Geophysical Research Letters

RESEARCH LETTER
10.1029/2020GL089928

 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 CO2 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. 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 CO2 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 carbon 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 ± 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 CO2 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 CO₂” (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 O₂ flux out of the ocean and a net CO₂ flux into the ocean, indicating a negative feedback to rising atmospheric CO₂. 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-PO₄ inventory) shows a negative correlation with atmospheric pCO₂ (Kwon et al., 2009) while EP has no meaningful relationship with atmospheric pCO₂ (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 CO₂ 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 O₂ and CO₂ under the transient conditions of a changing climate. Solving this question is important, if the marine feedback to atmospheric CO₂ 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 O₂ 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 (O₂^{pre}) 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, O₂ = O₂^{pre} − 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). O₂^{pre} is often approximated as the saturation concentration of oxygen (O₂^{sat}) in seawater at given atmospheric pressure, surface seawater temperature, and salinity. This is the concept of AOU, i.e., O₂ = O₂^{sat} − 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 O₂^{sat} 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 (∆F_{O₂}^{therm}) related to the change in oxygen solubility (i.e., ∆O₂^{sat}), and a residual associated with ∆AOU, 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),
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of COUPLED_IMPOSE with modiﬁed background vertical diffusivity. Technical details are provided in Text S1 and variants of COUPLED_SST with modiﬁed background vertical diffusivity. Technical details are provided in Text S1.

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., 2001; 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 (O2-sms) of the transient and the control simulation into a run without climate and circulation change, such that the O2-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 (O2-sms) of the climate change and the control simulation at model run time, such that the O2-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). 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 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).

Figure 1. Theoretical and simulated cumulative global oxygen ﬂuxes (Pmol O2) 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.

$\Delta F_{O_2}^{\text{biotic}}$ includes effects from circulation slow-down which have been projected to reduce the return of AOU back to the sea surface, including AOU that has been generated from organic matter breakdown long before climate change started.
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 ($\sim$3.46 Pmol O$_2$ by yr 2100). Changes in TOU and oxygen agree within 10% with a slightly larger time cumulative air-sea oxygen flux, $\Delta$F$_{O_2}^{\text{biotic}}$ (3.73 Pmol O$_2$ until yr 2100). Small differences between the cumulative $\Delta$F$_{O_2}^{\text{biotic}}$ 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$_{O_2}^{\text{biotic}}$. 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$_{O_2}^{\text{biotic}}$) 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$_{O_2}^{\text{biotic}}$, 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$_{O_2}^{\text{biotic}}$) (Figure 3a). When TOU increases, $\Delta$F$_{O_2}^{\text{biotic}}$ 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$_{O_2}^{\text{biotic}}$. For the same model runs, there is basically no meaningful relationship...
between the cumulative changes in \( \Delta EP \) and \( \Delta F_{O_2}^{\text{biotic}} \), 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 \( O_2 \)-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 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 \( O_2 \) (and \( CO_2 \), 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 (Garcia et al., 2014) which allow to derive a present-day state estimate of marine AOU (Garcia 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 \( \Delta AOU \) tends to underestimate \( \Delta TOU \) 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

![Figure 3](https://example.com/figure3.png)

**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) \( \Delta TOU \) versus \( \Delta F_{O_2}^{\text{biotic}} \) and (b) \( \Delta EP \) and \( \Delta F_{O_2}^{\text{biotic}} \), assuming that changes in TOU or EP would translate completely and immediately into an \( O_2 \) flux at the sea surface. The hatched area indicates where the signs of change of \( \Delta EP \) and \( \Delta F_{O_2}^{\text{biotic}} \) are inconsistent. Compare Table S1 for symbol legend.
reliable estimate of TOU (O₂ ΔTOU) 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 O₂ ΔAOU assumption; Figure S7). Improved procedures, e.g., the evaluated oxygen utilization, EOU (Duteil et al., 2013), may be used instead. The strong correlation between ΔTOU and ΔFbiotic (Figure 3a) as well the correlation between ΔAOU and ΔTOU (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 O₂-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 CO₂-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, r₁O₂ ≈ 1.4; Anderson & Sarmiento, 1994). The true CO₂-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 CO₂-flux from biological pump changes may be only 10%–20% of the potential CO₂-flux (Gruber et al., 2004).

We derive a first-order estimate of the steady-state CO₂-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 CO₂-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 CO₂-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 ± 0.5 GtC/yr; Le Quéré et al., 2016) this estimate of the CO₂-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).

Acknowledgments

We acknowledge discussions with colleagues from the “Biogeochemical Modelling” research units at GEOMAR. It was a discussion with our colleague Ulf Riebesell (GEOMAR) which stimulated the development of the modeling approach used in this study. W. K. acknowledges funding from Bundesministerium für Bildung und Forschung, Project BIOACID (FKZ 03F0728A). This is a contribution to the Collaborative Research Centre SFB 754, funded by the Deutsche Forschungsgemeinschaft (DFG).

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