

## OPINION

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

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## 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 (CO<sub>2</sub>). 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 CO<sub>2</sub>, 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 CO<sub>2</sub>. 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 CO<sub>2</sub>, 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 CO<sub>2</sub>. This feedback is notably small compared with anthropogenic CO<sub>2</sub> emissions and other carbon-climate feedbacks. In this Opinion paper, we advocate for a comprehensive view of the BCP's impact on atmospheric CO<sub>2</sub>, providing a prerequisite for assessing the effectiveness of marine CO<sub>2</sub> removal approaches that target marine biology.

## KEYWORDS

atmospheric CO<sub>2</sub>, 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 CO<sub>2</sub> and thus Earth's climate. This storage is partly determined by the ocean biological*

*carbon “pump” (BCP). Carbon dioxide (CO<sub>2</sub>) 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 CO<sub>2</sub> (Box 1,*

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### BOX 1 Ocean carbon chemistry and buffer capacity

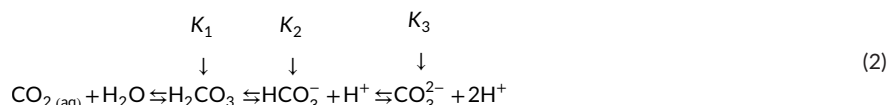
The exchange of  $\text{CO}_2$  between the ocean and the atmosphere is driven by the partial pressure difference of atmospheric  $p\text{CO}_{2(\text{atm})}$  and seawater  $p\text{CO}_{2(\text{aq})}$ . At thermodynamic equilibrium

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

$\text{CO}_2$  dissolves in seawater in proportion to its partial pressure  $p\text{CO}_{2(\text{aq})}$  and its solubility coefficient ( $K_0$ ), where  $K_0$  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  $\text{CO}_{2(\text{aq})}$  then rapidly (within minutes) chemically reacts with seawater, and dissociates to reach thermodynamic equilibrium, according to the salinity-, pressure- and temperature-dependent equilibrium constants  $K_1$ ,  $K_2$ ,  $K_3$  into carbonate species carbonic acid ( $\text{H}_2\text{CO}_3$ ), bicarbonate ( $\text{HCO}_3^-$ ) and carbonate ( $\text{CO}_3^{2-}$ ) (Zeebe & Wolf-Gladrow, 2001):



The carbonate species collectively are referred to as DIC, with  $\text{CO}_{2(\text{aq})}$  combining  $\text{CO}_2$  and  $\text{H}_2\text{CO}_3$ , 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  $\text{H}^+$ , and thus pH (a measure for  $\text{H}^+$ ) and determines the seawater's buffering capacity (Zeebe & Wolf-Gladrow, 2001): With high proportions of  $\text{HCO}_3^-$  and  $\text{CO}_3^{2-}$  an addition of  $\text{H}^+$  (Equation 2) is neutralized by reaction with  $\text{CO}_3^{2-}$  and  $\text{HCO}_3^-$ , with little pH change. With a high proportion of  $\text{CO}_{2(\text{aq})}$  the buffering capacity is low and any  $\text{H}^+$  additions result in a lowering of pH.

Under present conditions the equilibrium of Equation (2) is shifted toward  $\text{HCO}_3^-$ , ~89%, and  $\text{CO}_3^{2-}$ , ~11%, and only a small fraction of DIC, less than 1%, remains as  $\text{CO}_{2(\text{aq})}$  (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  $\text{CO}_{2(\text{atm})}$  dissolution and provides an efficient chemical buffer. Overall, the carbonate chemistry allows the ocean to take up large quantities of  $\text{CO}_2$ , 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  $\text{O}_2$  or  $\text{N}_2$ , the oceanic reservoir is much smaller than that of the atmosphere).

The ocean carbonate equilibria adjusts to perturbations. For example, the invasion of anthropogenic  $\text{CO}_2$ , or the remineralization of organic matter, will impact  $\text{CO}_{2(\text{aq})}$  but also the other two DIC species,  $\text{CO}_3^{2-}$  and  $\text{HCO}_3^-$  (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  $\text{CO}_3^{2-}$  following Equation (4), thus reducing the buffer capacity:



The efficiency of how much  $\text{CO}_2$  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  $p\text{CO}_{2(\text{atm})}$  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  $\text{CO}_2$  is amplified compared to that of ocean DIC. With the invasion of anthropogenic  $\text{CO}_2$  from the atmosphere the continued dissociation of  $\text{CO}_{2(\text{aq})}$  produces unbalanced protons,  $\text{H}^+$  (Equation 2) lowering pH. The  $\text{H}^+$  reacts with the  $\text{CO}_3^{2-}$ -ion, reducing the buffering capacity of seawater, and thereby shifting the DIC equilibrium speciation more toward the left, that is toward  $\text{CO}_{2(\text{aq})}$  (Equation 2), which equilibrates with the atmosphere. Hence, while the buffering capacity allows the ocean to absorb much more anthropogenic  $\text{CO}_2$  than was possible otherwise,  $R$  increases and the capacity reduces with continued uptake of  $\text{CO}_2$  ("buffer erosion"), and a larger share of  $\text{CO}_2$  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,  $\text{CO}_{2(\text{aq})}$ ,  $\text{HCO}_3^-$ , and  $\text{CO}_3^{2-}$ , 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  $\text{CO}_2$  that can effectively exchange between the atmosphere and ocean (referred to as the “atmosphere-ocean buffered carbon reservoir”  $C_{\text{buffer}}$ , with  $C_{\text{buffer}} = I_{\text{atm}} + I_{\text{oc}}$ , the sum of the atmospheric reservoir of  $\text{CO}_2$ ,  $I_{\text{atm}}$ , 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,  $C_{\text{buffer}}$ , 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  $C_{\text{buffer}}$  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  $\text{CO}_2$  emissions and climate change.

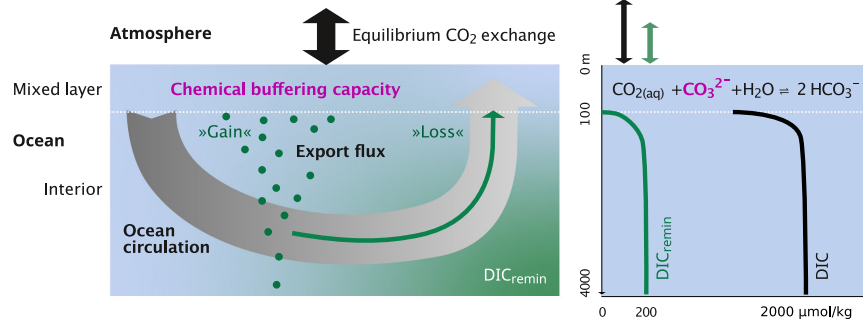
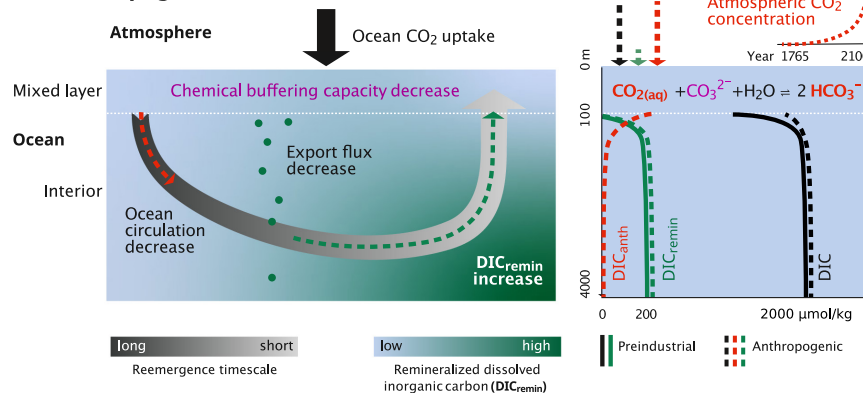
Equation 1), most of the carbon resides in the ocean in the form of carbonate ( $\text{CO}_3^{2-}$ ) and bicarbonate ( $\text{HCO}_3^-$ ) ions. The three carbon species are in thermodynamic equilibrium (Box 1, Equation 2), and in combination are referred to as dissolved inorganic carbon (DIC; Box 1, 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  $\text{CO}_2$ ,” 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  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  (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  $\text{CO}_2$  and long-term climate. It is an intuitive but unproven argument that the BCP will be of similar importance under ongoing anthropogenic  $\text{CO}_2$  emissions that perturb the Earth's carbon cycle. Yet, the relevance of the BCP for preindustrial atmospheric  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$ , 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  $\text{CO}_2$  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  $\text{CO}_2$  in high latitude cold waters, and two biologically operated pumps: the soft-tissue pump and the calcium-carbonate ( $\text{CaCO}_3$ ) pump that incorporate surface ocean  $\text{CO}_2$  in the sunlit upper ocean into organic particles and into the formation of  $\text{CaCO}_3$  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 ( $\text{DIC}_{\text{remin}}$ ).  $\text{DIC}_{\text{remin}}$  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  $\text{DIC}_{\text{remin}}$  (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  $\text{DIC}_{\text{remin}}$  is retained in the ocean interior, and the larger the reservoir of accumulated  $\text{DIC}_{\text{remin}}$  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  $\text{CO}_3^{2-}$ , Box 1) that controls the magnitude of the species of DIC that has a gaseous phase ( $\text{CO}_2(\text{aq})$ ) and that thus can exchange with the atmosphere. In a steady state, such as the preindustrial climate unperturbed by anthropogenic  $\text{CO}_2$  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  $\text{CO}_2$  to the atmosphere as a consequence of preindustrial weathering flux of alkalinity and DIC from land to ocean).  $\text{DIC}_{\text{remin}}$ , as a metric of the BCP and its impact on atmospheric  $\text{CO}_2$ , 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  $\text{CO}_2$  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  $\text{DIC}_{\text{remin}}$  (darker green shading to the left and green dashed line to the right), suggesting an intensified BCP, and a biogenically induced  $\text{CO}_2$  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  $\text{CO}_2$  (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 ( $\text{DIC}_{\text{anth}}$ , red dashed arrow and red dashed line).  $\text{DIC}_{\text{anth}}$  leads to an erosion of the buffer capacity (reduction of  $\text{CO}_3^{2-}$ ). 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 CO<sub>2</sub>, and climate. This perspective responds to this challenge and suggests a comprehensive concept of the BCP, and DIC<sub>remin</sub> 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 CO<sub>2</sub>?

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<sub>remin</sub> reservoir in the interior ocean is a balance of the fluxes due to a gain of DIC<sub>remin</sub> 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<sub>remin</sub> 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<sub>remin</sub> 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 CO<sub>2</sub> (CO<sub>2(aq)</sub>) component of DIC can interact with the atmosphere. The sequestration of DIC<sub>remin</sub> 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<sub>remin</sub> 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<sub>remin</sub> loss term, associated with reemergence to the mixed layer, is of equal importance as the gain of DIC<sub>remin</sub>, and thus critical to consider when determining the storage of ocean carbon and the role of the BCP in regulating atmospheric CO<sub>2</sub>.

Export flux alone is insufficient to assess ocean carbon storage by the BCP. There is an immense focus on the gain side of DIC<sub>remin</sub> 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 CO<sub>2</sub>. 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 CO<sub>2</sub> (e.g., reviews by Boyd et al., 2019; Iversen, 2023; Web of Science “BCP & climate/CO<sub>2</sub>” 54% of hits). However, the assumption of a universal relationship with atmospheric CO<sub>2</sub> 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 CO<sub>2</sub> 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<sub>remin</sub> is a useful metric for the BCP, and its impact on atmospheric CO<sub>2</sub>. While export flux is not representative for biological ocean storage (Figure S2a) and is not independently linked to atmospheric CO<sub>2</sub>, the reservoir of DIC<sub>remin</sub> 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<sub>remin</sub> in the ocean interior the smaller the atmospheric reservoir of CO<sub>2</sub>, with an approximately linear relationship (Figure 3c, though the relationship is not one-to-one, which we will discuss below). DIC<sub>remin</sub> 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<sub>remin</sub> (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 CO<sub>2</sub>.

If ocean circulation causes DIC<sub>remin</sub> to reemerge at the surface (“loss side”), it will not “just” outgas to the atmosphere to increase atmospheric CO<sub>2</sub> “one-to-one” (Figure 3c), because the seawater chemical buffering capacity shields atmospheric CO<sub>2</sub> against a change of DIC<sub>remin</sub>. The reemergence of DIC<sub>remin</sub> will result in a re-equilibration between the atmosphere and the ocean. The fraction of DIC<sub>remin</sub> that ends up in the atmosphere depends on the ocean’s carbon buffering capacity and the atmospheric pCO<sub>2</sub> (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 CO<sub>2</sub> (around a year, Emerson & Hedges, 2008), and regional sea ice coverage, can prevent complete equilibration between atmospheric CO<sub>2</sub> and surface ocean aqueous CO<sub>2</sub> (Eggleston & Galbraith, 2018; Khatiwala





**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 ( $\text{O}_2$ ), temperature and salinity. Upon the remineralization of organic matter,  $\text{O}_2$  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  $\text{O}_2$ . Although the assumption of surface  $\text{O}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  (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  $\text{CO}_2$  (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).

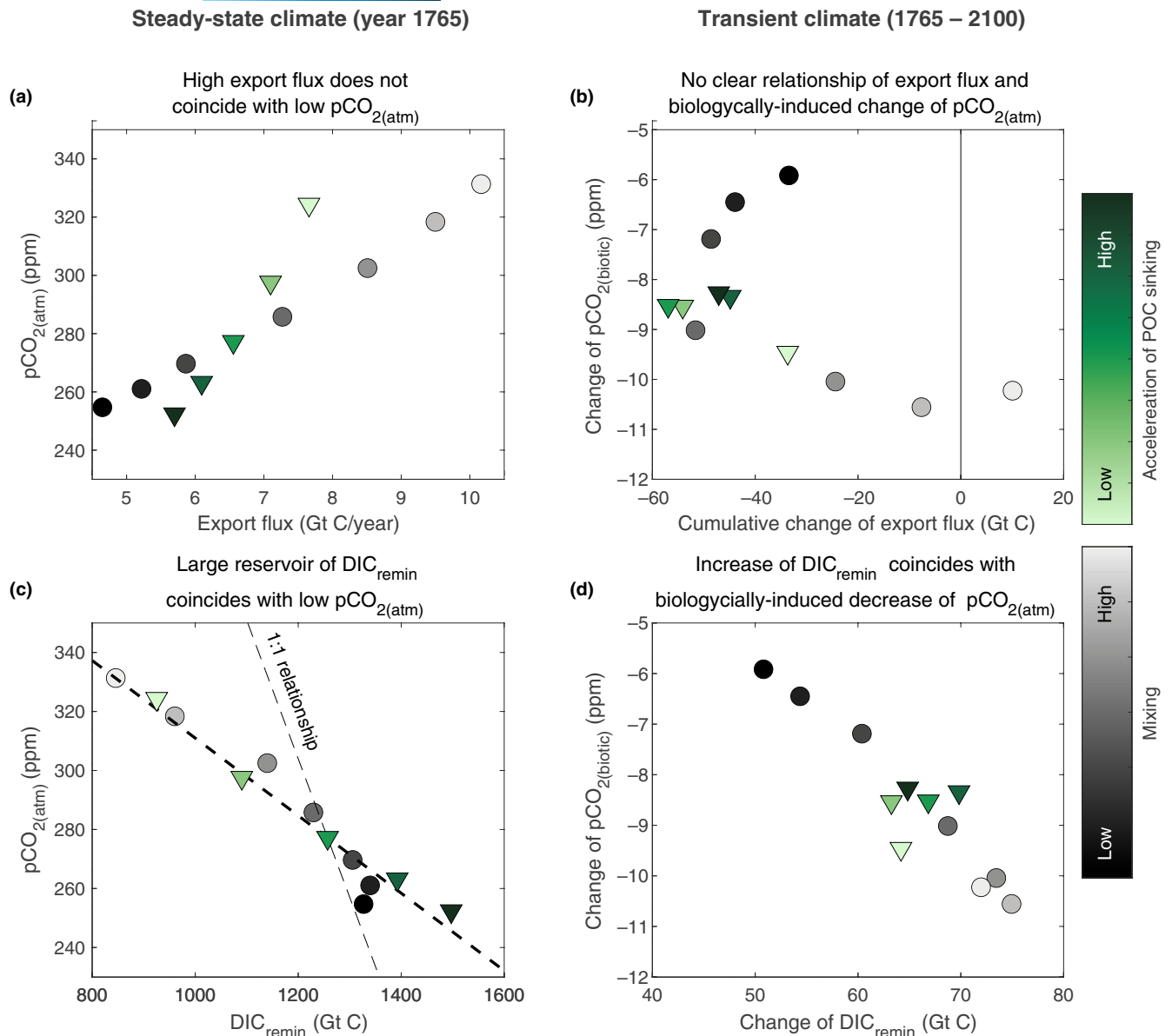
While the BCP therefore provides a negative feedback on anthropogenic climate change in the 21st century, this feedback is small compared with both the negative feedback of the invasion of anthropogenic  $\text{CO}_2$  into the ocean and to the positive feedback of the decreasing capacity of the surface ocean to take up more anthropogenic  $\text{CO}_2$  (“buffer erosion”,

Fassbender et al., 2017). The first-order ocean carbon response to the increase in atmospheric  $\text{CO}_2$  partial pressure is massive chemio-physical dissolution of anthropogenic  $\text{CO}_2$  in the ocean, hence mitigating climate change ( $\text{DIC}_{\text{anth}}$ , Figure 1b). The oceanic uptake of anthropogenic  $\text{CO}_2$  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  $\text{CO}_2$ , and an amplified change of atmospheric  $\text{CO}_2$  (Box 1, Equations 5 and 6). The effect of this “erosion” of the buffering capacity has been estimated to reduce the uptake of  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  levels, a process that would happen also if the marine carbon pumps did not exist. In comparison with anthropogenic  $\text{CO}_2$  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  $\text{CO}_2$  emissions in the ocean, and the resulting eroding capacity of the ocean to take up  $\text{CO}_2$ , 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<sub>2</sub> under transient anthropogenic climate at the centennial timescale (Figure 3c,d). Present-day anthropogenic CO<sub>2</sub> 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<sub>2</sub>. We wish to stress the value of research on export flux and flux attenuation. After all, DIC<sub>remin</sub> 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<sub>2</sub>, 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<sub>2</sub> (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 DIC<sub>remin</sub>. 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 DIC<sub>remin</sub> 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 DIC<sub>remin</sub>. 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 CO<sub>2</sub> under (left column) unperturbed preindustrial steady-state (zero anthropogenic CO<sub>2</sub> emissions) and (right column) perturbed anthropogenic transient climate (rising anthropogenic CO<sub>2</sub> emissions). Both support the use of remineralized dissolved inorganic carbon, DIC<sub>remin</sub>, as a proxy for the effect of the BCP on atmospheric CO<sub>2</sub>. Both, (a) in a steady state, after a re-equilibration to stable atmospheric pCO<sub>2</sub>, and (b) in a transient climate from preindustrial (1765) to 2100 a larger export flux does not correlate with a lower atmosphere CO<sub>2</sub> reservoir (pCO<sub>2(atm)</sub>); scatter plots of globally integrated export production ( $z = 130$  m) and atmospheric CO<sub>2</sub> (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<sub>remin</sub>, is associated with a lower atmosphere CO<sub>2</sub> 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<sub>2(atm)</sub> than in DIC<sub>remin</sub> (bold dashed line), as only part of DIC<sub>remin</sub> 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<sub>2(atm)</sub> with DIC<sub>remin</sub> to derive the biologically-induced changes of pCO<sub>2(atm)</sub>, referred to as pCO<sub>2(biotic)</sub> in (b) and (d). The change of pCO<sub>2(biotic)</sub> 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 O<sub>2</sub> to a change in CO<sub>2</sub> based on fixed stoichiometry and, using the relationship in (c), is adjusted with the factor of ~30% to account for the dependence of atmospheric CO<sub>2</sub> 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<sub>2(atm)</sub> (see also main text). The total change of pCO<sub>2(atm)</sub> (not shown) in (b) and (d), that includes the change of pCO<sub>2(biotic)</sub>, is dominated by anthropogenic CO<sub>2</sub> emissions, masking more subtle changes of pCO<sub>2(biotic)</sub>. 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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<sub>remin</sub> will be large as well. A potential increase of DIC<sub>remin</sub> may fade within decades (Siegel et al., 2021).

Fourth, DIC<sub>remin</sub> is a useful metric to evaluate the effect the BCP has on atmospheric CO<sub>2</sub>, as proposed by others (Koeve et al., 2020; Marinov et al., 2008; Wilson et al., 2022) (Figure 3c). The diagnostic DIC<sub>remin</sub> integrates over the gain and loss sides of marine biogenic carbon, and its impact on atmospheric pCO<sub>2</sub> can be quantified (Equation 6, Box 1, under steady state). In addition, DIC<sub>remin</sub> 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<sub>remin</sub> (<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<sub>remin</sub> is increasing in the global ocean (Schmidtko

et al., 2017) due to an increase in the reemergence timescale, and thus to a biologically driven reduction in atmospheric CO<sub>2</sub>. 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<sub>remin</sub>, the quantification of the associated atmospheric pCO<sub>2</sub> changes (“biotic” change of atmospheric ΔpCO<sub>2</sub>, pCO<sub>2(biotic)</sub>, Figure 3d) is less straightforward due to the anthropogenic CO<sub>2</sub> 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 pCO<sub>2</sub> the negative climate feedback due to enhanced storage of DIC<sub>remin</sub> 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 CO<sub>2</sub> 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<sub>remin</sub>, 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 CO<sub>2</sub>.

## 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.

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## 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>.

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