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Abruptly attenuated carbon sequestration with Weddell Sea dense waters towards the end of the 21st century

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Abstract

Antarctic Bottom Water formation, such as in the Weddell Sea, is an efficient vector for carbon sequestration on time scales of centuries. Possible changes in carbon sequestration under changing environmental conditions are unquantified to date, mainly due to difficulties in simulating the relevant processes on high-latitude continental shelves. Using a model setup including both ice-shelf cavities and oceanic carbon cycling, we demonstrate that by 2100, deep-ocean carbon accumulation in the southern Weddell Sea is abruptly attenuated to only 40% of the rate in the 1990s in a high-emission scenario, while still being 4-fold higher in the 2080s. Assessing deep-ocean carbon budgets and water mass transformations, we attribute this decline to an increased presence of Warm Deep Water on the southern Weddell Sea continental shelf, a 16% reduction in sea-ice formation, and a 79% increase in ice-shelf basal melt. Altogether, these changes lower the density and volume of newly formed bottom waters and reduce the associated carbon transport to the abyss.

19 Introduction

20 Due to its unique setting in the global overturning circulation¹, the Southern Ocean plays an important role in
21 the partitioning of carbon between the atmosphere and the deep ocean. Early box models^{2–4} and later also
22 general ocean circulation models⁵ demonstrated that the formation of Antarctic Bottom Water (AABW) at
23 high southern latitudes facilitates carbon sequestration on centennial to millennial time scales⁶ and therefore
24 exerts a strong control on global atmospheric CO₂ concentrations and climate. Despite this recognized im-
25 portance on climatically relevant time scales^{2–4}, no quantitative information exists to date about the amount
26 of carbon sequestered during the formation of AABW and its importance relative to deep carbon accumula-
27 tion through sinking biotic particles⁶. In fact, the difficulty of ocean models to correctly simulate all processes
28 involved in AABW formation^{7,8} and the scarcity of observational data in its formation regions on the Antarctic
29 continental shelves⁹ complicate both the assessment of present-day AABW formation and carbon seques-
30 tration rates, as well as the detection of climate change impacts. This is true even for the Weddell Sea in the
31 Atlantic sector of the Southern Ocean, which since the 1930s has been recognized as the most important
32 AABW formation region^{10,11} and is the best observed one to date¹².

33 Generally, the formation of AABW can be divided into two steps^{13–16}: First, open-ocean water masses
34 flowing into the southern Weddell Sea on the eastern flank of the cyclonic Weddell Gyre^{17,18} are transformed
35 to Dense Shelf Water (DSW) as a result of the buoyancy loss caused by atmosphere–ocean, sea ice–ocean,
36 and ice shelf–ocean interactions¹⁴ (Fig. 1). The densification of waters thereby predominantly occurs on
37 the southwestern Weddell Sea continental shelf as a result of heat loss and local sea-ice formation; it is
38 to some extent counteracted by precipitation and meltwater fluxes from the Filchner-Ronne and Larsen ice
39 shelves^{19–24}. Second, the DSW cascades down the continental slope forming either Weddell Sea Deep
40 Water (WSDW; potential temperature $-0.7^{\circ}\text{C} \leq \theta_0 < 0^{\circ}\text{C}$ ¹⁷) or Weddell Sea Bottom Water (WSBW; $\theta_0 < -$
41 0.7°C ¹⁷). Along the way, Warm Deep Water (WDW; the Weddell Sea variant of Circumpolar Deep Water
42 (CDW) with $\theta_0 > 0^{\circ}\text{C}$ ¹⁷) is entrained to ultimately form AABW, which then spreads throughout the abyss
43 of the global ocean^{13,14}. Integrating observations from 1973–2017, it has recently been suggested that,
44 on average, 4.5 ± 0.3 Sv of DSW formed on the Weddell Sea continental shelf in the first step entrain an-
45 other 3.9 ± 0.5 Sv of WDW on its way to the abyss, resulting in a total of 8.4 ± 0.7 Sv of AABW transported
46 northwards along the western flank of the Weddell Gyre¹⁶.

47 AABW formation in the Weddell Sea is highly variable in time^{25–27} and rather sensitive to changing envi-
48 ronmental conditions due to its close ties with buoyancy fluxes and density distributions^{14,27}. Both WSDW
49 and WSBW have been warming and freshening since the 1980s^{28–33}, which has at least partly been at-
50 tributed to property changes of newly formed DSW^{26,34}, possibly due to changes in sea-ice formation and
51 ice-shelf basal melt rates in the area³². For the 21st century, climate models project a slowdown or even
52 a complete shutdown of AABW formation under the high-emission RCP8.5 scenario⁷, as a consequence
53 of continuous warming and freshening of high-latitude waters³⁵. However, limited by the coarse resolution
54 on the Antarctic continental shelves (~ 50 km) and the absence of an ice-shelf component, many of these
55 models struggle to correctly reproduce AABW properties^{9,36} and often form AABW entirely via spurious deep
56 convection in the open ocean rather than via water mass transformations on the Weddell Sea continental
57 shelves south of the World Ocean Circulation Experiment (WOCE) transect SR4, which connects the tip
58 of the Antarctic Peninsula with the eastern Weddell Sea at Kapp Norvegia (Fig. 1)^{7,8,37}. The reduction of
59 AABW formation in response to the expected large freshwater discharge from ice shelves in the upcoming
60 decades³⁸ has recently been confirmed with higher-resolution ocean models, which better capture AABW
61 formation regions on the Antarctic shelf^{39,40}. These model experiments were, however, highly idealized with
62 prescribed freshwater input at the surface instead of the employment of a dynamic ice-shelf component in the
63 model. While ocean models including such a dynamic calculation of freshwater discharge in ice-shelf cavities
64 project an up to 15-fold increase in Weddell Sea ice-shelf basal melt rates by the year 2100^{41–46}, the relative
65 contribution of enhanced ice-shelf basal melt and reduced sea-ice formation^{42,45} to changes in Weddell Sea
66 DSW formation and the implications for carbon transfer to depth remain unquantified.

67 An improved understanding of Weddell Sea carbon cycling is urgently needed, as observations have
68 revealed substantial changes in carbon cycling in this area over the recent past^{9,47–51}: While the Weddell
69 Sea was a net source of carbon to the atmosphere in preindustrial times^{9,48}, it is currently a net sink of
70 ~ 33 –80 Tg C per year^{47,50,51}. Even though climate models suggest an up to 4-fold increase in CO₂ uptake
71 in the high-latitude Southern Ocean by the end of the 21st century⁵², it is still unclear how these projected
72 changes in air-sea CO₂ exchange might affect carbon sequestration in the deep ocean. Here, we fill this gap
73 by using a global ocean–sea ice–biogeochemical model^{53–57} with a representation of ice-shelf cavities⁵⁸ and
74 an eddy-permitting resolution on the southern Weddell Sea continental shelves. Forcing our ocean model
75 with atmospheric output from the AWI Climate Model⁵⁹, the comparison of a high-emission future scenario

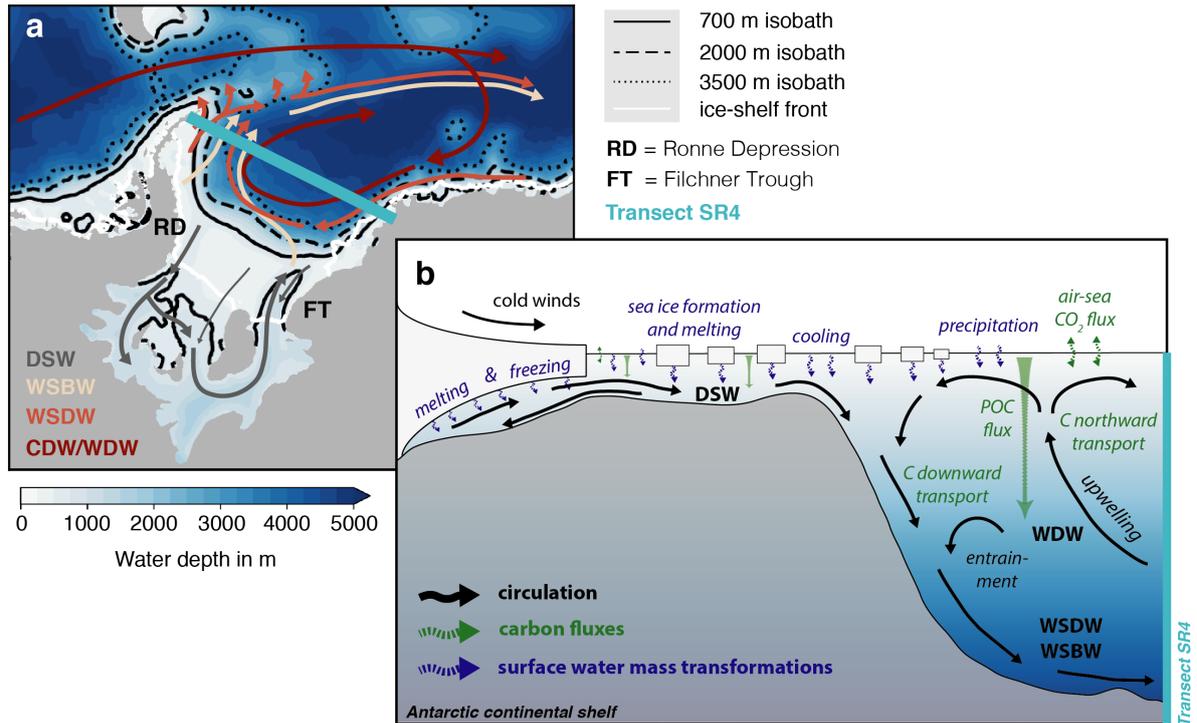


Figure 1: Sketch illustrating the major processes involved. **a** Water depth in m below the ocean surface in the Weddell Sea. Sketched on top is the general two-dimensional circulation in the area. The WOCE transect SR4 is marked in mint, and different water masses are distinguished by colors. **b** Typical section from the Antarctic continent to the transect SR4, with general features of the overturning circulation sketched in black. Highlighted in blue are surface water mass transformations by buoyancy fluxes, and carbon fluxes are marked in green. CDW: Circumpolar Deep Water, WDW: Warm Deep Water, WSDW: Weddell Sea Deep Water, WSBW: Weddell Sea Bottom Water, DSW: Dense Shelf Water, POC: particulate organic carbon.

76 (*simA*) with a control simulation in a constant climate (*simB*) suggests a reduction in deep-ocean carbon
 77 transfer in the southern Weddell Sea towards the end of the 21st century. We show that this can mainly be
 78 attributed to changes in water mass properties and water mass transformations on the southern continental
 79 shelf, which result in a reduced connectivity between the upper and the deep ocean, thereby diminishing the
 80 carbon transfer to the abyss with newly formed dense waters.

81 Results

82 **Deep-ocean carbon inventory and air-sea CO₂ exchange over the 21st century.** In the southern Weddell
 83 Sea south of the WOCE transect SR4, the total carbon inventory in the deep ocean below 2000 m increases
 84 by 0.75 Pg C between the years 1980 and 2100 under the high-emission SSP5-8.5 scenario (*simA*; Fig. 2a),
 85 which corresponds to 14% of the increase in the whole water column in this area (compare to upper-ocean
 86 carbon inventory in Supplementary Fig. 1). However, the accumulation in the deep ocean is not steady
 87 throughout the 21st century. While the deep-ocean accumulation rate of carbon amounts to 3.7 Tg C yr⁻¹
 88 in the 1990s, it increases to 14.7 Tg C yr⁻¹ in the 2080s, before abruptly declining to 1.5 Tg C yr⁻¹ in the
 89 2090s (grey bars in Fig. 2b). Over much of the 21st century, the deep-ocean carbon inventory also increases
 90 in the control simulation with a constant atmospheric CO₂ concentration and without climate-change forcing
 91 (*simB*; Fig. 2a), demonstrating that the deep ocean of the southern Weddell Sea is not fully equilibrated with
 92 the constant atmospheric CO₂ concentration (313 ppm) in this experiment, as expected from the chosen
 93 spin-up procedure (see Methods). Yet, the total increase by the year 2100 is small in *simB* (+0.27 Pg C)
 94 in comparison to *simA* (Fig. 2a), illustrating that the increase in *simA* is mostly attributable to the high CO₂
 95 and climate-change forcing scenario. Further, as we will show in the following, the mechanisms causing
 96 the changes in the deep-ocean carbon inventory in *simA* are robust, as corresponding changes in *simB* are
 97 much smaller or even opposite in sign. Any change in the deep-ocean accumulation rate of carbon can be

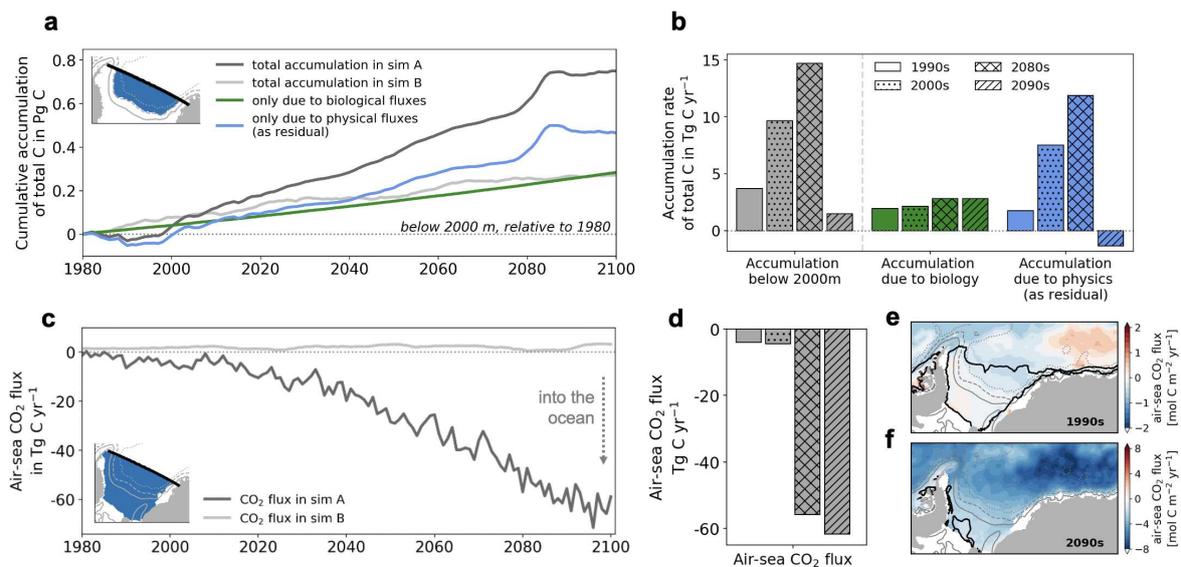


Figure 2: Deep-ocean carbon inventory and air-sea CO₂ exchange over the 21st century. **a** Cumulative carbon accumulation in Pg C below 2000 m in the southern Weddell Sea south of the WOCE transect SR4 (see blue area in inlet) in the model simulation *simA* (dark grey; historical + SSP5-8.5 scenario) and the control simulation *simB* (light grey). The contribution of biological and physical fluxes (calculated as residual) in *simA* are shown in green and blue, respectively. Biological fluxes are dominated by sinking particle fluxes (Supplementary Fig. 2). **b** Average annual total carbon accumulation rate (grey) and the contribution of biological (green) and physical (blue) fluxes in Tg C yr⁻¹ for the 1990s, 2000s, 2080s, and 2090s, as indicated by the hatching of the bars. **c** Annually integrated air-sea CO₂ flux in Tg C yr⁻¹ in the southern Weddell Sea south of the transect SR4 (see blue area in inlet) in *simA* (dark grey) and *simB* (light grey). **d** Air-sea CO₂ flux in *simA* averaged over selected decades (see panel **b** for legend). **e,f** Air-sea CO₂ flux in mol m⁻² yr⁻¹ in the Weddell Sea in the **e** 1990s and **f** 2090s. Isolines of 15% sea-ice cover in February in the respective decade are indicated by the black contours. Grey contours show the 700 m (solid), 2000 m (dashed), and 3500 m (dotted) isobaths. For panels **c-f**, a negative CO₂ flux denotes a flux into the ocean.

98 caused by changes in the downward transfer of carbon via biological fluxes (i.e., sinking particles and carbon
 99 fluxes at the sediment–water column–interface), changes in the physical transport of carbon, or changes in
 100 the upper-ocean carbon inventory due to changes in air-sea CO₂ exchange. While the southern Weddell Sea
 101 remains a small source of CO₂ to the atmosphere until the year 2100 in the control simulation (~2 Tg C yr⁻¹,
 102 see Fig. 2c), oceanic CO₂ uptake in this area in *simA* increases throughout the 21st century, amounting to
 103 62 Tg C yr⁻¹ in 2100 (Fig. 2c-f). As a consequence, also the upper ocean carbon inventory increases steadily
 104 (Supplementary Fig. 1).

105 At the same time, the deep-ocean carbon accumulation due to biological fluxes increases from 1.9 Tg C yr⁻¹
 106 in the 1990s to 2.8 Tg C yr⁻¹ in the 2090s (green bars in Fig. 2b). This increase is largely due to an enhanced
 107 sinking flux of particulate organic carbon (POC) with only a marginal contribution from sedimentary carbon
 108 release (Supplementary Fig. 2). The increased POC flux is the direct consequence of a 56% increase in
 109 biological productivity in the upper ocean south of SR4 (not shown), in response to warming and higher light
 110 availability due to the shrinking summer sea-ice cover by 2100 (Fig. 2e & f). Altogether, the steady increases
 111 in oceanic CO₂ uptake, in the upper-ocean carbon inventory, and in the downward carbon transfer with the
 112 biological pump imply that these fluxes cannot explain the simulated decline in deep-ocean carbon accumu-
 113 lation in the 2090s. Instead, this decline is dominated by changes in the physical fluxes of carbon in the
 114 model. While the deep-ocean carbon accumulation due to physical transport increases from 1.8 Tg C yr⁻¹
 115 in the 1990s to 11.9 Tg C yr⁻¹ in the 2080s, it dwindles and even changes sign in the 2090s, when all physical
 116 fluxes combined constitute a net loss of carbon from the deep ocean (1.3 Tg C yr⁻¹; blue bars in Fig. 2b).
 117 Taken together, by the end of the 21st century, the deep-ocean carbon inventory continues to increase - albeit
 118 at a much smaller rate compared to the previous decades - only due to the increased biological fluxes which
 119 outweigh the physically-driven decline.

120 **Disentangling the physical flux components contributing to deep-ocean carbon accumulation.** In

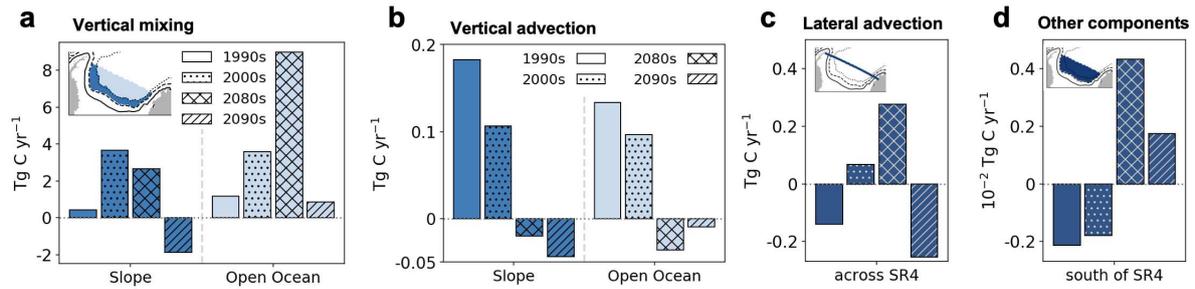


Figure 3: Divergence of physical flux components contributing to changes in the deep-ocean carbon inventory in the southern Weddell Sea. Positive fluxes denote an increase in the deep-ocean carbon inventory in the volume of interest due to the respective flux component. Changes in the total carbon inventory south of WOCE transect SR4 and below 2000 m in the model simulation *simA* (grey; historical + SSP5-8.5 scenario) due to **a** vertical mixing across 2000 m, **b** vertical advection across 2000 m, **c** lateral advection across the transect SR4, and **d** the sum of all other flux components, e.g., from the eddy parametrization. All fluxes are in Tg C yr⁻¹, but note that the fluxes in panel **d** are two orders of magnitudes smaller than those in panels **a-c**. All fluxes are shown for the 1990s, 2000s, 2080s, and 2090s, as indicated by the differences in hatching. Vertical fluxes in panels **a** & **b** are shown for the continental slope (dark blue) and the open ocean (light blue), which are separated at the 3500 m isobath (see inlet in panel **a**).

121 general, changes in the deep-ocean carbon accumulation rate due to physical transport can be due to lateral
 122 or vertical fluxes via advection or mixing. For the deep-ocean carbon budget considered here, the divergence
 123 of vertical fluxes typically dominates over the contribution by lateral fluxes (Fig. 3), as gradients in total carbon
 124 concentrations in the vertical exceed those in the lateral (Supplementary Fig. 3). In our model, vertical mixing
 125 is the dominant flux component in the southern Weddell Sea (Fig. 3a), with all others being at least one
 126 order of magnitude smaller (e.g., vertical and lateral advection; Fig. 3b-d). Consequently, vertical mixing as
 127 a signature of convection accounts for >90% of the total physically-driven carbon accumulation throughout
 128 much of the 20th and 21st century, and this flux component alone can explain most of the simulated evolution
 129 in deep-ocean carbon accumulation (compare Fig. 3a to blue bars in Fig 2b). While the slope region between
 130 the 2000 m and 3500 m isobaths contributes up to 50% to the downward transfer of carbon in the 2000s,
 131 the enhanced downward transfer in the 2080s can largely be attributed to enhanced downward mixing in
 132 the open ocean (~ 8 Tg C yr⁻¹; Fig. 3a and Supplementary Fig. 4), with only minor contributions from other
 133 components (Fig. 3b-d and Supplementary Fig. 5). The enhanced open-ocean downward mixing of carbon
 134 in the 2080s is the result of the downward mixing of relatively recently ventilated and thus carbon-enriched
 135 dense waters originating from regions upstream of the southern Weddell Sea (Supplementary Fig. 6 and
 136 Supplementary Section 1). In the 2090s, a much reduced open-ocean downward mixing (< 1 Tg C yr⁻¹) is
 137 outweighed by upward mixing along the slope and the two advective flux components, which all act to reduce
 138 the deep-ocean carbon inventory and thus explain the net loss of carbon from the deep ocean by physical
 139 fluxes in this decade (blue bars in Fig. 2b). In this context, the increasingly upwards-directed advective flux
 140 is in line with enhanced upwelling of deep waters resulting from the intensified upper ocean gyre circulation
 141 at the end of the 21st century (see barotropic stream function in Supplementary Fig. 5 and references^{9,60}
 142). Overall, the dominance of vertical physical fluxes in controlling the variability in carbon transfer to depth
 143 - in particular the attenuated transfer in the 2090s - implies that deep-ocean carbon accumulation rates are
 144 sensitive to physical processes in the overlying water column and upstream on the Weddell Sea continental
 145 shelves.

146 Indeed, bottom waters descending the continental slope in *simA* are less well connected to the upper
 147 ocean towards the end of the 21st century than they were before (Fig. 4a & c), which is explained in the
 148 following. To assess this connectivity, we use an age tracer, which tracks any water parcel's last contact with
 149 the atmosphere-ocean, sea ice-ocean, or ice shelf-ocean interface as it mixes with surrounding waters in
 150 the ocean interior in our model simulations (see Methods). Everywhere on the continental shelf south of the
 151 700 m isobath (solid black line in Fig. 4a), bottom waters are well ventilated in the 1990s, when >80% of the
 152 bottom waters have been in touch with one of these interfaces since the start of the simulation (purple colors
 153 in Fig. 4a). In comparison, bottom waters south of SR4 are far less well ventilated in the same decade both
 154 on the continental slope (50%) and in the open ocean ($< 30\%$), i.e., north of the 3500 m isobath (green colors
 155 north of the dotted black line in Fig. 4a). This is further illustrated by the far better mixed water column on
 156 the Weddell Sea continental shelf compared to in the open ocean (Supplementary Fig. 7), implying longer

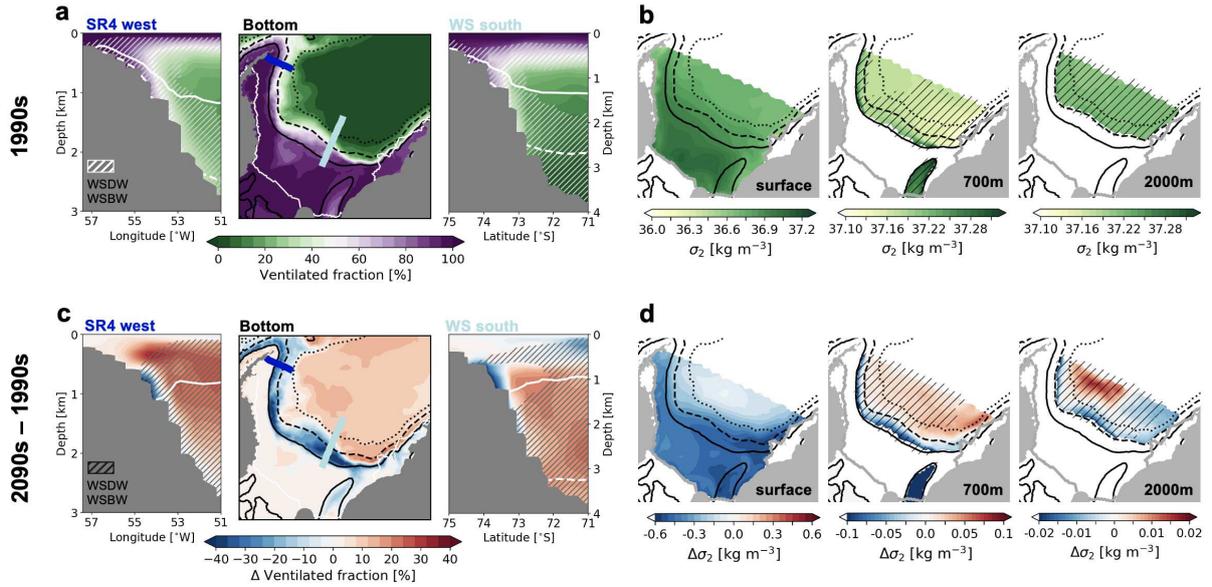


Figure 4: Bottom water ventilation and density distribution over the 21st century. **a** Age-tracer-based fraction of water that is ventilated at the bottom (middle) and across the continental slope in the western (SR4 west; left) and southern Weddell Sea (WS south; right) in the 1990s. The positions of the transects are indicated in the map as the dark blue (SR4 west) and the light blue line (WS south), respectively. **b** Distribution of potential density anomalies (σ_2 in kg m^{-3} , i.e., potential density referenced to 2000 dbar minus 1000 kg m^{-3}) at the surface, 700 m, and 2000 m in the 1990s. Note the different scales. **c,d** Same as panels **a,b**, but for the change in **c** the ventilated fraction and **d** σ_2 between the 2090s and the 1990s. In the transects in panels **a,c**, σ_2 isolines for the **a** 1990s and **c** 2090s are shown as the solid (37.2 kg m^{-3}) and dashed (37.25 kg m^{-3}) white contour, respectively. In the maps in panels **b,d**, black contours show the 700 m (solid), 2000 m (dashed), and 3500 m (dotted) isobaths. In all panels, hatching denotes the presence of Weddell Sea Deep Water and Weddell Sea Bottom Water in the **a,b** 1990s and **c,d** 2090s, defined in the model as waters with a potential temperature $< -0.2^\circ\text{C}$ and a practical salinity > 34.55 .

157 time scales associated with bottom water ventilation in the open ocean than on the continental shelf. In the
 158 2090s, the ventilation rate remains largely unchanged on the continental shelf, but declines profoundly along
 159 the slope (locally by more than 40%, Fig. 4b), demonstrating a reduced connectivity between the continental
 160 shelf and the deep ocean by the year 2100. Changes in the density distribution support this finding: While
 161 the densities at 700 m and 2000 m in the open ocean mostly increase in response to the intensification of the
 162 gyre circulation and the corresponding increase in upwelling over the 21st century (Supplementary Fig. 5),
 163 densities close to the continental slope decline by up to 0.2 kg m^{-3} and 0.033 kg m^{-3} at 700 m and 2000 m,
 164 respectively (potential density referenced to 2000 dbar; Fig. 4d). In fact, while isopycnals of high density,
 165 i.e., $\sigma_2 > 37.2 \text{ kg m}^{-3}$, are connected to the continental shelf sea in the 1990s (white isolines in Fig. 4a),
 166 providing a pathway of WSDW and WSBW into the abyss, this connectivity is absent by 2100 (Fig. 4c). As
 167 a consequence, this implies major changes in water mass properties and transformations on the southern
 168 Weddell Sea continental shelves, where new dense waters are typically formed.

169 **Changes in water mass properties and dense water formation on the Weddell Sea continental shelf.**
 170 Under the high-emission SSP5-8.5 scenario, water mass properties are projected to change throughout the
 171 water column on the southern Weddell Sea continental shelf (Fig. 5). While the decline in density is largest at
 172 the surface ($\Delta\sigma_2 < -0.5 \text{ kg m}^{-3}$ at the continental shelf break along the 700 m isobath; Fig. 5e & f and Fig. 4d),
 173 the average decline in bottom density on the shelf is still significant, amounting to 0.28 kg m^{-3} (Fig. 5a). This
 174 decline is due to a combination of a pronounced freshening (-0.31 in salinity; Fig. 5b) and warming ($+0.35^\circ\text{C}$;
 175 Fig. 5c) of bottom waters by the end of the 21st century. Concurrently, the total heat content on the shelf
 176 increases by 66% (Fig. 5d), reflecting both an increased presence of WDW on the shelf and the reduction of
 177 heat loss to the atmosphere. Most of these simulated changes can be attributed to the climate-change forcing
 178 scenario, as trends in these properties in the control experiment *simB* are much smaller or even opposite in
 179 sign (light grey bars in Fig. 5a-d). As a result, keeping the definition of the water masses unchanged, less
 180 DSW has temperature ($< -0.2^\circ\text{C}$) and salinity (> 34.55 ; see also Methods) properties of WSDW or WSBW in
 181 the 2090s as compared to in the 1990s. While most waters at the continental shelf break fulfill these criteria in

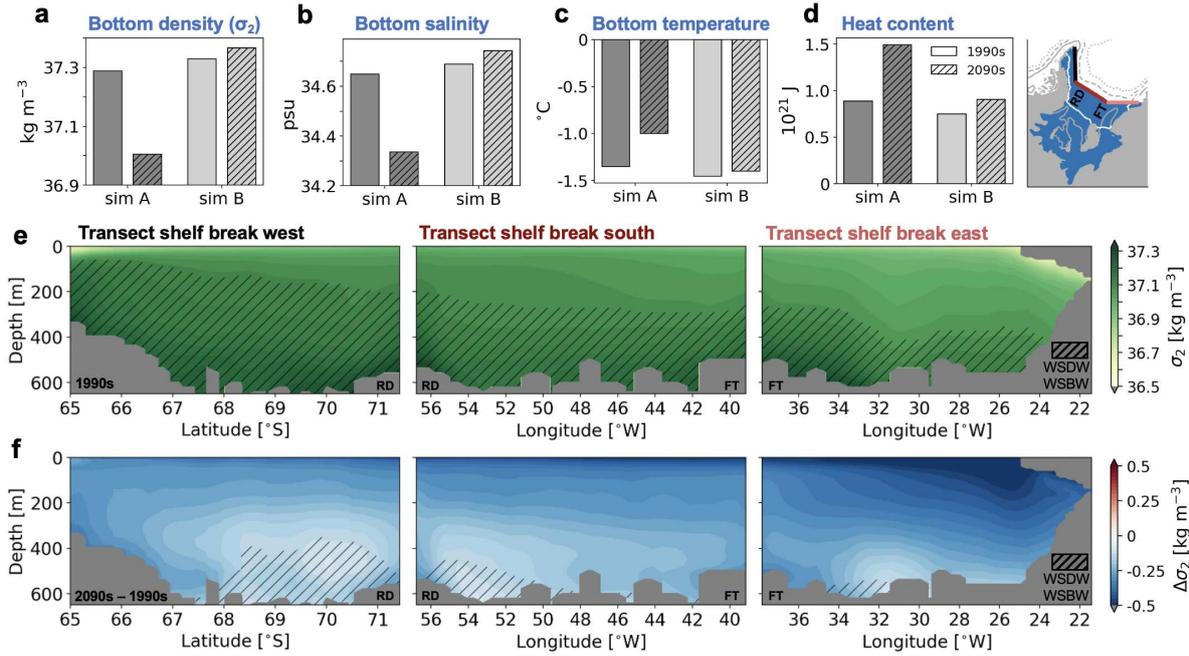


Figure 5: Changes in water mass properties on the Weddell Sea continental shelf. **a** Bottom potential density anomaly referenced to 2000 dbar (σ_2) in kg m^{-3} on the shelf (blue area in the map) in the 1990s (plain bar) and 2090s (hatched bar) in the experiment *simA* (dark grey; historical + SSP5-8.5 scenario) and in the control simulation *simB* (light grey). **b-d** Same as panel **a**, but for **b** bottom salinity, **c** bottom potential temperature in $^{\circ}\text{C}$, and **d** total heat content in 10^{21} J. **e** Distribution of potential density anomalies (σ_2 in kg m^{-3} , i.e., potential density referenced to 2000 dbar minus 1000 kg m^{-3}) at a transect along the continental shelf break (see black line in map) in the 1990s. **f** Same as panel **e**, but for the change in σ_2 between the 2090s and the 1990s. Hatching in panels **e** & **f** denotes the presence of Weddell Sea Deep Water and Weddell Sea Bottom Water in the **e** 1990s and **f** 2090s, defined in the model as waters with a potential temperature $< -0.2^{\circ}\text{C}$ and a practical salinity > 34.55 . The approximate positions of the Ronne Depression (RD) and the Filchner Trough (FT) are indicated.

182 the 1990s (61% of the total ocean area; Fig. 5e), the area covered by these dense waters has shrunk to only
 183 13% by the year 2100 (Fig. 5f), thereby ultimately affecting the water mass properties of newly formed AABW
 184 in the southern Weddell Sea. In fact, the reduction in bottom density at the shelf break is most pronounced
 185 where shelf water is exported to the abyss, namely in the Filchner Trough and in the northwestern Weddell
 186 Sea (-0.3 kg m^{-3} ; Fig. 5f), and is smallest in the Ronne Depression (-0.1 kg m^{-3}), where most newly formed
 187 dense waters enter the ice-shelf cavity and undergo freshening before leaving the shelf via the Filchner
 188 Trough (see Fig. 1 and reference¹⁹). Therefore, the overall lower density of DSW at the end of the 21st
 189 century directly affects the transfer of these dense waters from the continental shelf to the deep ocean (see
 190 white isolines in Fig. 4a) and suggests significant changes in water mass transformation on the continental
 191 shelf.

192 The densification of waters in the southern Weddell Sea can be assessed in the water mass transfor-
 193 mation (WMT) framework, which relates surface density distributions to buoyancy fluxes at the atmosphere-
 194 ocean, sea ice-ocean, or ice shelf-ocean interface and from which areas and formation rates of downwelling
 195 dense water masses can be derived (see Methods and references^{40,61-64}). Total WMT rates are largely posi-
 196 tive on the Weddell Sea continental shelf (black lines in Fig. 6a), indicating an overall densification of surface
 197 waters by buoyancy fluxes in this area, which is in agreement with observations¹⁷. In the 1990s, the forma-
 198 tion of dense waters on the southern Weddell Sea continental shelf amounts to 5.4 Sv in *simA* (peak in solid
 199 black line in Fig. 6a), fairly close to the recent observation-based estimate of $4.5 \pm 0.3 \text{ Sv}$ ¹⁶. In this region, it
 200 can mostly be attributed to net sea-ice growth (blue line in Fig. 6a), with only small modifications by ice-shelf
 201 freshwater fluxes (mint line in Fig. 6a), which counter the densification of waters by sea-ice formation and
 202 without which dense-water formation in the area would be $\sim 0.6 \text{ Sv}$ higher. In response to the environmental
 203 change over the course of the 21st century, sea-ice formation is projected to be 16% lower and ice-shelf
 204 basal melting 79% higher in the 2090s than in the 1990s (Fig. 6c & d). Southern Weddell Sea dense water

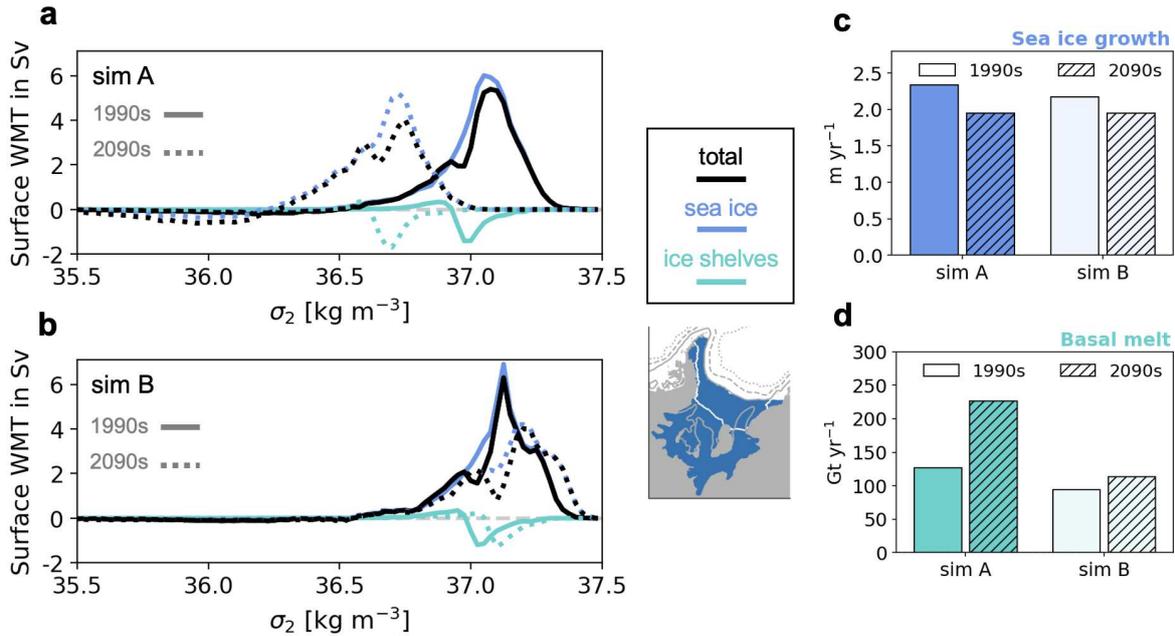


Figure 6: Water mass transformations due to surface buoyancy fluxes on the southern Weddell Sea continental shelf. **a, b** Surface water mass transformation rates (WMT) in Sverdrup (Sv; 1 Sv is $1 \cdot 10^6 \text{ m}^3 \text{ s}^{-1}$) as a function of the density anomaly (σ_2 ; potential density referenced to 2000 dbar; kg m^{-3}) due to the total buoyancy flux (black) and due to buoyancy fluxes from sea ice (blue) and ice shelves (mint) on the southern Weddell Sea continental shelf (see blue area in map) in the 1990s (solid) and 2090s (dotted) from **a** *simA* (historical + SSP5-8.5 scenario) and **b** the control simulation *simB*. Positive transformations denote a densification of surface waters due to buoyancy fluxes. Transformations due to heat fluxes and freshwater fluxes from evaporation minus precipitation are an order of magnitude smaller than those shown here (see Supplementary Fig. 8). **c** Sea-ice growth in m yr^{-1} and **d** ice-shelf basal melt rates in Gt yr^{-1} . The bars in panels **c** & **d** denote averages for the 1990s (plain) and the 2090s (hatched) in *simA* (darker colors) and *simB* (lighter colors), respectively.

205 formation in the 2090s in *simA* is 1.4 Sv lower than in the preceding century (Fig. 6a), but this decline has to
 206 at least partially be attributed to model drift, as dense water formation in the control experiment *simB* shows
 207 a similar decline in magnitude in the area of interest (Fig. 6b). In contrast, the simulated shift of dense water
 208 formation to lighter density classes in *simA* towards the end of the 21st century can clearly be attributed to
 209 climate change (Fig. 6a & b). The reduced sea-ice formation and increased freshwater discharge from ice
 210 shelves in the southern Weddell Sea are the dominant reasons for this shift, but property changes in the
 211 source waters upstream also play a role. Waters on the eastern Weddell Sea continental shelf experience
 212 pronounced freshening and particularly warming by the year 2100 (-0.026 in salinity and $+0.64 \text{ }^\circ\text{C}$, respec-
 213 tively; see Supplementary Fig. 9), and the 40% lower sea-ice formation and 8-fold higher basal melt rates
 214 result in much lighter waters flowing into the southern Weddell Sea in the 2090s than in the 1990s (Supple-
 215 mentary Fig. 10). Thereby, these lighter source waters amplify the shift towards lighter densities of newly
 216 formed dense waters in the southern Weddell Sea, where these become too light in our model experiments
 217 to sustain contemporary rates of carbon transfer to the deep ocean at the end of the 21st century.

218 Discussion

219 Using a model setup that, for the first time, includes both ice-shelf cavities and a description of the ocean
 220 carbon cycle, our results quantify the role of both physical and biological processes in deep-ocean carbon
 221 accumulation in the southern Weddell Sea. Over much of the 21st century, the carbon transfer to the abyss
 222 due to physical processes is up to four times higher than due to biological processes in the high-emission
 223 scenario, until the physically-driven transfer abruptly declines in the 2090s (Fig. 2). The simulated decline in
 224 dense-water transfer to the deep ocean in response to enhanced stratification is generally in line with pre-
 225 vious modelling experiments⁷. However, in contrast to some Earth System Models⁷, our model does not

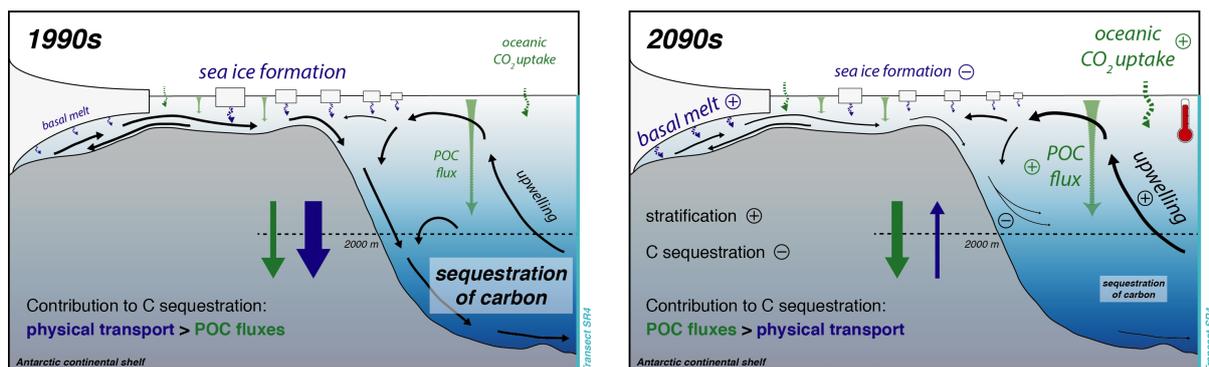


Figure 7: Sketch illustrating the simulated changes over the 21st century in the high-emission scenario. Compared to the 1990s, deep-ocean carbon sequestration in the southern Weddell Sea is reduced by 60%, which is largely attributed to a reduction in the physical transport of carbon to the abyss. In particular, sea-ice formation is reduced by 16%, and ice-shelf basal melt increases by 79%, which both act to increase the stratification of the water column. Despite the 10-fold increase in oceanic CO₂ uptake and a 47% increase in sinking fluxes of biotic particles (POC), the decline in physically-driven downward transport dominates, as newly formed lighter dense waters on the continental shelf are transferred to shallower depths in the 2090s, reducing carbon accumulation in the deep ocean. In the sketch, font sizes and arrow thicknesses in the 2090s are scaled to approximately represent the magnitude of the simulated changes.

226 suggest a complete shutdown of dense water formation by the end of the 21st century, but a less efficient
 227 transfer of newly formed dense waters from the Weddell Sea continental shelves to the abyss (Fig. 7). This
 228 discrepancy can be understood by looking at the mechanisms involved in dense water formation in the dif-
 229 ferent model experiments. Typically, the slowdown or shutdown of bottom water renewal simulated in Earth
 230 System Models occurs due to a reduction in (unrealistic) open-ocean deep convection in areas north of the
 231 transect considered in this study (Fig. 1)⁷. Instead, in our model experiments, pronounced freshening and
 232 warming of waters on the southern Weddell Sea continental shelf are largely responsible for this change. As
 233 the bottom water density decline is largest along pathways of dense water export from the southern shelves
 234 to the abyss (Filchner Trough and northwestern Weddell Sea shelf; see Fig. 1 & Fig. 5), bottom waters in the
 235 open-ocean southern Weddell Sea are effectively cut off from renewal with waters descending the continental
 236 slope, as the newly formed lighter dense waters end up at shallower depths. Although the downstream effects
 237 may be similar, namely less carbon sequestration in the high-latitude Southern Ocean, bottom water renewal
 238 is known to predominantly occur along the continental margins^{13–16}. Thus, our model experiments display
 239 a more realistic representation of the mechanisms involved in dense water formation and transfer to the
 240 deep ocean, which is indispensable when aiming to anticipate their response to the on-going environmental
 241 change.

242 In comparison to earlier modeling studies projecting an up to 15-fold increase in ice-shelf basal melt
 243 rates^{41–44}, the projected 79% increase in Weddell Sea ice-shelf basal melt by 2100 in our model is much
 244 more moderate. In fact, our projected increase is much closer to the values recently reported by Naughten
 245 et al.^{45,46}, who - like in this study - used atmospheric output from state-of-the-art climate projections to
 246 force their ocean model experiments. In their studies, ice-shelf basal melt rates in the Weddell Sea are
 247 projected to increase by 99% in the high-emission RCP8.5 scenario⁴⁵, and much higher atmospheric CO₂
 248 levels than those considered in our study are required to induce an up to five-fold increase in basal melt⁴⁶.
 249 Acknowledging that we have only used output from a single climate model here, our results are nevertheless
 250 in line with Naughten et al.^{45,46}, suggesting that earlier studies^{41–44} using an older forcing scenario may
 251 have been too prone to WDW intrusions onto the continental shelf and hence overestimated the future basal
 252 melt rate increase in the area (see also discussion in reference⁴⁶). While a cold bias in WDW in our model
 253 (Supplementary Fig. 11 & 12) might imply that our experiments underestimate the response of basal melt
 254 rates to the climate-change forcing, the simulated present-day basal melt rates in the Weddell Sea (127 Gt yr⁻¹
 255 in the 1990s) are within the range suggested by observations (192.6±96.6 Gt yr⁻¹⁶⁵). Furthermore, in our
 256 model experiment, the increase in basal melt rates accelerates towards the end of the 21st century (143 Gt yr⁻¹
 257 in the 2070s, 168 Gt yr⁻¹ in the 2080s, 226 Gt yr⁻¹ in the 2090s), suggesting that basal melt rates would likely
 258 continue to rise beyond 2100, further freshening the shelf and subsequently reducing the density of newly
 259 formed dense waters, possibly resulting in a continued low transfer of carbon to the abyss of the southern
 260 Weddell Sea.

261 As a result of the simulated changes in the physical environment (e.g., in sea-ice cover), the transfer of
262 carbon to the abyss with sinking biotic particles increases over the 21st century (Fig. 7). While the present-day
263 biological pump adjacent to the southern Weddell Sea continental shelves is thought to be efficient in trans-
264 ferring biotic particles to the deep ocean^{6,66}, several studies have suggested rather shallow remineralization
265 of those particles in the central Weddell Sea^{9,51,67}. In particular, MacGilchrist et al.⁵¹ have recently shown
266 that biological fluxes in the Weddell Sea significantly contribute to carbon accumulation above 2000 m (CDW
267 layer), but to a lesser extent to water masses below that, which is in line with our findings for the present
268 time. Yet, by the year 2100, the carbon inventory of the southern Weddell Sea below 2000 m changes from
269 being physically-controlled to being biologically-controlled in our model experiment, which also holds true
270 for the accumulation below 2500 m and 3000 m, respectively (Supplementary Fig. 13). This regime shift is
271 dominated by the decrease in the physically-driven downward carbon transfer (due to the increased stability
272 of the water column), which outweighs the increase in the biologically-driven transfer (due to more primary
273 productivity and sinking particle fluxes) and which results in deep-ocean carbon accumulation rates in the
274 2090s amounting to only 40% of those simulated in the 1990s. However, we acknowledge that we might
275 underestimate the future role of biotic particle fluxes in our model experiment. At high latitudes, phytoplank-
276 ton growth is generally limited by the availability of micronutrients, such as iron, and the rather short growing
277 season at these latitudes^{9,68}. While the latter will likely be prolonged by 2100 as a result of the shrinking sea
278 ice cover (Fig. 2f), iron supplied by meltwater from sea ice or icebergs was shown to be a source of iron for
279 high-latitude phytoplankton⁶⁹, suggesting substantial fertilization as melt rates increase over the 21st century.
280 This nutrient supply mechanism is currently not accounted for in our model, but might augment the biological
281 response to environmental change. Instead, here, the attenuation of deep-ocean carbon accumulation in the
282 southern Weddell Sea is controlled by changes in physical processes, namely the shift in water mass prop-
283 erties and transformations in the upper ocean, which act to reduce the vertical downward transfer of carbon
284 to the abyss with dense waters.

285 Rates of carbon sequestration - if given relative to the CO₂ uptake at the ocean surface - are an indicator
286 of the sequestration efficiency, but the sequestration depth is decisive for the storage permanence, which
287 describes how long the sequestered carbon will ultimately be locked away from the atmosphere. In the
288 Weddell Sea, a high storage permanence on the order of centuries or more is likely if the carbon is transferred
289 to the bottom of the ocean with WSBW along the continental slope^{6,51}. In contrast, the storage permanence
290 is likely much shorter if the carbon is only transferred to mid-depths, from where upwelling might bring the
291 freshly sequestered carbon to the surface again within a few years or decades (especially in the central
292 Weddell Sea)^{6,9,51}. Under the high-emission scenario considered in this study, the fraction of the oceanic
293 CO₂ uptake sequestered below 2000 m in the southern Weddell Sea declines from 93% in the 1990s to only
294 2% in the 2090s (Fig. 2). This reduced sequestration efficiency implies that an increasing amount of carbon
295 is stored at mid-depths and in the upper ocean over the 21st century (Supplementary Fig. 1). Indeed, most of
296 the CO₂ taken up at the surface in the southern Weddell Sea throughout the 21st century evades long-term
297 sequestration in the deep ocean, with cumulative deep-ocean carbon accumulation until 2100 amounting to
298 26% of the total CO₂ uptake south of the transect SR4. While it remains unclear how carbon sequestration
299 in the southern Weddell Sea evolves beyond the year 2100 under continuous climate-change forcing and
300 to what extent the attenuation of carbon sequestration rates in this region by 2100 is avoidable under a
301 lower-emission scenario, it is clear that a reduction in deep-ocean carbon accumulation will induce climate
302 feedbacks down the road as a consequence of the reduced storage permanence.

303 In summary, the evolution of deep-ocean carbon sequestration in the southern Weddell Sea is closely
304 tied to the evolution of buoyancy fluxes from sea ice and ice shelves and hence dense water formation in
305 the area. Therefore, based on our results, the crossing of any critical threshold in high-latitude freshwater
306 discharge, i.e., a tipping point above which newly formed dense waters are so light that they cease to reach
307 the abyss⁷⁰, will likely be associated with a concurrent cessation in carbon sequestration. Additional research
308 will be needed to elucidate whether such a tipping point has already been crossed by the end of our model
309 experiment, or whether this abrupt decline is a non-permanent early warning signal of the imminent crossing
310 of such a tipping point. Furthermore, it remains an open question whether such a tipping point can be
311 avoided under lower emission scenarios. In conclusion, the projected freshening of Weddell Sea shelf waters
312 and the associated reduction in bottom water renewal reduce their capacity to store carbon on centennial and
313 millennial time scales, with consequences for the partitioning of carbon between the ocean and atmosphere
314 and hence climate.

315 Methods

316 **Description of FESOM-REcoM.** We use the global Finite Element Sea Ice Ocean Model (FESOM) version
317 1.4⁵⁴ which includes a dynamic-thermodynamic sea-ice model⁵⁵ and an ice-shelf component⁵⁸. Ice-shelf
318 geometry and bottom topography are derived from RTopo-2⁷¹ and prescribed to be constant in our model
319 experiments. Coupled to FESOM is the Regulated Ecosystem Model version 2 (REcoM2)^{53,56,57}, which
320 resolves the biogeochemical cycling of carbon, nitrogen, silicon, iron, and oxygen with a total of 28 prognostic
321 tracers. The lower trophic level ecosystem is composed of two phytoplankton groups (silicifying diatoms and
322 a mixed nanophytoplankton group, of which a fraction calcifies) and two zooplankton groups. Stoichiometric
323 ratios are allowed to vary in REcoM2. Organic matter cycling is parametrized with one class of non-sinking
324 dissolved organic matter and two size classes of particulate organic matter, which are remineralized as
325 they sink through the water column. A fraction of the sinking particles reaches the sediment layer in the
326 model, from which they are released back into the water column in dissolved form with fixed remineralization
327 rates⁵³. Consequently, any change in the deep-ocean carbon inventory due to biological fluxes is caused
328 by changes in either the sinking particle flux across the depth horizon of interest (2000 m in this study) or
329 in the release of dissolved inorganic carbon from the sediments, with the former dominating in the southern
330 Weddell Sea (Supplementary Fig. 2). The *total carbon inventory* as assessed in this study refers to the sum
331 of the following model tracers: dissolved inorganic carbon, dissolved organic carbon, two classes of sinking
332 particulate organic carbon, particulate inorganic calcite, living particulate organic carbon associated with the
333 two phytoplankton and two zooplankton groups, and calcite associated with the nanophytoplankton group.

334 **Model setup, model assessment, and data sets for model evaluation.** For this study, all model experi-
335 ments are run on a mesh with enhanced horizontal grid resolution on the continental shelves of the Southern
336 Ocean, especially in the Weddell Sea. The horizontal resolution ranges from 4 km in the southern Weddell
337 Sea to ~80 km at the outer edge of the Weddell Gyre and increases to >100 km outside of the Southern
338 Ocean (Supplementary Fig. 14). The vertical is divided into 99 unevenly spaced z levels, of which 21 depth
339 levels are situated below 2000 m. The time step in our simulations is four minutes. We run transient simu-
340 lations with FESOM-REcoM for the years 1950-2100. At the ocean surface, we force the model with output
341 from the AWI Climate Model (AWI-CM) produced for the "Coupled Model Intercomparison Project Phase 6
342 (CMIP6)"⁵⁹. We use 3-hourly output of atmospheric momentum, radiation, and freshwater fluxes and daily
343 output of terrestrial freshwater runoff from the first ensemble member of the historical simulation until 2014
344 and from the SSP5-8.5 scenario simulation thereafter. We note that the SSP5-8.5 scenario assumes a con-
345 tinuously high usage of fossil fuel for the evolution of CO₂ emissions⁷², thereby assuming weaker climate
346 protection policies for the 21st century than currently in place⁷³. Nonetheless, the atmospheric CO₂ concen-
347 trations and the resulting future climate suggested by Earth System Models under the SSP5-8.5 scenario are
348 possible even under lower-emission scenarios as a result of the large uncertainty associated with carbon-
349 cycle feedbacks in these models⁷³. Atmospheric pCO₂ levels are taken from Meinshausen et al.⁷⁴ for the
350 historical period 1950-2014 and from O'Neill et al.⁷² for the period 2015-2100, consistent with the time series
351 used in the CMIP6 experiments. In our experiments, the physical tracers are initialized with FESOM output
352 from the historical simulation of the AWI-CM and the biogeochemical tracers with REcoM output from an
353 existing simulation for the "Regional Carbon Cycle Assessment and Processes 2 (RECCAP2)" project (un-
354 published). Thereby, at the start of our simulations, the physical and biogeochemical tracers have been spun
355 up for 850 years (FESOM) and 100 years (REcoM), respectively.

356 For this study, two model experiments were performed: *simA* is forced with varying climate and varying atmo-
357 spheric pCO₂ levels as described above, whereas *simB* is forced by repeating the atmospheric conditions of
358 the year 1950 (atmospheric pCO₂; 312.82 ppm⁷⁴) and 1955 (all other variables), allowing for an assessment
359 of the model drift. The year 1955 was chosen aiming to 1) minimize the warming signal in the chosen year
360 and 2) represent "normal" atmospheric conditions, which we identify by assessing the phase of the Southern
361 Annular Mode and El Niño Southern Oscillation in the first 20 years of the forcing. We acknowledge that in
362 the control simulation *simB*, the deep-ocean carbon inventory in the southern Weddell Sea is not in a steady
363 state at the start of the analysis period in 1980 (Fig. 2a), which can be attributed to the spin-up procedure.
364 In particular, atmospheric CO₂ concentrations have risen from the preindustrial 278 ppm to 313 ppm dur-
365 ing the spin-up, and another ~100 years are needed in *simB* for the deep-ocean carbon inventory to reach
366 quasi-equilibrium with this atmospheric CO₂ level (Fig. 2a). However, this does not affect the conclusions
367 drawn in this study because upper ocean processes are close to equilibrium already in 1980 (see Fig. 2c and
368 Supplementary Fig. 1) and because the climate-change signal in *simA* exceeds the drift in *simB* by far also
369 for the deep ocean (Fig. 2a).

370 Model output is generally stored at monthly frequency, with physical flux output being only available for se-
371 lected decades, namely between 1980-1999 and 2080-2099. For the budget analysis of the deep-ocean

372 carbon inventory in the southern Weddell Sea, vertical mixing fluxes are inferred from the change in the total
 373 carbon inventory, biological fluxes (see above), and the remaining physical flux components (lateral and ver-
 374 tical advection, horizontal diffusion, fluxes from the Gent-McWilliams parametrization, and the stabilization of
 375 the Taylor-Galerkin advection scheme⁵⁴). For model evaluation, we use available ship-observations of dis-
 376 solved inorganic carbon⁷⁵ and temperature & salinity¹² (see Supplementary Fig. 11, 12 & 15). Weddell Sea
 377 Deep Water (WSDW) and Weddell Sea Bottom Water (WSBW) in FESOM-REcoM are defined as waters with
 378 a potential temperature $<-0.2^{\circ}\text{C}$ and a practical salinity >34.55 , and we do not distinguish these two water
 379 masses in this study. The thresholds used here differ slightly from those in Fahrbach et al.¹⁷, who used 0°C
 380 as the temperature threshold and 34.6 and 34.63 as the salinity thresholds to distinguish WSDW and WSBW,
 381 respectively, from Warm Deep Water (WDW). The definition was chosen here to best reflect the simulated
 382 water mass structure both south of and at the transect SR4, thereby accounting for a slight fresh bias in the
 383 focus region and a cold bias in the WDW core in the model (Supplementary Fig. 11 & 12).

384 **Age tracer.** Our model experiments include an age tracer, which is initialized at zero everywhere in the model
 385 domain. Over the course of the simulations, the age of a given water parcel increases accordingly and is only
 386 reset when it comes in contact with the surface, with *surface* here being either the air–ocean, sea ice–ocean,
 387 or ice shelf–ocean interface. The age tracer is advected and mixed as any other model tracer, implying that
 388 the age of a water parcel can also decline (increase) by mixing with a water parcel of lower (higher) age,
 389 i.e., if the latter water parcel has been in touch with the surface more recently (longer ago) than the former.
 390 Hence, based on a water parcel’s age a , we calculate the ventilated fraction ϵ [%] of this water parcel at time
 391 t of the simulation as

$$\epsilon(t) = 100 \cdot \frac{t - a_t}{t}. \quad (1)$$

392 With this definition, a given water parcel with an age corresponding to the simulation time t is not ventilated
 393 at all, whereas an age of zero corresponds to 100% ventilated water. Consequently, a comparison of the
 394 age-tracer based ventilated fractions of bottom waters in the southern Weddell Sea between the 2090s and
 395 1990s reveals changes in the exchange of these waters with the ocean surface.

396 **Water mass transformation framework.** Here, we are mostly interested in the formation of dense waters
 397 on the Weddell Sea continental shelves. To that aim, we assess water mass transformations due to surface
 398 buoyancy fluxes on the continental shelf south of the WOCE transect SR4, which connects the tip of the
 399 Antarctic Peninsula with the eastern Weddell Sea (Fig. 1), and in the eastern Weddell Sea (see Fig. 6 and
 400 Supplementary Fig. 10 for the exact location of both shelf regions). Any change in the volume of waters in a
 401 given density class between the surface outcrop of these waters south of the transect SR4 and their volume
 402 flux across the transect SR4 is due to either 1) a change in the transport of this density class across SR4, 2)
 403 diapycnal mixing fluxes in the ocean interior, or 3) surface transformations causing a lateral diapycnal flux⁷⁶.
 404 In this context, the water mass transformation (WMT) framework relates the density distribution at the ocean
 405 surface to buoyancy fluxes, providing a framework to relate the formation of dense waters to heat fluxes or
 406 freshwater fluxes from evaporation minus precipitation, sea ice, or ice shelves^{40,61–64}.
 407 Discretizing the surface density (ρ) field into bins of 0.025 kg m^{-3} , heat fluxes Q_{net} and freshwater fluxes
 408 F_{net} transform water masses in the density bin ρ_k with a rate Ω [Sv] at any time t at the atmosphere-ocean
 409 or ice-ocean interface, following

$$\Omega(\rho_k, t) = -\frac{1}{\rho_{k+1} - \rho_k} \iint_A \frac{\alpha Q_{net}}{\rho_0 C_p} dA + \frac{1}{\rho_{k+1} - \rho_k} \iint_A \frac{\beta S F_{net}}{\rho_0} dA. \quad (2)$$

410 Here, A is the outcrop area between the density bins k and $k+1$, α and C_p are the thermal expansion coeffi-
 411 cient and the heat capacity, respectively, β and S are the haline contraction coefficient and the surface salinity,
 412 respectively, ρ_0 is the reference density, and F_{net} is composed of freshwater fluxes between atmosphere and
 413 ocean ($F_{Atm \rightarrow Ocean}$), sea ice and ocean ($F_{Seaice \rightarrow Ocean}$), and ice shelves and ocean ($F_{Iceshelf \rightarrow Ocean}$):

$$F_{net} = F_{Atm \rightarrow Ocean} + F_{Seaice \rightarrow Ocean} + F_{Iceshelf \rightarrow Ocean}. \quad (3)$$

414 The convergence (divergence) of waters in a given density class implies downwelling (upwelling) of these to
 415 satisfy mass continuity. We use the potential density referenced to 2000 dbar (ρ_2) as the density coordinate
 416 and display the density anomaly throughout this manuscript ($\sigma_2 = \rho_2 - 1000 \text{ kg m}^{-3}$). While different density
 417 coordinates have been used by other authors in the past^{40,63}, the qualitative results presented here are
 418 insensitive to this choice. Here, we compute WMT rates in the southern Weddell Sea based on monthly
 419 model output for the 1990s and 2090s.

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429 Data availability

430 The model output needed to reproduce the results presented here will be uploaded to PANGAEA upon ac-
431 ceptance of the manuscript. Codes and full model output are available upon request from the corresponding
432 author.

433 Author contributions

434 C.N., J.H., and M.H. conceived the study. C.N. set up the model simulations, with help from R.T. and J.H.
435 C.N. performed the analysis. All authors contributed to the interpretation of the results and the writing of the
436 manuscript.

437 Competing interests

438 The authors declare no competing interests.

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