

OPINION

Misconceptions of the marine biological carbon pump in a changing climate: Thinking outside the “export” box

Ivy Frenger¹  | Angela Landolfi²  | Karin Kvale^{1,3}  | Christopher J. Somes¹  |
Andreas Oschlies¹  | Wanxuan Yao¹  | Wolfgang Koeve¹ 

¹Biogeochemical Modelling, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

²National Research Council of Italy, CNR-ISMAR, Rome, Italy

³GNS Science, Te Pū Ao, Lower Hutt, New Zealand

Correspondence

Ivy Frenger, Biogeochemical Modelling, GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstr. 1-3, D-24148 Kiel, Germany.

Email: ifrenger@geomar.de

Angela Landolfi, National Research Council of Italy, CNR-ISMAR, Via Fosso del Cavaliere, 100, 00133 Rome, Italy. Email: angela.landolfi@cnr.it

Funding information

New Zealand Ministry of Business, Innovation, and Employment, Grant/Award Number: C05X1702 and ANTA1801; Deutsche Forschungsgemeinschaft, Grant/Award Number: 445549720

Abstract

The marine biological carbon pump (BCP) stores carbon in the ocean interior, isolating it from exchange with the atmosphere and thereby coregulating atmospheric carbon dioxide (CO₂). As the BCP commonly is equated with the flux of organic material to the ocean interior, termed “export flux,” a change in export flux is perceived to directly impact atmospheric CO₂, and thus climate. Here, we recap how this perception contrasts with current understanding of the BCP, emphasizing the lack of a direct relationship between global export flux and atmospheric CO₂. We argue for the use of the storage of carbon of biological origin in the ocean interior as a diagnostic that directly relates to atmospheric CO₂, as a way forward to quantify the changes in the BCP in a changing climate. The diagnostic is conveniently applicable to both climate model data and increasingly available observational data. It can explain a seemingly paradoxical response under anthropogenic climate change: Despite a decrease in export flux, the BCP intensifies due to a longer reemergence time of biogenically stored carbon back to the ocean surface and thereby provides a negative feedback to increasing atmospheric CO₂. This feedback is notably small compared with anthropogenic CO₂ emissions and other carbon-climate feedbacks. In this Opinion paper, we advocate for a comprehensive view of the BCP's impact on atmospheric CO₂, providing a prerequisite for assessing the effectiveness of marine CO₂ removal approaches that target marine biology.

KEYWORDS

atmospheric CO₂, biological carbon pump, carbon cycle, climate change, export flux, marine carbon sequestration, marine carbon storage, ocean circulation

1 | MOTIVATION

The storage of carbon in the ocean regulates atmospheric CO₂ and thus Earth's climate. This storage is partly determined by the ocean biological

carbon “pump” (BCP). Carbon dioxide (CO₂) is a greenhouse gas that traps warmth near the Earth's surface. Through air–sea gas exchange, it is in continuous contact with the surface layer of the oceanic carbon reservoir. While the air–sea exchange happens through CO₂ (Box 1,

Ivy Frenger and Angela Landolfi should be considered joint first author.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *Global Change Biology* published by John Wiley & Sons Ltd.

BOX 1 Ocean carbon chemistry and buffer capacity

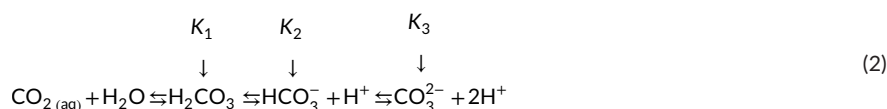
The exchange of CO₂ between the ocean and the atmosphere is driven by the partial pressure difference of atmospheric pCO_{2(atm)} and seawater pCO_{2(aq)}. At thermodynamic equilibrium

$$p\text{CO}_{2(\text{atm})} = p\text{CO}_{2(\text{aq})}$$

CO₂ dissolves in seawater in proportion to its partial pressure pCO_{2(aq)} and its solubility coefficient (K₀), where K₀ depends on temperature, salinity, and pressure (Weiss, 1974), fundamentally following Henry's Law:

$$[\text{CO}_{2(\text{aq})}] = K_0 p\text{CO}_{2(\text{aq})} \quad (1)$$

Different to other gasses, dissolved carbon dioxide CO_{2(aq)} then rapidly (within minutes) chemically reacts with seawater, and dissociates to reach thermodynamic equilibrium, according to the salinity-, pressure- and temperature-dependent equilibrium constants K₁, K₂, K₃ into carbonate species carbonic acid (H₂CO₃), bicarbonate (HCO₃⁻) and carbonate (CO₃²⁻) (Zeebe & Wolf-Gladrow, 2001):



The carbonate species collectively are referred to as DIC, with CO_{2(aq)} combining CO₂ and H₂CO₃, species that are difficult to separate:

$$\text{DIC} = [\text{CO}_{2(\text{aq})}] + [\text{HCO}_3^-] + [\text{CO}_3^{2-}] \quad (3)$$

The relative proportion of the carbonate species is related to the system's unbalanced H⁺, and thus pH (a measure for H⁺) and determines the seawater's buffering capacity (Zeebe & Wolf-Gladrow, 2001): With high proportions of HCO₃⁻ and CO₃²⁻ an addition of H⁺ (Equation 2) is neutralized by reaction with CO₃²⁻ and HCO₃⁻, with little pH change. With a high proportion of CO_{2(aq)} the buffering capacity is low and any H⁺ additions result in a lowering of pH.

Under present conditions the equilibrium of Equation (2) is shifted toward HCO₃⁻, ~89%, and CO₃²⁻, ~11%, and only a small fraction of DIC, less than 1%, remains as CO_{2(aq)} (Zeebe & Wolf-Gladrow, 2001). Importantly, only the latter has a gas phase and can exchange with the atmosphere. This particular speciation creates favorable conditions for CO_{2(atm)} dissolution and provides an efficient chemical buffer. Overall, the carbonate chemistry allows the ocean to take up large quantities of CO₂, resulting in a large background DIC independently of the BCP, and makes the ocean carbon reservoir dominate the atmospheric one (for other gasses that do not react with sea water, such as O₂ or N₂, the oceanic reservoir is much smaller than that of the atmosphere).

The ocean carbonate equilibria adjusts to perturbations. For example, the invasion of anthropogenic CO₂, or the remineralization of organic matter, will impact CO_{2(aq)} but also the other two DIC species, CO₃²⁻ and HCO₃⁻ (Equation 2). The net effect of this reaction is often summarized as an acid-base neutralization (Eggleston & Galbraith, 2018; Zeebe & Wolf-Gladrow, 2001) and, importantly, consumes CO₃²⁻ following Equation (4), thus reducing the buffer capacity:



The efficiency of how much CO₂ is converted into the carbonate species, is measured by the Revelle factor (Revelle & Suess, 1957), or "buffer factor" R,

$$R = \left(\frac{\Delta p\text{CO}_{2(\text{atm})}}{p\text{CO}_{2(\text{atm})}} \right) / \left(\frac{\Delta \text{DIC}}{\text{DIC}} \right) \quad (5)$$

that is, the ratio of the relative change of pCO_{2(atm)} to the relative change of DIC in seawater. Given the present surface ocean conditions, R varies between 8 and 15 (Sabine et al., 2004), with an average of 10. This factor tells us that, for these conditions, a relative change in the atmospheric CO₂ is amplified compared to that of ocean DIC. With the invasion of anthropogenic CO₂ from the atmosphere the continued dissociation of CO_{2(aq)} produces unbalanced protons, H⁺ (Equation 2) lowering pH. The H⁺ reacts with the CO₃²⁻-ion, reducing the buffering capacity of seawater, and thereby shifting the DIC equilibrium speciation more toward the left, that is toward CO_{2(aq)} (Equation 2), which equilibrates with the atmosphere. Hence, while the buffering capacity allows the ocean to absorb much more anthropogenic CO₂ than was possible otherwise, R increases and the capacity reduces with continued uptake of CO₂ ("buffer erosion"), and a larger share of CO₂ ends up in the atmosphere.

Similarly, the buffer factor is important to the response of $p\text{CO}_{2(\text{atm})}$ to a perturbation of $\text{DIC}_{\text{remin}}$, $\Delta\text{DIC}_{\text{remin}}$. For example, in the hypothetical case of a biological extinction, $\Delta\text{DIC}_{\text{remin}}$ will affect the three DIC species, $\text{CO}_{2(\text{aq})}$, HCO_3^- , and CO_3^{2-} , according to the dynamical chemical buffer. Given that of the three species only $\text{CO}_{2(\text{aq})}$ exchanges with the atmosphere, only a limited fraction of $\Delta\text{DIC}_{\text{remin}}$ will outgas to the atmosphere. Thus, the chemical buffering acts as a gatekeeper of air-sea exchange, and thus also of the partitioning of $\Delta\text{DIC}_{\text{remin}}$ between the ocean and the atmosphere. Analytical approximations show that the absolute change of $\text{CO}_{2(\text{atm})}$, $\Delta p\text{CO}_{2(\text{atm})}$, is proportional to $\Delta\text{DIC}_{\text{remin}}$, times a factor that accounts for the initial $p\text{CO}_{2(\text{atm})}$, $p\text{CO}_{2(\text{atm}_{\text{ini}})}$ (Goodwin et al., 2007; Ito & Follows, 2005; Marinov et al., 2008), and the amount of CO_2 that can effectively exchange between the atmosphere and ocean (referred to as the “atmosphere-ocean buffered carbon reservoir” C_{buffer} , with $C_{\text{buffer}} = I_{\text{atm}} + I_{\text{oc}}$, the sum of the atmospheric reservoir of CO_2 , I_{atm} , and the ocean reservoir weighted by the buffer factor, $I_{\text{oc}} = \text{DIC}/R$):

$$\Delta p\text{CO}_{2(\text{atm})} = - \frac{p\text{CO}_{2(\text{atm}_{\text{ini}})} \Delta\text{DIC}_{\text{remin}}}{C_{\text{buffer}}} \quad (6)$$

The approximation is valid for perturbations smaller than roughly 1000 GtC. For perturbations larger than roughly 1000 GtC, the relationship of $\text{DIC}_{\text{remin}}$ and $\text{CO}_{2(\text{atm})}$ remains valid but is better estimated with an exponential function (Goodwin et al., 2007; Marinov et al., 2008). The assumption of a constant buffered atmospheric-ocean carbon reservoir, C_{buffer} , where an increase of DIC is accompanied by an increase of the buffer factor, R , and a shift to a larger fraction of $\text{CO}_{2(\text{aq})}$, and larger $\text{CO}_{2(\text{atm})}$, is valid up to several 1000 Gt C (Goodwin et al., 2007). Considering estimates of the preindustrial C_{buffer} of a preindustrial state in Equation (6), several 10% of a change of $\text{DIC}_{\text{remin}}$ outgasses to the atmosphere, in our model it is around 30% (Figure 3c) in the long-term steady state. This fraction is not straightforward to quantify in a transient state due to the invasion of anthropogenic CO_2 emissions and climate change.

Equation 1), most of the carbon resides in the ocean in the form of carbonate (CO_3^{2-}) and bicarbonate (HCO_3^-) ions. The three carbon species are in thermodynamic equilibrium (Box 1, Equation 2), and in combination are referred to as dissolved inorganic carbon (DIC; Box 1, Equation 3; Figure 2a). The partitioning of carbon among the ocean and atmosphere has varied over Earth's history on millennial timescales, with changes in this partitioning amplifying past variations in climate, for example, glacial cycles (Broecker et al., 1982; Sarmiento & Orr, 1991; Sigman & Boyle, 2000). Similarly, alterations in the partitioning are thought to have the potential to amplify or mitigate anthropogenic climate change (Arora et al., 2020; Heinze et al., 2019; Lenton, 2000). Of continuous interest in this context are changes in the ocean BCP (Henson et al., 2022; Iversen, 2023; Siegel et al., 2023) (Figure 1a), that is commonly associated with “carbon sequestration,” “atmospheric CO_2 ,” and “climate” (see Figure S1b). The BCP sequesters organic carbon in the ocean interior that subsequently is decomposed back to DIC and thus contributes to enriching the deep ocean reservoir with DIC (Figure 2b). By doing so, the BCP isolates ocean carbon from contact with the atmosphere and contributes to reducing the atmospheric CO_2 concentration compared with a hypothetical world without BCP.

While there is some uncertainty in terms of magnitude, research agrees that the BCP is important for setting atmospheric CO_2 under preindustrial steady-state climate. It is an easy pitfall to then project this importance of the preindustrial BCP onto anthropogenic transient climate. The importance of the BCP in an unperturbed, preindustrial climate is demonstrated by idealized model experiments in which a die-off of ocean biology results in a new equilibrium of the ocean-atmosphere carbon reservoirs, with loss of ocean carbon to the atmosphere that has the potential to almost double preindustrial atmospheric CO_2 (Kvale et al., 2021; Maier-Reimer et al., 1996; Sarmiento & Orr, 1991). Despite substantial quantitative spread, it

is thus recognized that the BCP plays an important role in the atmosphere-ocean carbon partitioning and, therefore, is fundamental to the regulation of atmospheric CO_2 and long-term climate. It is an intuitive but unproven argument that the BCP will be of similar importance under ongoing anthropogenic CO_2 emissions that perturb the Earth's carbon cycle. Yet, the relevance of the BCP for preindustrial atmospheric CO_2 cannot be simply projected onto the near-future under anthropogenic perturbation, as we recap here.

We argue that the role of the BCP for the transient response of atmospheric CO_2 to anthropogenic emissions is overrated due to the BCP often being equated with export flux. The flux of organic material from the sunlit surface ocean layer toward the interior ocean, “export flux,” is a common metric for the BCP (Boyd & Trull, 2007; Buesseler et al., 2020; Eppley & Peterson, 1979; Henson et al., 2011). Recent refinements of the BCP into multiple pumps (Boyd et al., 2019; Siegel et al., 2023) still ultimately focus on the downward pumping, or “export,” of carbon. The export flux is thought to decrease under climate change (Henson et al., 2022). While this flux is essential to ecosystem functioning, it is only the first step that contributes to the storage of DIC of biological origin (referred to here as accumulated remineralized DIC, $\text{DIC}_{\text{remin}}$) in the ocean interior (Gnanadesikan & Marinov, 2008). Inferring solely based on the export flux the changes of $\text{DIC}_{\text{remin}}$ is like trying to explain the balance of a bank account by keeping track only of the deposits, leading to incorrect estimates in terms of magnitude and also in terms of the sign of change of $\text{DIC}_{\text{remin}}$. Recognizing this is a prerequisite if we wish to assess the relation of the BCP to atmospheric $p\text{CO}_2$ in a changing world.

In light of the increasing interest in marine climate engineering approaches that seek to enhance the BCP (National Academies of Sciences, Engineering, and Medicine, 2022), and in particular the export flux as a means to enhance the oceanic uptake of anthropogenic CO_2 , or recent concerns about how ocean plastics pollution might

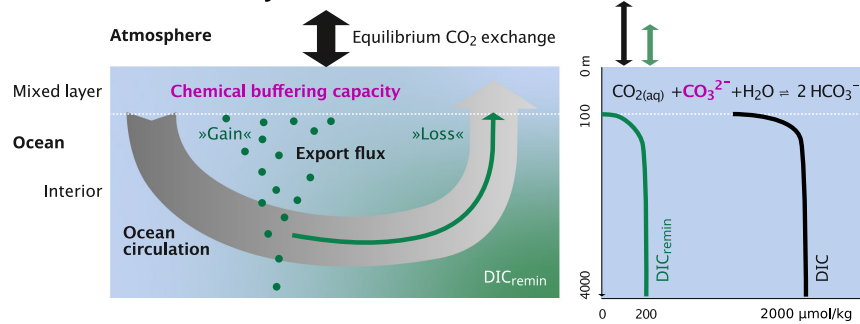
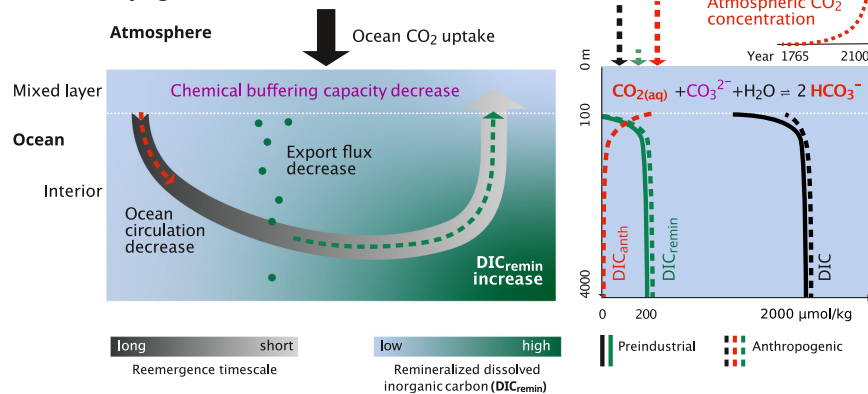
(a) Preindustrial steady-state climate**(b) Anthropogenic transient climate**

FIGURE 1 Thinking out of the export box: an integrated view of the marine biological carbon pump (BCP). The ocean DIC reservoir is the result of the dissolution of atmospheric CO₂ in, and reaction with seawater (Box 1), plus the effects of three “carbon pumps” (Volk & Hoffert, 1985) that enrich the interior ocean with carbon relative to the surface ocean, effectively isolating carbon from the exchange with the atmosphere. The three pumps consist of the solubility pump that operates via increased solubility of CO₂ in high latitude cold waters, and two biologically operated pumps: the soft-tissue pump and the calcium-carbonate (CaCO₃) pump that incorporate surface ocean CO₂ in the sunlit upper ocean into organic particles and into the formation of CaCO₃ shells that sink or are transported passively to the ocean interior. As the reactive organic material, representing only around 1% of total ocean carbon (DeVries, 2022; Friedlingstein et al., 2022), is transferred to the interior ocean and remineralized back to DIC, the biologically operated pumps contribute to maintain the surface ocean mixed layer-to-interior ocean DIC gradient. Here, we focus on the soft-tissue pump. For a review of the full ocean carbon cycle, see for example DeVries (2022). (a) In a preindustrial climate, here taken to be steady-state (in equilibrium), the BCP “gain side” and “loss side” balance. The export flux of organic matter (that includes dissolved organic matter) to the ocean interior (green dots) is remineralized to inorganic DIC (DIC_{remin}). DIC_{remin} accumulates (green gradient) as waters move in the ocean interior with the ocean circulation (illustrated as wide arrow). Ultimately ocean circulation allows the reemergence of DIC_{remin} (thin green arrow) from the ocean interior to the surface ocean mixed layer, where it can exchange with the atmosphere (arrows at the ocean surface). The longer the timescale to reemergence (gray gradient along the wide circulation arrow) the longer DIC_{remin} is retained in the ocean interior, and the larger the reservoir of accumulated DIC_{remin} becomes. Note that the reemergence timescale differs from the local ventilation age, that is the time the waters already have spent in the ocean interior (Primeau, 2005). The exchange with the atmosphere upon reemergence to the mixed layer is regulated by the chemical buffering capacity (strongly correlated with CO₃²⁻, Box 1) that controls the magnitude of the species of DIC that has a gaseous phase (CO_{2(aq)}) and that thus can exchange with the atmosphere. In a steady state, such as the preindustrial climate unperturbed by anthropogenic CO₂ emissions, the net air–sea flux is zero in an ocean–atmosphere model system (in the real Earth system the ocean is a small source of CO₂ to the atmosphere as a consequence of preindustrial weathering flux of alkalinity and DIC from land to ocean). DIC_{remin} as a metric of the BCP and its impact on atmospheric CO₂, contributes less than 10% to total DIC but canonically more than half to the surface-to-interior gradient of DIC (e.g., DeVries, 2022, green and black solid lines to the right; see also Figure 2; Box 1). (b) With the anthropogenic perturbation of increasing atmospheric CO₂ and global warming the system enters a non-steady, “transient” state. The gain side (export flux) is expected to globally decrease. Also the loss side flux is expected to decrease as stratification intensifies and circulation slows down. The reduction of the gain is smaller than the reduction of the loss, resulting in a net increase in DIC_{remin} (darker green shading to the left and green dashed line to the right), suggesting an intensified BCP, and a biogenically induced CO₂ influx into the ocean (dashed green arrow at the air–sea interface). The intensification contributes less to the change of DIC (black dashed line), relative to changes mostly due to the invasion of anthropogenic CO₂ (red dashed arrow at the air–sea interface), which dissolves in the ocean, and enters the ocean interior independently of the BCP with circulation and mixing (DIC_{anth}, red dashed arrow and red dashed line). DIC_{anth} leads to an erosion of the buffer capacity (reduction of CO₃²⁻). Note that the magnitudes of profiles, gradients, and sizes of arrows and reservoirs illustrate relative importance but are not to scale.

alter the marine carbon cycle (Galgani & Loisel, 2021), the scientific community needs to agree on principal constituents of the BCP and discuss the link between the BCP, atmospheric CO₂, and climate. This perspective responds to this challenge and suggests a comprehensive concept of the BCP, and DIC_{remin} as a convenient metric to assess the BCP and its role in climate.

2 | TAKING A STEP BACK: WHAT IS THE BIOLOGICAL CARBON PUMP AND HOW DOES IT RELATE TO ATMOSPHERIC CO₂?

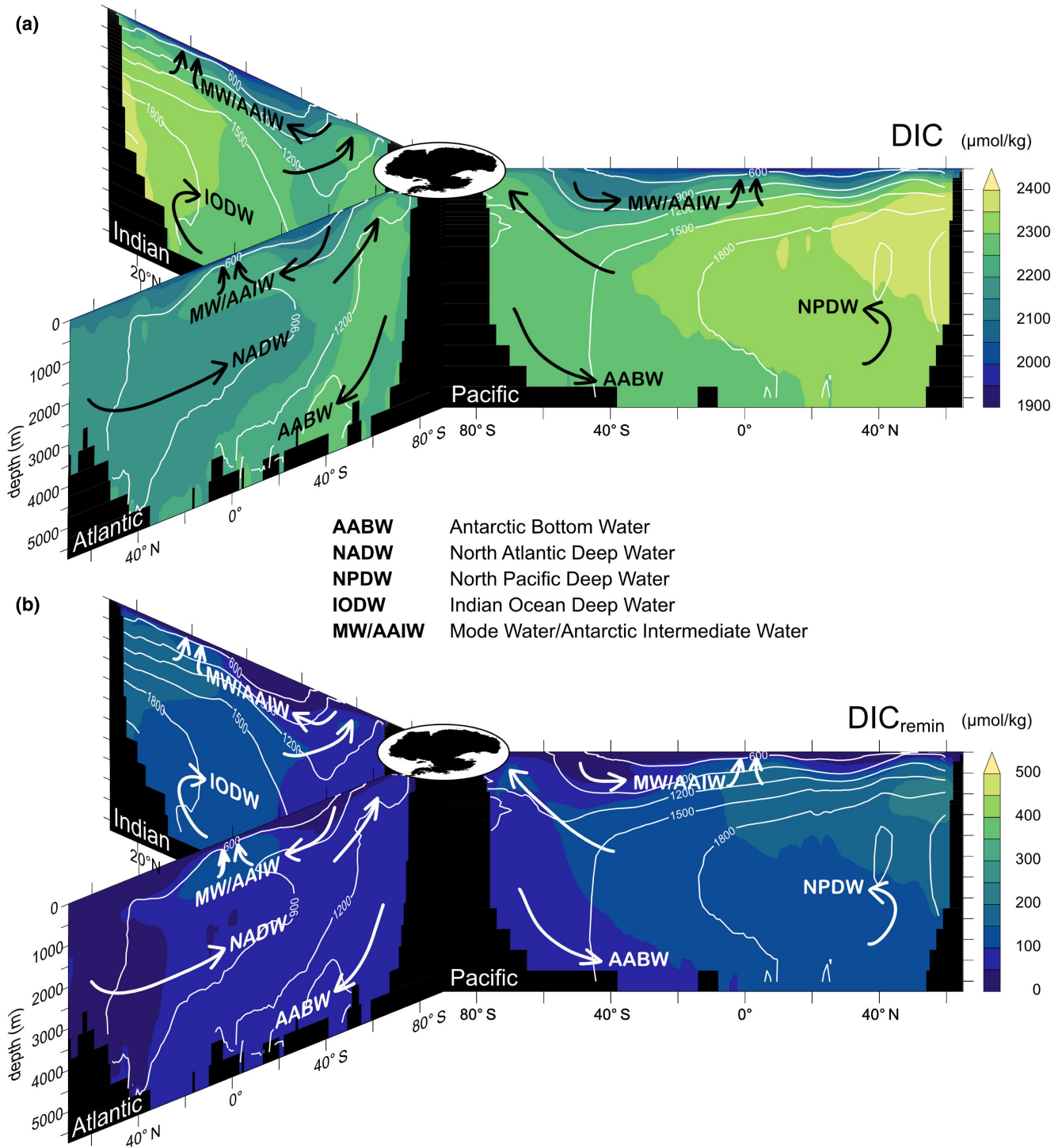
Ocean carbon storage due to the BCP is the net result of physical and biogeochemical processes. The enrichment of DIC of biological origin, the DIC_{remin} reservoir in the interior ocean is a balance of the fluxes due to a gain of DIC_{remin} stemming from the remineralization of organic carbon, and its loss due to its reemergence from the ocean interior via the ocean circulation back to the surface ocean mixed layer (Lévy et al., 2013) (Figure 1a). Integrated below the sunlit biologically productive surface ocean, the gain of DIC_{remin} is equivalent to the flux of particulate and dissolved organic carbon, commonly referred to as “export (production)” (here referred to as export flux). Once organic material is remineralized to DIC_{remin} in the ocean interior below the mixed layer, it commences its journey with ocean circulation and ultimately “is lost” back to the surface ocean mixed layer, where the aqueous CO₂ (CO_{2(aq)}) component of DIC can interact with the atmosphere. The sequestration of DIC_{remin} in the ocean interior (Boyd et al., 2019; DeVries et al., 2012; Siegel et al., 2023) depends on the local timescales of reemergence, that is the mean time it takes for a molecule of DIC_{remin} to return from the interior back to the ocean surface mixed layer (Holzer & Hall, 2000; Primeau, 2005; Siegel et al., 2021). We do not have a direct observation of this timescale. In a constant circulation model, it has been estimated to range from short annual timescales in regions of persistent upwelling up to centennial and millennial timescales in regions of deep and bottom water formation (DeVries et al., 2012; Siegel et al., 2021). The DIC_{remin} loss term, associated with reemergence to the mixed layer, is of equal importance as the gain of DIC_{remin}, and thus critical to consider when determining the storage of ocean carbon and the role of the BCP in regulating atmospheric CO₂.

Export flux alone is insufficient to assess ocean carbon storage by the BCP. There is an immense focus on the gain side of DIC_{remin} in the ocean interior, in particular on the export flux of organic material and its vertical attenuation depending on, among others, temperature, aggregation or disaggregation processes, oxygen sensitivity of organic matter degradation, or ecosystem structure (e.g., Boyd, 2015; Henson et al., 2022; Siegel et al., 2023; Web of Science keywords “biological carbon pump” as of October 2022, 1821 hits, in 40% of cases linked to “export”). In contrast, the loss side of the BCP and its contribution to the ocean carbon reservoir is less appreciated (e.g., DeVries et al., 2012; Gnanadesikan & Marinov, 2008; Web of Science “BCP & outgassing/released”, 9%, and “BCP & storage/reservoir” 9%). In a conceptual short circuit, export flux could be incorrectly

thought to dominate the relationship between the BCP and atmospheric CO₂. A research motivation commonly evoked in articles and proposals is that better constraining the export flux to the interior ocean could allow us to make more accurate predictions of atmospheric CO₂ (e.g., reviews by Boyd et al., 2019; Iversen, 2023; Web of Science “BCP & climate/CO₂” 54% of hits). However, the assumption of a universal relationship with atmospheric CO₂ does not hold for export flux (Marinov et al., 2008) (Figure 3a), nor for the flux of organic material across a deeper ocean layer (Figure S2c). In particular, with a larger export flux in a steady-state climate, atmospheric CO₂ may be larger instead of smaller. Although counterintuitive at first glance this can be explained by considering the loss side of the BCP.

Because it integrates the fluxes of organic matter export (gain) and circulation (loss) side of the BCP, DIC_{remin} is a useful metric for the BCP, and its impact on atmospheric CO₂. While export flux is not representative for biological ocean storage (Figure S2a) and is not independently linked to atmospheric CO₂, the reservoir of DIC_{remin} is (Ito & Follows, 2005; Koeve et al., 2020; Kwon et al., 2011). In an ocean-atmosphere system without anthropogenic emissions, the larger the ocean reservoir of DIC_{remin} in the ocean interior the smaller the atmospheric reservoir of CO₂, with an approximately linear relationship (Figure 3c, though the relationship is not one-to-one, which we will discuss below). DIC_{remin} is stoichiometrically related to biological consumption of oxygen and can be conveniently estimated based on the accumulated oxygen consumption in the ocean interior, referred to as apparent oxygen utilization (AOU; Figure 2b). As a fingerprint of accumulated biological remineralization, AOU accounts for all of the remineralized organic matter, independent of how it was transferred to the ocean interior, including via gravitational settling of particles, zooplankton vertical migration, and physical transport and mixing processes (Siegel et al., 2023). Unlike export flux (Figure S2a), or similarly the flux of organic matter to the deeper ocean interior (see flux of particulate organic matter, at 1000m in Figure S2c) AOU provides a universal robust estimate of DIC_{remin} (Anderson & Sarmiento, 1994; Keeling et al., 2010; Koeve et al., 2020; Wilson et al., 2022) (with quantifiable uncertainty well below that of export flux, as we will detail later) and thus allows to qualitatively infer, based on observations, the impact of the BCP on atmospheric CO₂.

If ocean circulation causes DIC_{remin} to reemerge at the surface (“loss side”), it will not “just” outgas to the atmosphere to increase atmospheric CO₂ “one-to-one” (Figure 3c), because the seawater chemical buffering capacity shields atmospheric CO₂ against a change of DIC_{remin}. The reemergence of DIC_{remin} will result in a re-equilibration between the atmosphere and the ocean. The fraction of DIC_{remin} that ends up in the atmosphere depends on the ocean’s carbon buffering capacity and the atmospheric pCO₂ (Box 1, Equation 6), and is only around a quarter to a third (Archer et al., 1997; Goodwin et al., 2007; Marinov et al., 2008) in the contemporary ocean. Though of lesser importance, non-instantaneous gas exchange of CO₂ (around a year, Emerson & Hedges, 2008), and regional sea ice coverage, can prevent complete equilibration between atmospheric CO₂ and surface ocean aqueous CO₂ (Eggleston & Galbraith, 2018; Khatiwala



et al., 2019). Ocean CO_2 -buffer capacity and incomplete air-sea equilibration also apply to the gain side of the BCP: the CO_2 fixed by photosynthesis and exported into the ocean interior by sinking particles is only partly replaced by CO_2 from the atmosphere.

To summarize, an integrative understanding of the BCP has to equally consider processes that contribute to gain and loss of $\text{DIC}_{\text{remin}}$, as well as the state or change of surface ocean chemistry which translate changes of $\text{DIC}_{\text{remin}}$ to changes of $\text{pCO}_{2(\text{atm})}$. As such, the ocean chemical buffering capacity acts as a gatekeeper of ocean-atmosphere CO_2 uptake and release (Gruber et al., 2004; Ito

& Follows, 2005) (Figure 1a). We next turn to what the above implies for the impact of the BCP on atmospheric CO_2 under anthropogenic climate change.

3 | THE BCP UNDER ANTHROPOGENIC CLIMATE CHANGE IN THE 21ST CENTURY

Anthropogenic transient climate change is projected to induce a reduction in export flux and, at the same time, an increase in the $\text{DIC}_{\text{remin}}$

FIGURE 2 Observational estimate of the contribution of the biological carbon pump to the ocean carbon reservoir. (a) Dissolved inorganic carbon (DIC) from climatological observations (Global Ocean Data Analysis Project, GLODAP, Lauvset et al., 2016), zonally averaged for the Pacific (right side), Atlantic and Indian Ocean (left side) basins; white contours mark $\Delta^{14}\text{C}$ -based “ages” (years) (Matsumoto, 2007) from GLODAP observations. The ocean average DIC is around 2000 $\mu\text{mol}/\text{kg}$; note that the scale only starts at 1900 $\mu\text{mol}/\text{kg}$ DIC concentration, representative for minimum zonal mean surface concentrations, illustrating the high background DIC concentrations, and emphasizing the enrichment of DIC in the interior ocean due to the carbon pumps; and (b) Accumulated remineralized DIC ($\text{DIC}_{\text{remin}}$) that is carbon of biological origin based on climatological observations (World Ocean Atlas, WOA, Garcia et al., 2018) of oxygen (O_2), temperature and salinity. Upon the remineralization of organic matter, O_2 is consumed and carbon, C, and nutrients (nitrogen and phosphate, P) are released in their inorganic forms in quasi-constant proportions $\text{C}:\text{P}:\text{O}_2 = 117:1:-170$ (Anderson & Sarmiento, 1994). Making use of the quasi-constant proportions, $\text{DIC}_{\text{remin}}$ in the ocean can be calculated based on Apparent Oxygen Utilization (AOU, from WOA). AOU is a measure of the difference between the oxygen concentration that is expected based on oxygen solubility and the observed oxygen concentration, with $\text{DIC}_{\text{remin}} = r \text{AOU} = r (\text{O}_2 - \text{O}_{2(\text{sat})})$, and $r = \text{C}:\text{O} = 0.688$, assuming saturation when waters left the ocean surface ($\text{O}_{2(\text{sat})}$), and the actual in-situ observed O_2 . Although the assumption of surface O_2 concentration in equilibrium with the atmosphere might not always be valid (Duteil et al., 2013; Ito et al., 2004), uncertainties associated for example with $\text{O}_{2(\text{sat})}$ (Duteil et al., 2013) or the O:C ratio (Körtzinger et al., 2001) are relatively small, leaving $\text{DIC}_{\text{remin}}$ with an estimated error of less than 10% that is well constrained compared to estimates of the export flux with an uncertainty of more than a factor of two (Henson et al., 2011). The pattern of $\text{DIC}_{\text{remin}}$ illustrates a higher contribution of $\text{DIC}_{\text{remin}}$ in particular in older waters such as in the north Pacific where waters have not exchanged with the atmosphere for more than 1000 years, and a lower contribution of $\text{DIC}_{\text{remin}}$ in comparatively younger waters such as mode and intermediate waters and North Atlantic Deep Water.

reservoir in this century. With an increase of $\text{DIC}_{\text{remin}}$, the BCP acts as a negative carbon-climate feedback and slightly dampens anthropogenic climate change. This is in contrast to the growing concern that a reduction of export flux (Bopp et al., 2013; Wilson et al., 2022) (Figures 1b and 3b) could enhance atmospheric CO_2 and provide a positive feedback to global warming (Bopp & Le Quéré, 2009; Henson et al., 2022). The reasoning underlying such concerns is that due to a warming-driven increase in stratification, surface nutrient supply and thus phytoplankton production will be reduced. However, a warming-driven increase in stratification and a more sluggish ventilation will also reduce the loss side of the BCP (Bopp & Le Quéré, 2009; Henson et al., 2022) so that the rate of reemergence to the surface ocean mixed layer of remineralized carbon and subsequent outgassing is reduced (DeVries et al., 2017). Models suggest that the effect of a more sluggish ventilation on the BCP “loss side” wins over a reduced export flux “gain side,” thereby enhancing the accumulation of $\text{DIC}_{\text{remin}}$ in the ocean interior, and reducing atmospheric CO_2 (Wilson et al., 2022; Figures 1b and 3d; Figure S2b,d). A dominance of the change of the “loss side” under the anthropogenic transient climate is supported also by an increase of AOU (Schmidtko et al., 2017), provoked by a more sluggish ventilation. As discussed above, an increase in AOU corresponds to an increase of accumulated $\text{DIC}_{\text{remin}}$. Using observed changes of AOU over the past five decades to estimate the change of $\text{DIC}_{\text{remin}}$, under the assumption of a constant stoichiometric ratio (Thomas, 2002) (see also caption Figure 2), and further roughly accounting for the vast capacity of seawater to absorb CO_2 (chemical buffering capacity, Box 1), one arrives at a very rough estimate of around 0.1 Gt C/year of net-additional ocean carbon uptake under contemporary anthropogenic global warming due to the BCP (Koeve et al., 2020).

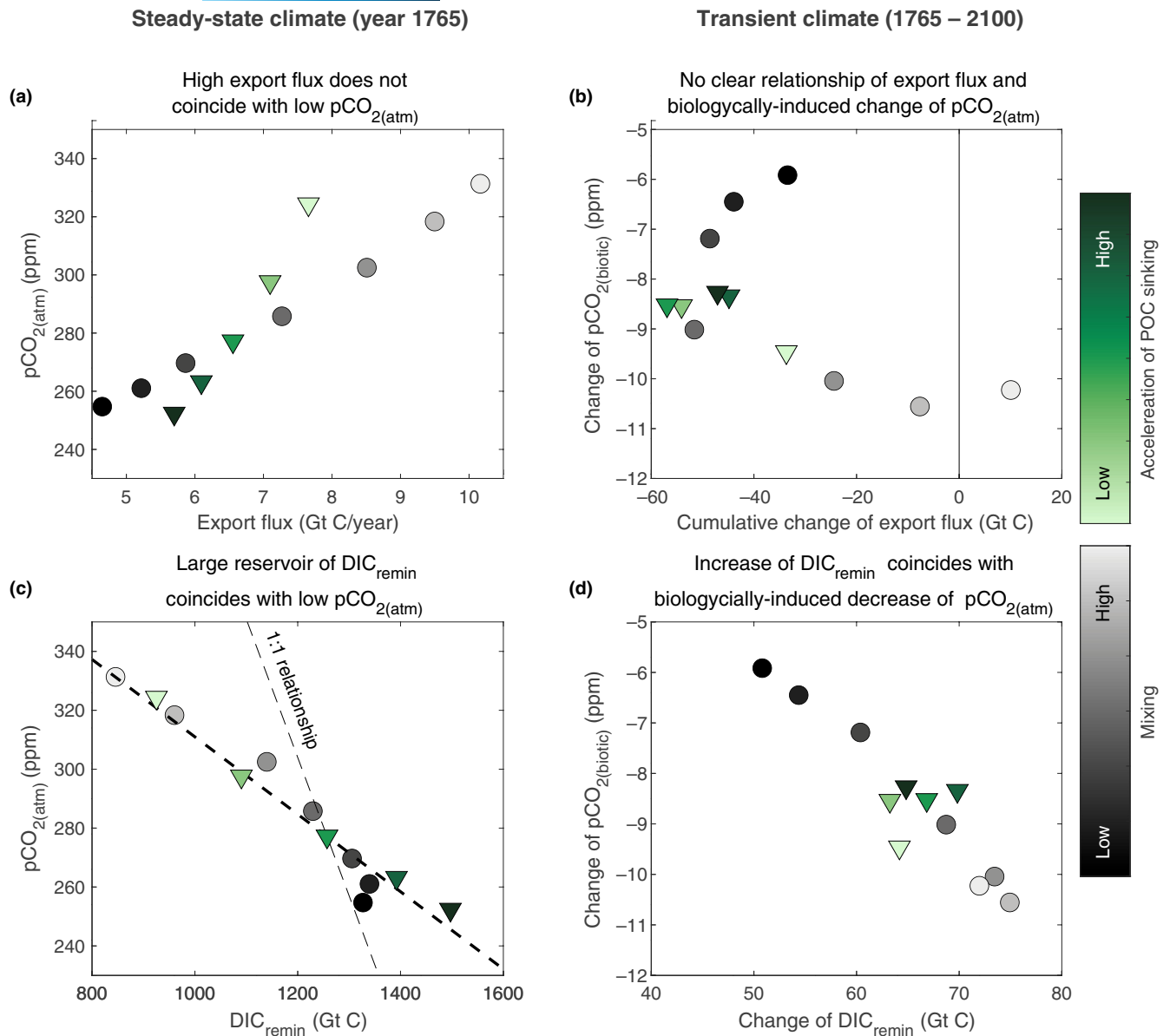
While the BCP therefore provides a negative feedback on anthropogenic climate change in the 21st century, this feedback is small compared with both the negative feedback of the invasion of anthropogenic CO_2 into the ocean and to the positive feedback of the decreasing capacity of the surface ocean to take up more anthropogenic CO_2 (“buffer erosion”,

Fassbender et al., 2017). The first-order ocean carbon response to the increase in atmospheric CO_2 partial pressure is massive chemio-physical dissolution of anthropogenic CO_2 in the ocean, hence mitigating climate change (DIC_{anth} , Figure 1b). The oceanic uptake of anthropogenic CO_2 at the same time diminishes the ocean’s buffering capacity (Fassbender et al., 2017; Sarmiento et al., 1995) (Box 1, Equation 4): While causing the ocean carbon reservoir to be large in the first place, the buffering capacity is dynamic and shifts with the addition of carbon toward a reduced capacity to absorb CO_2 , and an amplified change of atmospheric CO_2 (Box 1, Equations 5 and 6). The effect of this “erosion” of the buffering capacity has been estimated to reduce the uptake of CO_2 by the ocean under a high emissions scenario by a factor of two by the end of the century (Rodgers et al., 2020). The dissolution of anthropogenic CO_2 in the ocean and resulting changes in the buffer capacity are the result of an ongoing re-equilibration of the ocean DIC reservoir with rising atmospheric CO_2 levels, a process that would happen also if the marine carbon pumps did not exist. In comparison with anthropogenic CO_2 dissolution (around 2 Gt C/year averaged over a similar time period, Friedlingstein et al., 2022), enhanced $\text{DIC}_{\text{remin}}$ in the ocean interior due to the perturbation of the BCP in a changing climate is estimated to be an order of magnitude smaller (see above), consistently in observations and for global climate models (Koeve et al., 2020; Wilson et al., 2022). Thus, we expect chemio-physical dissolution of anthropogenic CO_2 emissions in the ocean, and the resulting eroding capacity of the ocean to take up CO_2 , to be of substantially greater importance on the centennial timescale than changes to the BCP.

4 | CONCLUDING REMARKS AND WAY FORWARD

In summary, we emphasize the following points:

First, the importance of the BCP in the preindustrial unperturbed ocean does not inform about its role in ongoing anthropogenic climate



change. While the BCP is substantial to the partitioning of carbon between the ocean and atmosphere in a preindustrial, steady-state climate, this importance does not translate to a similar relative role for atmospheric CO_2 under transient anthropogenic climate at the centennial timescale (Figure 3c,d). Present-day anthropogenic CO_2 uptake overwhelms more subtle potential changes of the BCP (Koeve et al., 2020).

Second, at all timescales, export flux alone is a misleading quantity for defining the BCP and diagnosing its effects on atmospheric CO_2 . We wish to stress the value of research on export flux and flux attenuation. After all, $\text{DIC}_{\text{remin}}$ would not exist without biological processes, and understanding export flux is integral to understanding ecosystem functioning in the ocean interior. But if one wishes to link the BCP to atmospheric CO_2 , export flux as a single metric is a poor predictor: export flux (a flux), and more broadly the flux of organic material, lacks a clear relationship to atmospheric CO_2 (a reservoir) in both the preindustrial steady state and in the present anthropogenic

transient climate (Figure 3a,b; Figure S2a–d). This applies also to how a potentially altered export flux due to plastic pollution could impact $\text{DIC}_{\text{remin}}$. Independent of the timescale, along with export flux, we need to consider the circulation-driven reemergence flux, that is the balance between the gain side and the loss side of $\text{DIC}_{\text{remin}}$ as a comprehensive concept of the BCP.

Third, a lopsided focus on export flux is detrimental for the exponentially growing research field of climate engineering approaches. It has been hypothesized that marine-based climate engineering techniques increase export flux, that is the gain side, without—in the short term—changing the circulation and the loss side, thus enhancing the negative climate feedback of the BCP. Commonly proposed techniques to do so are iron fertilization (de Baar et al., 2005) or artificial upwelling (Jürchott et al., 2023; Oschlies et al., 2010). The thought is that such techniques would, by enhancing export production, also lead to an increase of $\text{DIC}_{\text{remin}}$. Regardless of whether unintended side-effects may dominate such efforts (Oschlies et al., 2010), the

FIGURE 3 Relationship between the biological carbon pump (BCP) and atmospheric CO₂ under (left column) unperturbed preindustrial steady-state (zero anthropogenic CO₂ emissions) and (right column) perturbed anthropogenic transient climate (rising anthropogenic CO₂ emissions). Both support the use of remineralized dissolved inorganic carbon, DIC_{remin}, as a proxy for the effect of the BCP on atmospheric CO₂. Both, (a) in a steady state, after a re-equilibration to stable atmospheric pCO₂, and (b) in a transient climate from preindustrial (1765) to 2100 a larger export flux does not correlate with a lower atmosphere CO₂ reservoir (pCO_{2(atm)}); scatter plots of globally integrated export production ($z = 130$ m) and atmospheric CO₂ (freely evolving), for model set-ups that vary in terms of the organic matter vertical sinking (downward pointing triangles in green shading) or their ocean circulation mixing coefficient K_v (circles in gray shading; different K_v result in differences in circulations, Duteil & Oschlies, 2011; Koeve et al., 2020). In contrast to export flux, both (c) in an unperturbed, and (d) in a transient climate a larger reservoir of accumulated remineralized carbon, DIC_{remin}, is associated with a lower atmosphere CO₂ reservoir; note that the magnitude of the change in the oceanic and atmospheric reservoirs is not one-to-one (evaluated for the same unit, for example, Gt C, thin dashed line) but considerably lower in atmospheric pCO_{2(atm)} than in DIC_{remin} (bold dashed line), as only part of DIC_{remin} escapes to the atmosphere, the remainder stays in the ocean due to the seawater buffer capacity (see also main text and Box 1). The slope (~30%) of the bold dashed line is similar to the one derived from earlier theoretical considerations and idealized ocean-atmosphere models (Ito & Follows, 2005; Marinov et al., 2008) (Box 1). The slope is used here as an empirical estimate of the change of pCO_{2(atm)} with DIC_{remin} to derive the biologically-induced changes of pCO_{2(atm)}, referred to as pCO_{2(biotic)} in (b) and (d). The change of pCO_{2(biotic)} is estimated (i) as the cumulative biogenic oxygen flux between the ocean and the atmosphere (corresponding to a reservoir change) since preindustrial times (1765) until 2100 that then is (ii) converted from O₂ to a change in CO₂ based on fixed stoichiometry and, using the relationship in (c), is adjusted with the factor of ~30% to account for the dependence of atmospheric CO₂ on the ocean buffering capacity (Box 1, Equations 4–6); note that this approach of applying the relationship from (c) to (d) does not consider the changes in the surface ocean buffer capacity due to rising pCO_{2(atm)} (see also main text). The total change of pCO_{2(atm)} (not shown) in (b) and (d), that includes the change of pCO_{2(biotic)}, is dominated by anthropogenic CO₂ emissions, masking more subtle changes of pCO_{2(biotic)}. Simulations are based on the intermediate complexity Earth system model UVic (Keller et al., 2012; Koeve et al., 2020), using explicit modeling techniques that allow a separation of effects of individual processes on atmospheric CO₂ in an idealized modeling framework (e.g., Bernardello et al., 2014; Koeve et al., 2020). Simulations are spun up for several 1000 years to a steady-state. Transient simulations follow historical CO₂ emissions, and further strongly increasing emissions until 2100 according to the Representative Concentration Pathway (RCP8.5) scenario. In the transient simulations (b, d) land effects are not considered to avoid compensating effects, and allow for an attribution of changes to the ocean. Data are available from (Koeve, 2023).

evaluation of effectiveness and permanence of a potential enhancement of the BCP should not be based on export production alone (Gnanadesikan & Marinov, 2008) but needs to account for the loss term. Even if a change of export flux is large, the change of reemerging DIC_{remin} will be large as well. A potential increase of DIC_{remin} may fade within decades (Siegel et al., 2021).

Fourth, DIC_{remin} is a useful metric to evaluate the effect the BCP has on atmospheric CO₂, as proposed by others (Koeve et al., 2020; Marinov et al., 2008; Wilson et al., 2022) (Figure 3c). The diagnostic DIC_{remin} integrates over the gain and loss sides of marine biogenic carbon, and its impact on atmospheric pCO₂ can be quantified (Equation 6, Box 1, under steady state). In addition, DIC_{remin} also has the advantage (in contrast to export flux) that it can be estimated rather conveniently and robustly based on oxygen observations (Figure 2b). Such observations are becoming increasingly available from biogeochemical Argo floats for the upper 2000 m. Deep observations below 2000 m presently are covered mostly by decadal cruises (GO-SHIP program, <https://www.go-ship.org>). A standing array of Deep Argo floats, combined with an implementation of biogeochemical sensors on these floats, would complement the latter by providing higher coverage. This would be a major step forward in assessing the spatio-temporal evolution of DIC_{remin} (<https://argo.ucsd.edu/expansion/deep-argo-mission>) and, consequently, the state of the BCP.

Finally, the fact that the current ocean is losing oxygen at a rapid speed, a phenomenon known as ocean deoxygenation (Oschlies et al., 2017), and that most of this oxygen loss is attributed to changes in AOU, indicates that DIC_{remin} is increasing in the global ocean (Schmidt

et al., 2017) due to an increase in the reemergence timescale, and thus to a biologically driven reduction in atmospheric CO₂. Note that this is so despite a likely decline in export production (Wilson et al., 2022). Also, while this contemporary change of the BCP constitutes a negative feedback on climate, it is small compared with other climate feedbacks, and we anticipate it to remain so until 2100 in light of the continued high rate of anthropogenic emissions. While the impact of the BCP on transient marine carbon storage can be quantified based on AOU and DIC_{remin}, the quantification of the associated atmospheric pCO₂ changes (“biotic” change of atmospheric ΔpCO₂, pCO_{2(biotic)}, Figure 3d) is less straightforward due to the anthropogenic CO₂ invasion and buffer erosion. It requires specific methodological developments that take into account these transient conditions. Qualitatively, we expect with continued buffer erosion under high atmospheric pCO₂ the negative climate feedback due to enhanced storage of DIC_{remin} to be reduced.

We conclude that clarifying our perception of the BCP is essential to progressing our understanding of the role of BCP in climate. Acknowledging the lack of a clear relationship between export flux and atmospheric CO₂ has the potential to reconcile different concepts of the BCP within our research community. It will provide the basis to agree on common assessment techniques. Applying common diagnostics such as the reservoir of carbon of biological origin, DIC_{remin}, across observational and modeling communities, as well as biological, chemical, and physical marine research fields is a path forward, promising advances in understanding, and a systematic quantification of temporal and spatial scales of BCP relevance to atmospheric CO₂.

AUTHOR CONTRIBUTIONS

Ivy Frenger: Conceptualization; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **Angela Landolfi:** Conceptualization; investigation; methodology; project administration; writing – original draft; writing – review and editing. **Karin Kvale:** Writing – original draft; writing – review and editing. **Christopher J. Somes:** Methodology; visualization; writing – review and editing. **Andreas Oschlies:** Writing – review and editing. **Wanxuan Yao:** Writing – review and editing. **Wolfgang Koeve:** Conceptualization; data curation; formal analysis; investigation; methodology; supervision; validation; visualization; writing – original draft; writing – review and editing.

ACKNOWLEDGMENTS

K.K. acknowledges support from the New Zealand Ministry of Business, Innovation and Employment (MBIE) within the Antarctic Science Platform, grant ANTA1801. K.K. also acknowledges support from the New Zealand Ministry of Business, Innovation and Employment through the Global Change through Time programme (Strategic Science Investment Fund, contract C05X1702). C.S. was supported by the Deutsche Forschungsgemeinschaft (project no. 445549720). We acknowledge discussions with colleagues at Geomar and beyond, in particular within the pathfinder group “biological carbon pump.” We thank Rita Erven for supporting us with the illustration of [Figure 1](#), and Tianfei Xue, Haichao Guo, and Malte Jürchott for comments that helped to clarify the manuscript and Figures. This is a contribution to the Helmholtz POF IV Program, Subtopic 6.3–“The future biological carbon pump.”

CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interest.

DATA AVAILABILITY STATEMENT

The observational data for [Figure 2](#) (WOA, GLODAP) is publicly available at <https://www.ncei.noaa.gov/products/world-ocean-atlas> (Garcia et al., 2018) and <https://www.glodap.info/index.php/mapped-data-product> (Lauvset et al., 2016). Model output shown in [Figure 3](#) and respective model code are partly published with (Koeve et al., 2020) and data that support the findings of this study are openly available in <https://doi.org/10.6084/m9.figshare.24635115>.

ORCID

Ivy Frenger  <https://orcid.org/0000-0002-3490-7239>
 Angela Landolfi  <https://orcid.org/0000-0002-5000-7863>
 Karin Kvale  <https://orcid.org/0000-0001-8043-5431>
 Christopher J. Somes  <https://orcid.org/0000-0003-2635-7617>
 Andreas Oschlies  <https://orcid.org/0000-0002-8295-4013>
 Wanxuan Yao  <https://orcid.org/0000-0003-3938-1237>
 Wolfgang Koeve  <https://orcid.org/0000-0002-2298-9230>

REFERENCES

- Anderson, L. A., & Sarmiento, J. L. (1994). Redfield ratios of remineralization determined by nutrient data analysis. *Global Biogeochemical Cycles*, 8(1), 65–80. <https://doi.org/10.1029/93GB03318>
- Archer, D., Khesghi, H., & Maier-Reimer, E. (1997). Multiple timescales for neutralization of fossil fuel CO₂. *Geophysical Research Letters*, 24(4), 405–408. <https://doi.org/10.1029/97GL00168>
- Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein, P., Schwinger, J., Bopp, L., Boucher, O., Cadule, P., Chamberlain, M. A., Christian, J. R., Delire, C., Fisher, R. A., Hajima, T., Ilyina, T., Joetjzer, E., Kawamiya, M., Koven, C. D., ... Ziehn, T. (2020). Carbon-concentration and carbon-climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences*, 17(16), 4173–4222. <https://doi.org/10.5194/bg-17-4173-2020>
- Bernardello, R., Marinov, I., Palter, J. B., Sarmiento, J. L., Galbraith, E. D., & Slater, R. D. (2014). Response of the ocean natural carbon storage to projected twenty-first-century climate change. *Journal of Climate*, 27(5), 2033–2053. <https://doi.org/10.1175/JCLI-D-13-00343.1>
- Bopp, L., & Le Quéré, C. (2009). Ocean carbon cycle. In *Surface ocean-lower atmosphere processes* (pp. 181–195). American Geophysical Union (AGU). <https://doi.org/10.1029/2008GM000780>
- Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., & Vichi, M. (2013). Multiple stressors of ocean ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences*, 10(10), 6225–6245. <https://doi.org/10.5194/bg-10-6225-2013>
- Boyd, P. W. (2015). Toward quantifying the response of the oceans' biological pump to climate change. *Frontiers in Marine Science*, 2, 77. <https://doi.org/10.3389/fmars.2015.00077>
- Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., & Weber, T. (2019). Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature*, 568(7752), 327–335. <https://doi.org/10.1038/s41586-019-1098-2>
- Boyd, P. W., & Trull, T. W. (2007). Understanding the export of biogenic particles in oceanic waters: Is there consensus? *Progress in Oceanography*, 72(4), 276–312. <https://doi.org/10.1016/j.pocean.2006.10.007>
- Broecker, W. S., Beng, Z., & Peng, T. (1982). *Tracers in the sea*. Lamont-Doherty Geological Observatory, Columbia University.
- Buesseler, K. O., Boyd, P. W., Black, E. E., & Siegel, D. A. (2020). Metrics that matter for assessing the ocean biological carbon pump. *Proceedings of the National Academy of Sciences of the United States of America*, 117(18), 9679–9687. <https://doi.org/10.1073/pnas.1918114117>
- de Baar, H. J. W., Boyd, P. W., Coale, K. H., Landry, M. R., Tsuda, A., Assmy, P., Bakker, D. C. E., Bozec, Y., Barber, R. T., Brzezinski, M. A., Buesseler, K. O., Boyé, M., Croot, P. L., Gervais, F., Gorbunov, M. Y., Harrison, P. J., Hiscock, W. T., Laan, P., Lancelot, C., ... Wong, C.-S. (2005). Synthesis of iron fertilization experiments: From the iron age in the age of enlightenment. *Journal of Geophysical Research: Oceans*, 110(C9), C09S16. <https://doi.org/10.1029/2004JC002601>
- DeVries, T. (2022). The ocean carbon cycle. *Annual Review of Environment and Resources*, 47(1), 317–341. <https://doi.org/10.1146/annurev-enviro-120920-111307>
- DeVries, T., Holzer, M., & Primeau, F. (2017). Recent increase in oceanic carbon uptake driven by weaker upper-ocean overturning. *Nature*, 542(7640), 215–218. <https://doi.org/10.1038/nature21068>
- DeVries, T., Primeau, F., & Deutsch, C. (2012). The sequestration efficiency of the biological pump. *Geophysical Research Letters*, 39(13), L13601. <https://doi.org/10.1029/2012GL051963>
- Duteil, O., Koeve, W., Oschlies, A., Bianchi, D., Galbraith, E., Kriest, I., & Matear, R. (2013). A novel estimate of ocean oxygen

- utilisation points to a reduced rate of respiration in the ocean interior. *Biogeosciences*, 10(11), 7723–7738. <https://doi.org/10.5194/bg-10-7723-2013>
- Duteil, O., & Oschlies, A. (2011). Sensitivity of simulated extent and future evolution of marine suboxia to mixing intensity. *Geophysical Research Letters*, 38(6), L06607. <https://doi.org/10.1029/2011GL046877>
- Eggleston, S., & Galbraith, E. D. (2018). The devil's in the disequilibrium: Multi-component analysis of dissolved carbon and oxygen changes under a broad range of forcings in a general circulation model. *Biogeosciences*, 15(12), 3761–3777. <https://doi.org/10.5194/bg-15-3761-2018>
- Emerson, S., & Hedges, J. (2008). *Chemical oceanography and the marine carbon cycle*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511793202>
- Eppley, R. W., & Peterson, B. J. (1979). Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, 282, 677–680. <https://doi.org/10.1038/282677a0>
- Fassbender, A. J., Sabine, C. L., & Palevsky, H. I. (2017). Nonuniform ocean acidification and attenuation of the ocean carbon sink. *Geophysical Research Letters*, 44(16), 8404–8413. <https://doi.org/10.1002/2017GL074389>
- Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I. T., Olsen, A., Peters, G. P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S. R., Alkama, R., ... Zheng, B. (2022). Global carbon budget 2022. *Earth System Science Data*, 14(11), 4811–4900. <https://doi.org/10.5194/essd-14-4811-2022>
- Galgani, L., & Loiselle, S. A. (2021). Plastic pollution impacts on marine carbon biogeochemistry. *Environmental Pollution*, 268, 115598. <https://doi.org/10.1016/j.envpol.2020.115598>
- Garcia, H., Weathers, K., Paver, C., Smolyar, I., Boyer, T., Locarnini, M., Zweng, M., Mishonov, A., Baranova, O., Seidov, D., & Reagan, J. (2018). *World ocean atlas 2018, Vol. 3: Dissolved oxygen, apparent oxygen utilization, and dissolved oxygen saturation* (A. Mishonov Tech. Ed.). NOAA atlas NESDIS.
- Gnanadesikan, A., & Marinov, I. (2008). Export is not enough: Nutrient cycling and carbon sequestration. *Marine Ecology Progress Series*, 364, 289–294. <https://doi.org/10.3354/meps07550>
- Goodwin, P., Williams, R. G., Follows, M. J., & Dutkiewicz, S. (2007). Ocean-atmosphere partitioning of anthropogenic carbon dioxide on centennial timescales. *Global Biogeochemical Cycles*, 21(1), GB1014. <https://doi.org/10.1029/2006GB002810>
- Gruber, N., Friedlingstein, P., Field, C. B., Valentini, R., Heimann, M., Richey, J. E., Lankao, P. R., Schulze, E.-D., & Chen, C. T. A. (2004). The vulnerability of the carbon cycle in the 21st century: An assessment of carbon-climate-human interactions. In C. B. Field & M. R. Raupach (Eds.), *The global carbon cycle: Integrating humans, climate, and the natural world* (pp. 45–76). Island Press. <https://hdl.handle.net/11858/00-001M-0000-000E-D19D-5>
- Heinze, C., Eyring, V., Friedlingstein, P., Jones, C., Balkanski, Y., Collins, W., Fichetef, T., Gao, S., Hall, A., Ivanova, D., Knorr, W., Knutti, R., Löw, A., Ponater, M., Schultz, M. G., Schulz, M., Siebesma, P., Teixeira, J., Tselioudis, G., & Vancoppenolle, M. (2019). ESD reviews: Climate feedbacks in the earth system and prospects for their evaluation. *Earth System Dynamics*, 10(3), 379–452. <https://doi.org/10.5194/esd-10-379-2019>
- Henson, S. A., Laufkötter, C., Leung, S., Giering, S. L. C., Palevsky, H. I., & Cavan, E. L. (2022). Uncertain response of ocean biological carbon export in a changing world. *Nature Geoscience*, 15, 248–254. <https://doi.org/10.1038/s41561-022-00927-0>
- Henson, S. A., Sanders, R., Madsen, E., Morris, P. J., Moigne, F. L., & Quartly, G. D. (2011). A reduced estimate of the strength of the ocean's biological carbon pump. *Geophysical Research Letters*, 38(4), L04606. <https://doi.org/10.1029/2011GL046735>
- Holzer, M., & Hall, T. M. (2000). Transit-time and tracer-age distributions in geophysical flows. *Journal of the Atmospheric Sciences*, 57(21), 3539–3558. [https://doi.org/10.1175/1520-0469\(2000\)057<3539:TTATAD>2.0.CO;2](https://doi.org/10.1175/1520-0469(2000)057<3539:TTATAD>2.0.CO;2)
- Ito, T., & Follows, M. J. (2005). Preformed phosphate, soft tissue pump and atmospheric CO₂. *Journal of Marine Research*, 63(4), 813–839. <https://doi.org/10.1357/0022240054663231>
- Ito, T., Follows, M. J., & Boyle, E. A. (2004). Is AOU a good measure of respiration in the oceans? *Geophysical Research Letters*, 31(17), L17305. <https://doi.org/10.1029/2004GL020900>
- Iversen, M. H. (2023). Carbon export in the ocean: A biologist's perspective. *Annual Review of Marine Science*, 15(1), 357–381. <https://doi.org/10.1146/annurev-marine-032122-035153>
- Jürchott, M., Oschlies, A., & Koeve, W. (2023). Artificial upwelling—A refined narrative. *Geophysical Research Letters*, 50(4), e2022GL101870. <https://doi.org/10.1029/2022GL101870>
- Keeling, R. F., Körtzinger, A., & Gruber, N. (2010). Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, 2(1), 199–229. <https://doi.org/10.1146/annurev.marine.010908.163855>
- Keller, D. P., Oschlies, A., & Eby, M. (2012). A new marine ecosystem model for the University of Victoria Earth System Climate Model. *Geoscientific Model Development*, 5(5), 1195–1220. <https://doi.org/10.5194/gmd-5-1195-2012>
- Khatiwala, S., Schmittner, A., & Muglia, J. (2019). Air-sea disequilibrium enhances ocean carbon storage during glacial periods. *Science Advances*, 5(6), eaaw4981. <https://doi.org/10.1126/sciadv.aaw4981>
- Koeve, W. (2023). Misconceptions of the marine biological carbon pump in a changing climate: Thinking outside the “export” box [dataset]. *Figshare*. <https://doi.org/10.6084/m9.figshare.24635115.v2>
- Koeve, W., Kähler, P., & Oschlies, A. (2020). Does export production measure transient changes of the biological carbon pump's feedback to the atmosphere under global warming? *Geophysical Research Letters*, 47(22), e2020GL089928. <https://doi.org/10.1029/2020GL089928>
- Körtzinger, A., Hedges, J. I., & Quay, P. D. (2001). Redfield ratios revisited: Removing the biasing effect of anthropogenic CO₂. *Limnology and Oceanography*, 46(4), 964–970. <https://doi.org/10.4319/lo.2001.46.4.0964>
- Kvale, K., Koeve, W., & Mengis, N. (2021). Calcifying phytoplankton demonstrate an enhanced role in greenhouse atmospheric CO₂ regulation. *Frontiers in Marine Science*, 7, 583989. <https://doi.org/10.3389/fmars.2020.583989>
- Kwon, E. Y., Sarmiento, J. L., Toggweiler, J. R., & DeVries, T. (2011). The control of atmospheric pCO₂ by ocean ventilation change: The effect of the oceanic storage of biogenic carbon. *Global Biogeochemical Cycles*, 25(3), GB3026. <https://doi.org/10.1029/2011GB004059>
- Lauvset, S. K., Key, R. M., Olsen, A., van Heuven, S., Velo, A., Lin, X., Schirnick, C., Kozyr, A., Tanhua, T., Hoppema, M., Jutterström, S., Steinfeldt, R., Jeansson, E., Ishii, M., Perez, F. F., Suzuki, T., & Watelet, S. (2016). A new global interior ocean mapped climatology: The 1° × 1° GLODAP version 2. *Earth System Science Data*, 8(2), 325–340. <https://doi.org/10.5194/essd-8-325-2016>
- Lenton, T. M. (2000). Land and ocean carbon cycle feedback effects on global warming in a simple Earth system model. *Tellus B*, 52(5), 1159–1188. <https://doi.org/10.1034/j.1600-0889.2000.01104.x>
- Lévy, M., Bopp, L., Karleskind, P., Resplandy, L., Ethe, C., & Pinsard, F. (2013). Physical pathways for carbon transfers between the surface mixed layer and the ocean interior. *Global Biogeochemical Cycles*, 27(4), 1001–1012. <https://doi.org/10.1002/gbc.20092>
- Maier-Reimer, E., Mikolajewicz, U., & Winguth, A. (1996). Future Ocean uptake of CO₂: Interaction between ocean circulation and biology. *Climate Dynamics*, 12(10), 711–722. <https://doi.org/10.1007/s003820050138>
- Marinov, I., Gnanadesikan, A., Sarmiento, J. L., Toggweiler, J. R., Follows, M., & Mignone, B. K. (2008). Impact of oceanic circulation on

- biological carbon storage in the ocean and atmospheric pCO₂. *Global Biogeochemical Cycles*, 22(3), GB3007. <https://doi.org/10.1029/2007GB002958>
- Matsumoto, K. (2007). Radiocarbon-based circulation age of the world oceans. *Journal of Geophysical Research: Oceans*, 112(C9), C09004. <https://doi.org/10.1029/2007JC004095>
- National Academies of Sciences, Engineering, and Medicine. (2022). *A research strategy for ocean-based carbon dioxide removal and sequestration*. The National Academies Press. <https://doi.org/10.17226/26278>
- Oschlies, A., Duteil, O., Getzlaff, J., Koeve, W., Landolfi, A., & Schmidtko, S. (2017). Patterns of deoxygenation: Sensitivity to natural and anthropogenic drivers. *Philosophical Transactions. Series A, Mathematical, Physical, and Engineering Sciences*, 375(2102), 20160325. <https://doi.org/10.1098/rsta.2016.0325>
- Oschlies, A., Pahlow, M., Yool, A., & Matear, R. J. (2010). Climate engineering by artificial ocean upwelling: Channelling the sorcerer's apprentice. *Geophysical Research Letters*, 37(4), L04701. <https://doi.org/10.1029/2009GL041961>
- Primeau, F. (2005). Characterizing transport between the surface mixed layer and the ocean interior with a forward and adjoint global ocean transport model. *Journal of Physical Oceanography*, 35(4), 545–564. <https://doi.org/10.1175/JPO2699.1>
- Revelle, R., & Suess, H. E. (1957). Carbon dioxide exchange between atmosphere and ocean and the question of an increase of atmospheric CO₂ during the past decades. *Tellus*, 9(1), 18–27. <https://doi.org/10.1111/j.2153-3490.1957.tb01849.x>
- Rodgers, K. B., Schlunegger, S., Slater, R. D., Ishii, M., Frölicher, T. L., Toyama, K., Plancherel, Y., Aumont, O., & Fassbender, A. J. (2020). Reemergence of anthropogenic carbon into the ocean's mixed layer strongly amplifies transient climate sensitivity. *Geophysical Research Letters*, 47(18), e2020GL089275. <https://doi.org/10.1029/2020GL089275>
- Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., Wanninkhof, R., Wong, C. S., Wallace, D. W. R., Tilbrook, B., Millero, F. J., Peng, T.-H., Kozyr, A., Ono, T., & Rios, A. F. (2004). The oceanic sink for anthropogenic CO₂. *Science*, 305(5682), 367–371. <https://doi.org/10.1126/science.1097403>
- Sarmiento, J. L., Le Quéré, C., & Pacala, S. W. (1995). Limiting future atmospheric carbon dioxide. *Global Biogeochemical Cycles*, 9(1), 121–137. <https://doi.org/10.1029/94GB01779>
- Sarmiento, J. L., & Orr, J. C. (1991). Three-dimensional simulations of the impact of Southern Ocean nutrient depletion on atmospheric CO₂ and ocean chemistry. *Limnology and Oceanography*, 36(8), 1928–1950. <https://doi.org/10.4319/lo.1991.36.8.1928>
- Schmidtko, S., Stramma, L., & Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature*, 542(7641), 335–339. <https://doi.org/10.1038/nature21399>
- Siegel, D. A., DeVries, T., Cetinić, I., & Bisson, K. M. (2023). Quantifying the ocean's biological pump and its carbon cycle impacts on global scales. *Annual Review of Marine Science*, 15(1), 329–356. <https://doi.org/10.1146/annurev-marine-040722-115226>
- Siegel, D. A., DeVries, T., Doney, S. C., & Bell, T. (2021). Assessing the sequestration time scales of some ocean-based carbon dioxide reduction strategies. *Environmental Research Letters*, 16(10), 104003. <https://doi.org/10.1088/1748-9326/ac0be0>
- Sigman, D. M., & Boyle, E. A. (2000). Glacial/interglacial variations in atmospheric carbon dioxide. *Nature*, 407(6806), 859–869. <https://doi.org/10.1038/35038000>
- Thomas, H. (2002). Remineralization ratios of carbon, nutrients, and oxygen in the North Atlantic Ocean: A field databased assessment. *Global Biogeochemical Cycles*, 16(3), 1051. <https://doi.org/10.1029/2001GB001452>
- Volk, T., & Hoffert, M. I. (1985). Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO₂ changes. In E. T. Sundquist & W. S. Broecker (Eds.), *Geophysical monograph series*. American Geophysical Union. <https://doi.org/10.1029/GM032p0099>
- Weiss, R. F. (1974). Carbon dioxide in water and seawater: The solubility of a non-ideal gas. *Marine Chemistry*, 2(3), 203–215. [https://doi.org/10.1016/0304-4203\(74\)90015-2](https://doi.org/10.1016/0304-4203(74)90015-2)
- Wilson, J. D., Andrews, O., Katavouta, A., de Melo Virissimo, F., Death, R. M., Adloff, M., Baker, C. A., Blackledge, B., Goldsworth, F. W., Kennedy-Asser, A. T., Liu, Q., Sieradzan, K. R., Vosper, E., & Ying, R. (2022). The biological carbon pump in CMIP6 models: 21st century trends and uncertainties. *Proceedings of the National Academy of Sciences of the United States of America*, 119(29), e2204369119. <https://doi.org/10.1073/pnas.2204369119>
- Zeebe, R. E., & Wolf-Gladrow, D. A. (2001). *CO₂ in seawater: Equilibrium, kinetics, isotopes*. Elsevier Oceanography Book Series, 65, 346 pp, Amsterdam.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Frenger, I., Landolfi, A., Kvale, K., Somes, C. J., Oschlies, A., Yao, W., & Koeve, W. (2024). Misconceptions of the marine biological carbon pump in a changing climate: Thinking outside the “export” box. *Global Change Biology*, 30, e17124. <https://doi.org/10.1111/gcb.17124>