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## RESEARCH LETTER

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### Key Points:

- Apparent oxygen utilization is proposed to quantify the feedback of the biological carbon pump to the atmosphere in a warming ocean
- Changes in export production are unrelated to changes in biotic oxygen air-sea gas exchange
- The CO<sub>2</sub>-flux due to changes of the biological carbon pump over the recent decades is negligible compared to the total marine CO<sub>2</sub> uptake

### Supporting Information:

- Supporting Information S1

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## Does Export Production Measure Transient Changes of the Biological Carbon Pump's Feedback to the Atmosphere Under Global Warming?

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**Abstract** In a widely-held conception, the biological carbon pump (BCP) is equal to the export of organic matter out of the euphotic zone. Using global ocean-atmosphere model experiments we show that the change in export production is a poor measure of the biological pump's feedback to the atmosphere. The change in global true oxygen utilization (TOU), an integrative measure of the imprint of the BCP on marine oxygen, however, is in good agreement with the net change in the biogenic air-sea flux of oxygen. Since TOU correlates very well with apparent oxygen utilization (AOU) in our experiments, we propose to measure the change of AOU from data of global float programs to monitor the feedback of the BCP to the atmosphere. For the current ocean we estimate that BCP changes effect a CO<sub>2</sub> uptake by the ocean in the range of 0.07 to 0.14 GtC/yr.

**Plain Language Summary** The biological carbon pump is an important element of marine carbon cycling and climate control on millennium timescales. In a widely-held conception the export of organic carbon from the productive surface layer of the ocean is used as the essential measure of this carbon pump. Using numerical ocean modeling, we show here that the change in export production is, however, a poor measure of the biological carbon pump's feedback to the atmosphere on centennial timescales. In the contrary, we find that an oxygen-based measure, the apparent oxygen utilization can be used to quantify the impact of biological pump changes on the atmosphere. Since the apparent oxygen utilization is easily accessible from an existing network of marine floats, our study suggests that the atmospheric impact of any future changes of the biological carbon pump can be monitored and quantified. For past decades our study proposes a negligible CO<sub>2</sub> feedback to climate from biological carbon processing.

## 1. Introduction

The biological carbon pump (hereafter BCP, also coined soft tissue pump; Volk & Hoffert, 1985) is often equated with the export of organic matter out of the euphotic zone (Boyd & Trull, 2007; Harrison et al., 2018; Keeling et al., 2010; Yool et al., 2007). Attempts to quantify the “efficiency” or the “strength” of the biological pump often use export production (EP) as its essential measure. The fraction of net primary production vertically exported from the surface layer has been explored extensively in its relationships with temperature, nutrient availability, or net primary productivity, and with respect to its global patterns (Buesseler, 1998; Eppley & Peterson, 1979; Henson et al., 2011, 2012; Laws et al., 2000). In climate models, net primary production and EP have been used to quantify changes of marine ecosystems and the reaction of the biological pump to future climate change (Cabre et al., 2015; Laufkötter et al., 2015, 2016; Taucher & Oschlies, 2011). Models consistently project a decrease of global EP by on average 12% ( $\Delta EP = -0.68 \pm 0.54$  GtC/yr) until the end of this century for a business-as-usual emission scenario (Cabre et al., 2015). The ultimate drivers of this reduction are increasing density stratification (Bopp et al., 2002; Sarmiento et al., 1998), caused by surface ocean warming, increased moisture fluxes, and mixed layer shoaling. These physical changes reduce nutrient supply from the deep ocean, followed by decreasing net primary production, phytoplankton biomass, and ultimately export (Cabre et al., 2015), in particular in the low latitudes, while export increases in the high latitudes. The projected net global decrease in EP has been suggested to potentially sustain a positive feedback to atmospheric CO<sub>2</sub> concentrations (Cabre et al., 2015), i.e., to potentially amplify climate change (Resplandy, 2018).

This view is contrasted by observations and model projections of a widespread ocean deoxygenation until the end of this century (Bopp et al., 2013) and beyond (Oschlies et al., 2019; Shaffer et al., 2009;

Yamamoto et al., 2015). The overwhelming part of the projected marine oxygen inventory loss until the end of this century is due to an increase in apparent oxygen utilization (AOU) (Bopp et al., 2017). AOU is an integrative measure of the (oxic) degradation of organic matter and provides a measure of the amount of “respired carbon” or “respiratory CO<sub>2</sub>” (Keeling et al., 2010; Kwon et al., 2011), i.e., dissolved inorganic carbon stored in the ocean interior after having been processed by the biological carbon pump (Bernardello et al., 2014; Körtzinger et al., 1998; Peng et al., 1998). Increase in AOU has been identified as the major cause of ocean oxygen loss (deoxygenation) (Bopp et al., 2002; Emerson et al., 2004; Oschlies et al., 2017; Schmidtko et al., 2017). A global increase in AOU is hence consistent with a net O<sub>2</sub> flux out of the ocean and a net CO<sub>2</sub> flux into the ocean, indicating a negative feedback to rising atmospheric CO<sub>2</sub>. This proposes that global-warming related changes of the biological carbon pump may mitigate, rather than amplify, climate change. The same or comparable climate models, hence propose contradicting responses of the BCP to climate change, only depending on the choice of the metric to quantify the change of the BCP.

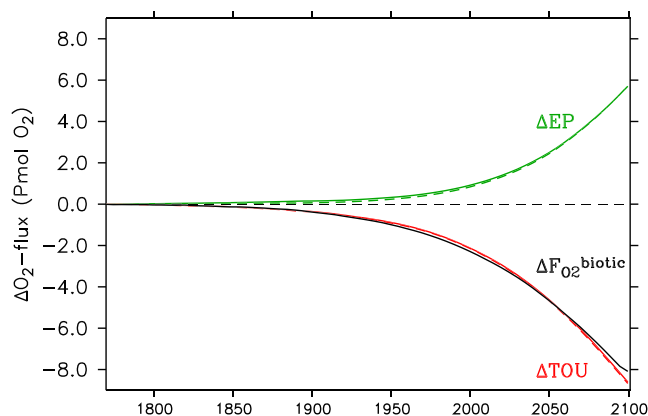
In idealized steady-state model simulations, the global integral of AOU (or its stoichiometric equivalent remineralized-PO<sub>4</sub> inventory) shows a negative correlation with atmospheric pCO<sub>2</sub> (Kwon et al., 2009) while EP has no meaningful relationship with atmospheric pCO<sub>2</sub> (Gnanadesikan & Marinov, 2008), an observation which can be explained by a strong regional decoupling of EP and AOU, evident from the regional variability of the “sequestration efficiency” (DeVries et al., 2012). Hence, AOU rather than EP provides a good indicator of the biotically driven oceanic carbon storage in steady state, which is in agreement with the original definition of the “strength” of the soft tissue pump given by Volk and Hoffert (1985). However, the Holocene steady state is in transition to the Anthropocene (Crutzen, 2002a, 2002b; Steffen et al., 2011), an era of rapidly changing climate and oceans (Hoegh-Guldberg et al., 2014). On transient timescales, a change in AOU, for example, in the deep ocean, may not immediately be reflected in an exchange of oxygen or CO<sub>2</sub> between ocean and atmosphere. For a marine process to qualify as a feedback to the atmosphere, however, an actual flux change at the air-sea boundary must occur. So far, this has neither been shown for transient changes in AOU nor for transient changes of EP.

In this paper, we use the University of Victoria (UVic) Earth System model of intermediate complexity to explore whether the cumulative change in EP or the change in AOU provide the better measure of the impact of the BCP on atmospheric O<sub>2</sub> and CO<sub>2</sub> under the transient conditions of a changing climate. Solving this question is important, if the marine feedback to atmospheric CO<sub>2</sub> and climate is to be monitored and understood. We do this by comparing changes of AOU and EP with a new objective model metric, the biogenic O<sub>2</sub>-flux between atmosphere and ocean, which we will introduce in the next section.

## 2. Conceptual Approach

Oxygen in the interior ocean can be described as the difference between preformed oxygen (O<sub>2</sub><sup>pre</sup>) and the oxygen debt from the oxidation of organic matter accumulated since last contact with the atmosphere. We refer to this oxygen debt as true oxygen utilization (TOU); hence, O<sub>2</sub> = O<sub>2</sub><sup>pre</sup> – TOU. Preformed oxygen is the oxygen contained in seawater when it subducted from the surface into the ocean interior. It is controlled by rapid gas exchange between the surface ocean and the atmosphere, i.e., by the thermodynamic conditions of the surface ocean, its temperature and salinity, and in polar regions by the degree of ice coverage (Ito et al., 2004). O<sub>2</sub><sup>pre</sup> is often approximated as the saturation concentration of oxygen (O<sub>2</sub><sup>sat</sup>) in seawater at given atmospheric pressure, surface seawater temperature, and salinity. This is the concept of AOU, i.e., O<sub>2</sub> = O<sub>2</sub><sup>sat</sup> – AOU (Sarmiento & Gruber, 2006).

The direct physical impact of global warming on marine oxygen, i.e., decreasing solubility with rising temperature, is usually quantified by the change of O<sub>2</sub><sup>sat</sup> in the ocean (Ito et al., 2017; Schmidtko et al., 2017). The change in AOU combines effects associated with changing primary production, EP, respiration, but also circulation, which ventilates (provides oxygen to) the ocean interior and thereby replaces the oxygen debt from biological processes. In an idealized ocean-atmosphere model setting, the change of the air-sea oxygen flux at the sea surface can similarly be split into a thermodynamic component (ΔF<sub>O<sub>2</sub></sub><sup>therm</sup>) related to the change in oxygen solubility (i.e., ΔO<sub>2</sub><sup>sat</sup>), and a residual associated with ΔAOU, to the extent that it causes an oxygen flux change at the sea surface. Since this residual oxygen flux is directly or indirectly related to either the production of oxygen (net primary production) or the oxidation of organic matter (respiration),



**Figure 1.** Theoretical and simulated cumulative global oxygen fluxes (Pmol O<sub>2</sub>) in UVic model experiment COUPLED\_SST (solid lines) and COUPLED (dashed lines) between 1770 and 2100. Simulated air-sea oxygen flux ( $\Delta F_{O_2}^{\text{biotic}}$ , black solid line), theoretical cumulative flux (green lines) derived from cumulative export-production change (Figure S3b), and theoretical air-sea flux derived from TOU inventory change (red lines, Figure S3b). Theoretical fluxes are computed assuming that the changes in cumulative export or TOU, respectively, result in an immediate and equivalent flux at the air-sea boundary. Following conventions, a flux into the ocean is positive. TOU is integrated below  $z = 130$  m, export production is quantified at  $z = 130$  m. For carbon flux to oxygen conversion, we apply the model's ratio of mole oxygen produced per mole organic carbon formed ( $r = 1.5$ ). An increase in TOU constitutes a loss of oxygen from the ocean, hence a negative flux at the atmosphere-ocean interface.

we refer to it as biogenic ( $\Delta F_{O_2}^{\text{biotic}}$ ).  $\Delta F_{O_2}^{\text{biotic}}$  includes effects from circulation slow-down which have been projected to reduce the return flux of AOU back to the sea surface, including AOU that has been generated from organic matter breakdown long before climate change started.

In the global-warming model runs used in this study we explicitly exclude the thermodynamic warming component on marine oxygen by assimilating the annual mean temperature difference between a transient climate change run COUPLED and its constant climate control run CTRL (supporting information Figures S1 and S2) for the computation of oxygen gas exchange and solubility (see Text S1; Table S1). Transient changes in simulated oxygen gas exchange between ocean and atmosphere presented in this study are hence due to  $\Delta F_{O_2}^{\text{biotic}}$  only. Accordingly, we can use the biogenic oxygen air-sea flux changes as a reference metric of BCP changes in our model, against which we compare changes in (cumulative) EP and changes in AOU (TOU).

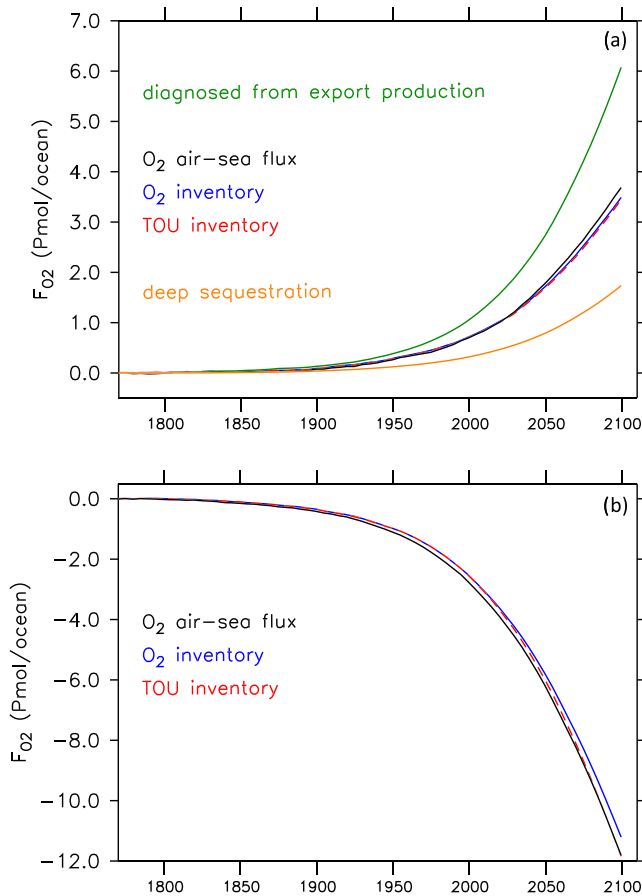
### 3. Experimental Approach

We use an ocean-sea-ice-atmosphere version of the UVic Earth System model of intermediate complexity version 2.9 (Keller et al., 2012; Weaver et al., 2001) supplemented with idealized tracers of TOU (Ito et al., 2004; Koeve & Kähler, 2016) and ideal age (England, 1995; Koeve et al., 2015). With this model we carried out a series of model experiments under the RCP 8.5 climate change scenario (see Text S1 and Table S1 for details): COUPLED\_SST is a transient run in which we apply SST for gas exchange from the preindustrial state control run

(CTRL). CTRL\_IMPOSE is an experiment in which we assimilate the annual mean difference of biotic oxygen sinks-minus-sources (O<sub>2</sub>-sms) of the transient and the control simulation into a run without climate and circulation change, such that the O<sub>2</sub>-sms of this run very much resembles that of the coupled transient experiment. COUPLED\_IMPOSE is a model experiment with changing climate and circulation in which we assimilate the annual mean difference of oxygen sinks minus sources (O<sub>2</sub>-sms) of the climate change and the control simulation at model run time, such that the O<sub>2</sub>-sms of the run COUPLED\_IMPOSE very much resembles that of CTRL. We also carry out several variants of CTRL\_IMPOSE and COUPLED\_IMPOSE in which assimilation is done only in restricted regions (see Table S1) and variants of COUPLED\_SST with modified background vertical diffusivity. Technical details are provided in Text S1.

### 4. Results

In experiment COUPLED\_SST EP decreases during the experiment (yr 1770 to 2100) (Figure S3a) while AOU and TOU, which we track by an idealized model tracer (Ito et al., 2004), increase (Figure S3b). We convert cumulative EP and TOU into equivalent oxygen flux units (Figure 1) assuming the changes to cause an immediate flux response. Carbon export flux is converted to oxygen units by applying the model's ratio of mole oxygen produced per mole organic carbon formed ( $r = 1.5$ ). TOU change is converted to biotic oxygen flux (positive downward) by multiplying with  $(-1)$ . For an immediate flux response the simulated cumulative decrease in EP hence would translate into an oxygen flux from the atmosphere into the ocean (Figure 1, green line), while the simulated increase in TOU would translate into an oxygen air-sea flux out of the ocean (Figure 1, red line). The true biogenic oxygen air-sea flux ( $\Delta F_{O_2}^{\text{biotic}}$ ) in COUPLED\_SST (Figure 1, black line) is out of the ocean and almost identical to the equivalent air-sea flux of the TOU change. In contrast, the theoretical O<sub>2</sub>-flux equivalent to the cumulative export-production change has the wrong sign compared with the modeled O<sub>2</sub>-flux at the air-sea boundary. This picture is consistent with earlier work (Bopp et al., 2002; Yamamoto et al., 2015) which showed that the direct biotic effect of reduced EP on oxygen and AOU is overcompensated by the effects of a circulation slow-down and increasing interior-ocean residence time.



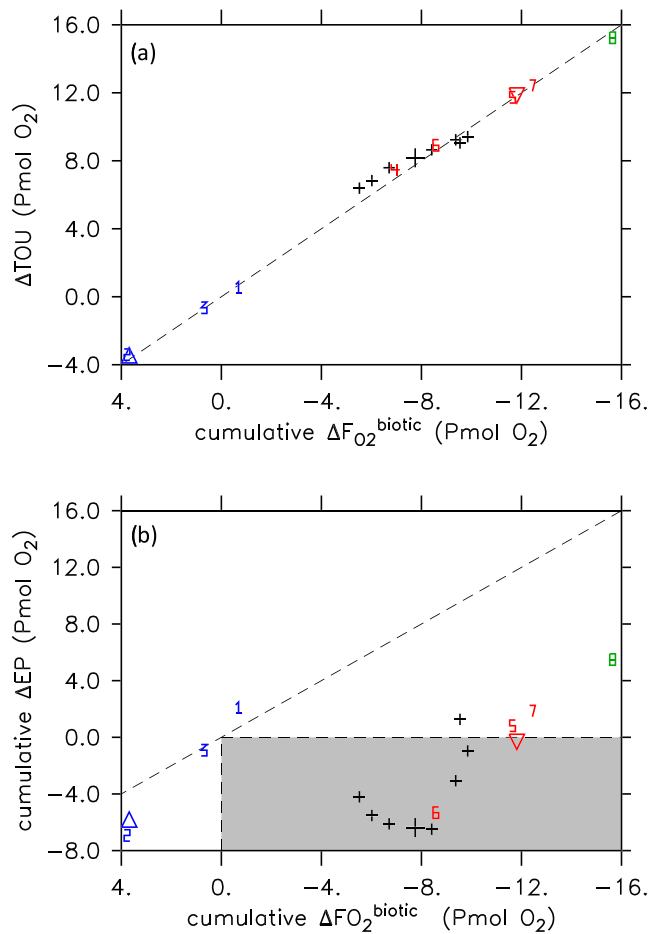
**Figure 2.** Disentangling direct and indirect effects of the biological carbon pump changes on oxygen and TOU inventory as well as oxygen fluxes. All numbers are presented in units of cumulative oxygen flux at the air sea boundary. (a) Experiment CTRL\_IMPOSE (no circulation change, but with imposed changes of biological rates affecting  $O_2$ -sms like in COUPLED, compare Figure S4a): simulated oxygen air-sea flux  $\Delta F_{O_2}^{biotic}$  (black), change in oxygen inventory (blue), theoretical air-sea flux derived from change in TOU inventory (dashed red), cumulative theoretical  $O_2$ -flux (green) derived from cumulative change in export production, cumulative theoretical  $O_2$ -flux (orange) derived from cumulative change of respiration below 1,000 m (so-called sequestration flux). (b) Experiment COUPLED\_IMPOSE (circulation change affects oxygen and TOU, but biological rates affecting  $O_2$ -sms are like in CTRL; compare Figure S4b). Theoretical fluxes are computed assuming that the changes in cumulative export, sequestration flux, or TOU, respectively, result in an equivalent flux at the air-sea boundary without any time delay. For carbon flux to oxygen conversion, we apply the model's ratio of mole oxygen produced per mole organic carbon formed ( $r = 1.5$ ). Following conventions, a flux into the ocean is positive. Inventory changes of  $O_2$  and TOU are global integrals, export production is quantified at  $z = 130$  m.

We isolate the direct effects of changing biological rates from the effect of a changing circulation on tracer accumulation in experiment CTRL\_IMPOSE. The globally integrated  $O_2$ -sms in the interior ocean from this run very much resembles that of the transient climate change run COUPLED (Figure S4a, see Text S1 for details). The ocean gains oxygen in this run (globally, about 3.48 Pmol  $O_2$  by yr 2100) (Figure 2a), which is due to a reduction of the TOU ( $-3.46$  Pmol  $O_2$  by yr 2100). Changes in TOU and oxygen agree within 10% with a slightly larger time cumulative air-sea oxygen flux,  $\Delta F_{O_2}^{biotic}$  (3.73 Pmol  $O_2$  until yr 2100). Small differences between the cumulative  $\Delta F_{O_2}^{biotic}$  and the oxygen inventory change are explained by differences in oxygen and TOU inventory changes in the upper ocean and the ocean interior (not shown), i.e., as a small hysteresis effect. EP, the integral of  $O_2$ -sms below 130 m in this run, decreases over the course of the experiment (Figure S3), which is consistent with an ocean gaining oxygen. However, the time-cumulative integral of EP change is larger by a factor of two (equivalent oxygen demand of 6.69 Pmol  $O_2$  by yr 2100) compared to simulated oxygen air-sea exchange and oxygen inventory changes. This overestimate of biogenic oxygen flux by the EP metric is likely explained by shallow respiration, e.g. within the winter mixed layer (Koeve, 2001). Organic matter sequestration flux across 1,000 m, sometimes suggested to better represent long term sequestration of carbon from the BCP (Barange et al., 2017; Lampitt et al., 2008), is 1.84 Pmol  $O_2$  by yr 2100, about a factor two too low in comparison with the observed inventory changes of oxygen (or TOU), or  $\Delta F_{O_2}^{biotic}$ . Should a reduction of the BCP magnitude occur without circulation change, it would contribute to oxygenate the ocean. In such a situation both the changes in EP and the deep ocean carbon sequestration flux ( $z = 1,000$  m) would be weak predictors of the  $O_2$ -flux induced by the changes of the BCP, either overestimating or underestimating it by about a factor of two. However, at least the signs of change of EP, sequestration flux and the oxygen flux at the ocean-atmosphere boundary would be consistent.

We also perform the “counter” experiment (COUPLED\_IMPOSE), i.e., a run with changing climate and circulation in which we assimilate the annual mean difference of oxygen sinks minus sources ( $O_2$ -sms) of COUPLED and CTRL at model run time, such that the  $O_2$ -sms of the run COUPLED\_IMPOSE very much resembles that of CTRL (Figure S4b, see Text S1 for details). In this run, again, the decrease in oxygen, the increase in TOU, and the loss of oxygen to the atmosphere ( $\Delta F_{O_2}^{biotic}$ ) are consistent, with little hysteresis (Figure 2b; red inverse triangle in Figure 3a). Similar to earlier work (Bopp et al., 2002; Yamamoto et al., 2015), the effect of circulation change on TOU (and oxygen) tracer accumulation (isolated in COUPLED\_IMPOSE) overcompensates the direct biotic effect of changing biological rates (isolated in CTRL\_IMPOSE) on TOU and oxygen concentrations, as evident from COUPLED\_SST (Figure 1). In all three cases (COUPLED\_SST,

CTRL\_IMPOSE, and COUPLED\_IMPOSE)  $\Delta TOU$  is a very good measure of  $\Delta F_{O_2}^{biotic}$ , the biotic component of changing air-sea  $O_2$ -fluxes (Figures 1 and 2).

Using a larger number of transient model simulations (for details, see Table S1) we find very good agreement between the change of the global TOU inventory between 1770 and 2100 ( $\Delta TOU$ ) and the cumulative biogenic oxygen air-sea exchange ( $\Delta F_{O_2}^{biotic}$ ) (Figure 3a). When TOU increases,  $\Delta F_{O_2}^{biotic}$  is negative and vice versa. The dashed line in Figure 3a indicates the line of perfect agreement between the simulated changes in TOU and cumulative  $\Delta F_{O_2}^{biotic}$ . For the same model runs, there is basically no meaningful relationship



**Figure 3.** Time integrated (yr 1765 to 2100) change of (a) TOU and (b) export production (in oxygen equivalents) versus the cumulative biogenic air-sea oxygen flux. Dashed lines indicate the respective equivalence points (1:1 relationship) of (a)  $\Delta\text{TOU}$  versus  $\Delta\text{F}_{\text{O}_2}^{\text{biotic}}$  and (b)  $\Delta\text{EP}$  and  $\Delta\text{F}_{\text{O}_2}^{\text{biotic}}$ , assuming that changes in TOU or EP would translate completely and immediately into a  $\text{O}_2$  flux at the sea surface. The hatched area indicates where the signs of change of  $\Delta\text{EP}$  and  $\Delta\text{F}_{\text{O}_2}^{\text{biotic}}$  are inconsistent. Compare Table S1 for symbol legend.

biases (Kähler & Bauerfeind, 2001). Additionally, accounting for the contribution of dissolved organic matter to export (Hansell et al., 2002) is difficult. Accordingly, monitoring changes of EP appears to be extremely challenging for the real ocean. With respect to biotically induced air-sea fluxes of  $\text{O}_2$  (and  $\text{CO}_2$ , s.b.), we may be lucky that there is no need to monitor EP since it is no suitable measure of the biological carbon pump's feedback to the atmosphere under global warming.

In contrast, computing AOU from high-quality data of temperature, salinity, and oxygen is a more straightforward task (García & Gordon, 1992). Data archives hold a huge body of historical data (García et al., 2014) which allow to derive a present-day state estimate of marine AOU (García et al., 2005) and further allow to quantify its change over the last 50 years (Schmidtko et al., 2017). Currently existing and deployed technology of oxygen-sensor equipped Argo floats (Jayne et al., 2017; Johnson et al., 2009) is available to quantify and monitor changes in oxygen and AOU in the future. Model studies (Duteil et al., 2013; Ito et al., 2004) have indicated that AOU may overestimate TOU globally by up to 25%, due to incomplete equilibration at the formation time of deep water (Körtzinger et al., 2004; Wolf et al., 2018). In our model experiments, the change in AOU and the change in TOU are highly correlated (Figure S5), though  $\Delta\text{AOU}$  tends to underestimate  $\Delta\text{TOU}$  in the COUPLED model experiment by 25%. This appears to be related to a change in polar sea ice cover which can prevent complete equilibration of surface seawater with the atmosphere, a major

between the cumulative changes in  $\Delta\text{EP}$  and  $\Delta\text{F}_{\text{O}_2}^{\text{biotic}}$ , respectively (Figure 3b). Almost all data points are very far from the 1:1 relationship, which in this plot represents the theoretical case that (only) changes in EP would cause an oxygen flux at the air-sea boundary (i.e., increasing EP would cause an oxygen flux out of the ocean). Actually, for many model runs (indicated by the gray hatched area), even the sign of change of EP and that of the simulated biogenic oxygen air-sea flux do not agree.

The change in EP hence turns out to be an unreliable measure of the transient development of the biogenic  $\text{O}_2$ -flux at the ocean atmosphere boundary, while the change in TOU represents it almost perfectly. This holds for the standard simulation (COUPLED\_SST, thick black + in Figure 2), sensitivity runs with differing circulations (small black +), runs where the circulation is as in CTRL, but changing biological rates are imposed globally (blue triangle) or in specific regions (blue numbers, see Table S1 for details), as well as for runs in which circulation changes affect the accumulation of the TOU tracer and of oxygen, but biological rates from CTRL are assimilated at model run time either globally (red triangle) or in specific regions (red numbers, see Table S1 for details).

## 5. Discussion

With a suite of idealized model experiments, we cover a wide range of possible future EP and TOU changes and circulation states. We find the robust result that the change in global TOU provides a reliable quantitative measure of the oxygen fluxes at the air-sea boundary which are induced by changes of the BCP. At the same time, change in EP does not inform about the influence of the BCP on the atmosphere. This is consistent with the finding from idealized steady-state model simulations (Gnanadesikan & Marinov, 2008) and related to a strong regional decoupling of the export of organic matter and its impact on the storage of its degradation products (DeVries et al., 2012; Marinov et al., 2006). It is shown here for the first time that this also holds for transient model simulations under a business-as-usual climate change scenario.

Measuring EP in the ocean is an ambitious task. There is large regional and temporal variability requiring extremely dense measurement coverage, and there are notorious technical issues plaguing the methods to sample sinking particles quantitatively (Scholten et al., 2001) and without

reason identified for  $O_2^{\text{sat}}$  (AOU) to overestimate  $O_2^{\text{pre}}$  (TOU) (Duteil et al., 2013; Ito et al., 2004). Polar sea ice cover is projected to decrease during the 21st century for high emission scenarios, like the one used here (RCP 8.5) (Figure S6), which should have the effect to make AOU ( $O_2^{\text{sat}}$ ) a more reliable estimate of TOU ( $O_2^{\text{pre}}$ ) over the course of our model experiments. The smaller change in AOU compared to TOU in our experiments is hence an artifact of the default procedure to compute AOU (the  $O_2^{\text{sat}}$  assumption; Figure S7). Improved procedures, e.g., the evaluated oxygen utilization, EOU (Duteil et al., 2013), may be used instead. The strong correlation between  $\Delta\text{TOU}$  and  $\Delta F_{O_2}^{\text{biotic}}$  (Figure 3a) as well the correlation between  $\Delta\text{AOU}$  and  $\Delta\text{TOU}$  (Figure S5) suggest that changes of AOU (eventually EOU) monitored from a continued Argo float program with oxygen sensors provides the unique opportunity to monitor changes of the biological pump in the ocean and its influence on the atmosphere.

## 6. Conclusions and Outlook

Re-emphasizing the original proposal of Volk and Hoffert (1985) that the biological carbon pump can be best quantified by its contribution to the vertical surface-to-bottom DIC gradient, we here showed that the effect of transient changes of this pump on the atmosphere is best quantified by changes of AOU, a property linearly related to that DIC gradient and easily measured in the ocean. In contrast, we found that changes of EP show no clear relationship with the biogenic  $O_2$ -flux between atmosphere and ocean and hence has no predictive capacity to quantify changes of the biological pump relevant to the atmosphere and climate.

This study addresses the feedback of the biological carbon pump to the atmosphere in terms of an air-sea oxygen flux. Of real interest is the associated carbon flux. Biogenic oxygen fluxes between the ocean and the atmosphere are directly related to a stoichiometrically equivalent potential  $CO_2$  flux of biogenic origin, which can be easily computed by dividing the biogenic oxygen flux by the ocean mean oxygen-to-carbon ratio (the oxygen demand of organic matter degradation,  $r_{O_2:C} = 1.4$ ; Anderson & Sarmiento, 1994). The true  $CO_2$  flux attributable to changes of the biological-physical pump, will, however, be considerably different. This is due to the buffering effect of surface ocean seawater (Ito & Follows, 2005). In steady state, the true  $CO_2$ -flux from biological pump changes may be only 10%–20% of the potential  $CO_2$ -flux (Gruber et al., 2004).

We derive a first-order estimate of the steady-state  $CO_2$ -flux attributable to biological carbon pump changes from the observed rate of ocean deoxygenation (Schmidtko et al., 2017). Over the recent 50 years the rate of ocean deoxygenation (961 Tmol per decade; Schmidtko et al., 2017) is mainly due to an increase in AOU (831 Tmol per decade), which is equivalent to a potential  $CO_2$ -flux into the ocean of +594 Tmol C per decade. Using the steady-state buffer correction of this flux taken from Gruber et al. (2004) this translates into an ultimate true  $CO_2$ -flux into the ocean attributable to the biological pump of 0.7 to 1.4 GtC per decade or 0.07 to 0.14 GtC/yr. Compared with the mean total marine uptake for 2006 to 2015 ( $2.6 \pm 0.5$  GtC/yr; Le Quéré et al., 2016) this estimate of the  $CO_2$ -flux attributable to changes of the biological carbon pump (soft tissue pump) appears negligible.

## Data Availability Statement

Model output is available from <http://data.geomar.de> (<http://hdl.handle.net/20.500.12085/396970fe-3529-430c-a774-55ccc681795e>).

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