milliliters of HCl 6 N in a hermetic reaction chamber (22.4 cm³) that is connected to a manometer MANO MEX2-420 that measures the amount of outgassed CO₂. The system is calibrated so that 100 mg of CaCO₃ (100%) trigger a pressure rise to 1 bar. Total organic carbon and nitrogen contents together with organic matter fractionation processes only. The data that support the findings of this study are available from the corresponding author (S.D.-A.) upon reasonable request.

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