Does export production measure transient changes of the biological carbon pump under global warming?

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1. Plain language summary:

The biological carbon pump is an important element of marine carbon cycling and climate control on millennium time scales. 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 modelling, 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 time scales. 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 neglectable CO2-feedback to climate from biological carbon processing.

2. Abstract/first paragraph

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 biological carbon pump 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 lead to an uptake of CO_2 by the ocean in the range of 0.07 to 0.14 GtC/yr.

3. Introduction

The biological carbon pump (hereafter BCP, also coined soft tissue pump, [*Volk and Hoffert*, 1985]) is often equated with the export of organic matter out of the euphotic zone [*Boyd and 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 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 and Peterson*, 1979; *Henson et al.*, 2012; *Henson et al.*, 2011; *Laws et al.*, 2000]. In climate models, net primary production and export production 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.*, 2016; *Laufkötter et al.*, 2015; *Taucher and Oschlies*, 2011]. Models consistently projects a decrease of global export production (EP) by on average 12 % (ΔEP = -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; *J. L. Sarmiento et al.*, 1998], caused by surface ocean warming and 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 export production has been suggested to potentially sustain a positive feedback to atmospheric CO_2 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_2' [*Keeling et al.*, 2010; *E. Y. 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]. A global increase in AOU is consistent with a net O_2 flux out of the ocean and a net CO_2 flux into the ocean, hence a negative feedback to rising atmospheric CO_2. 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 idealised steady-state model simulations, the global integral of AOU (or its stoichiometric equivalent remineralised-PO_4 inventory) shows a negative correlation with atmospheric pCO_2 [*E Y Kwon et al.*, 2009] while export production has no meaningful relationship with atmospheric pCO_2 [*Gnanadesikan and Marinov*, 2008], an observation which can be explained by a strong regional decoupling of export production and AOU, evident from the regional variability of the 'sequestration efficiency' [*DeVries et al.*, 2012]. Hence AOU rather than export production 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; b; *Steffen et al.*, 2011], an era of rapidly changing climate and oceans [*Hoegh-Guldberg et al.*, 2014]. On transient time scales, a change in AOU, for example in the deep ocean, may not immediately be reflected in an exchange of oxygen or CO_2 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 export production.

In this paper, we use the UVic Earth System model of intermediate complexity to explore whether the cumulative change in export production or the change in AOU provide the better measure of the impact of the BCP on atmospheric O_2 and CO_2 under the transient conditions of a changing climate. Solving this question is important, if the marine feedback

to atmospheric CO_2 and climate is to be monitored and understood. We do this by comparing changes of AOU and export production with a new objective model metric, the biogenic O_2-flux between atmosphere and ocean, which we will introduce in the next section.

4. Results

Oxygen in the interior ocean can be described as the difference between preformed oxygen (O_2^{pre}) and the oxygen debt accumulated since last contact with the atmosphere from the oxidation of organic matter. We refer to this oxygen debt as true oxygen utilization (TOU), hence $O_2 = O_2^{pre} – TOU$. Preformed oxygen is the oxygen contained in sea water 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_2^{pre} is often approximated as the saturation concentration of oxygen (O_2^{sat}) in seawater at given atmospheric pressure, surface seawater temperature and salinity. This is the concept of apparent oxygen utilization (AOU), i.e. $O_2 = O_2^{sat} – AOU$ [*J L Sarmiento and 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_2^{sat} in the ocean [*Ito et al.*, 2017; *Schmidtko et al.*, 2017]. The change in AOU combines effects associated with changing primary production, export production, respiration, but also circulation, which ventilates (provides oxygen to) the ocean interior and thereby replaces the oxygen debt from biological processes. In an idealised 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_{O2}^{therm}) related to the change in oxygen solubility (i.e. ΔO_2^{sat}), 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), we refer to it as biogenic (ΔF_{O2}^{biotic}). ΔF_{O2}^{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 (see Suppl. Methods, Tab. S1) 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 (Figs. S1, S2) for the computation of oxygen gas exchange and solubility. Transient changes in simulated oxygen gas exchange between ocean and atmosphere presented in this study are hence due to ΔF_{O2}^{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) export production and changes in AOU (TOU).

In experiment COUPLED_SST, a transient run with SST for gas exchange like in CTRL (see Tab. S1), export production decreases during the experiment (1770-2100) (Fig. S3a) while AOU and TOU, which we track by an idealised model tracer [*Ito et al.*, 2004], increase (Fig. S3b). We convert cumulative export production and TOU into equivalent oxygen flux units (Fig. 1) assuming the changes to cause an immediate flux response. Cumulative change in export production would translate into an oxygen flux from the atmosphere into the ocean (Fig. 1, green line), while the change in TOU would translate into an oxygen air-sea flux out of the ocean (Fig. 1, red line). The true biogenic oxygen air-sea flux (ΔF_{O2}^{biotic}) in COUPLED_SST (Fig. 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_2-flux equivalent to the cumulative export-production change has the wrong sign compared with the modelled O_2-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 export production on oxygen and AOU is overcompensated by the effects of a circulation slow-down and increasing interior-ocean residence time.

We isolate the direct effects of changing biological rates from the effect of a changing circulation on tracer accumulation in experiment CTRL_IMPOSE. In this experiment, we assimilate the annual mean difference of biotic oxygen sinks-minus-sources (O_2-sms) of

COUPLED and CTRL into a run without climate and circulation change. The globally integrated O_2-sms in the interior ocean from this run very much resembles that of the transient climate change run COUPLED (Fig. S4a, see Supplementary Methods (S1) for details). The ocean gains oxygen in this run (globally, about 3.48 Pmol O_2 by yr 2100) (Fig. 2a), which is due to a reduction of the true oxygen utilization (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, ΔF_{O2}^{biotic} (3.73 Pmol O_2 until yr 2100). Small differences between the cumulative ΔF_{O2}^{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. Export production, the integral of O_2-sms below 130m in this run, decreases over the course of the experiment (Fig. S3), which is consistent with an ocean gaining oxygen. However, the time-cumulative integral of export production 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 export production metric is likely explained by shallow respiration, e.g. within the winter mixed layer [*Koeve*, 2001]. Organic matter sequestration flux across 1000m, 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 ΔF_{O2}^{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 export production and the deep ocean carbon sequestration flux (z=1000m) 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 export production, 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 (Fig. S4b**,** see Supplementary Methods (S1) for details). In this run, again, the decrease in oxygen, the increase in TOU and

200 the loss of oxygen to the atmosphere (ΔF_{O2}^{biotic}) are consistent, with little hysteresis (Fig. 2b;
201 red inverse triangle in Fig 3a). Similar to earlier work [*Bopp et al.*, 2002; *Yamamoto et al.*,
202 2015], the effect of circulation change on TOU (and oxygen) tracer accumulation (isolated in
203 COUPLED_IMPOSE) overcompensates the direct biotic effect of changing biological rates
204 (isolated in CTRL_IMPOSE) on TOU and oxygen concentrations, as evident from
205 COUPLED_SST (Fig. 1). In all three cases (COUPLED_SST, CTRL_IMPOSE, COUPLED_IMPOSE)
206 ΔTOU is a very good measure of ΔF_{O2}^{biotic}, the biotic component of changing air-sea O_2-fluxes
207 (Fig. 1, 2).
208
209 Using a larger number of transient model simulations (for details see Tab. S1) we find very
210 good agreement between the change of the global TOU inventory between 1770 and 2100
211 (ΔTOU) and the cumulative biogenic oxygen air-sea exchange (ΔF_{O2}^{biotic}) (Fig. 3a). When TOU
212 increases ΔF_{O2}^{biotic} is negative and vice versa. The dashed line in Fig. 3a indicates the line of
213 perfect agreement between the simulated changes in TOU and cumulative ΔF_{O2}^{biotic}. For the
214 same model runs, there is basically no meaningful relationship between the cumulative
215 changes in export production (ΔEP) and ΔF_{O2}^{biotic}, respectively (Fig. 3b). Almost all data
216 points are very far from the 1:1 relationship, which in this plot represents the theoretical
217 case that (only) changes in export production would cause an oxygen flux at the air-sea
218 boundary (i.e. increasing export production would cause an oxygen flux out of the ocean).
219 Actually, for many model runs (indicated by the grey hatched area), even the sign of change
220 of export production and that of the simulated biogenic oxygen air-sea flux do not agree.
221
222 The change in export production hence turns out to be an unreliable measure of the
223 transient development of the biogenic O_2-flux at the ocean atmosphere boundary, while the
224 change in TOU represents it almost perfectly. This holds for the standard simulation
225 (COUPLED_SST, thick black + in Fig. 2), sensitivity runs with differing circulations (small black
226 +), runs where the circulation is as in CTRL, but changing biological rates are imposed
227 globally (blue triangle) or in specific regions (blue numbers, see Tab. S1 for details), as well
228 as for runs in which circulation changes affect the accumulation of the TOU tracer and of
229 oxygen, but biological rates from CTRL are assimilated at model run time either globally (red
230 triangle) or in specific regions (red numbers, see Tab. S1 for details).
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5. Discussion

By a suite of idealised model experiments we cover a wide range of possible future export production 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 export production does not inform about the influence of the BCP on the atmosphere. This is consistent with the finding from idealised steady state model simulations [*Gnanadesikan and 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 export production 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 and Bauerfeind*, 2001]. Additionally, accounting for the contribution of DOM to export [*Hansell et al.*, 2002] is difficult. Accordingly, monitoring changes of export production 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 export production since it is no suitable measure of biological pump change anyway.

In contrast, computing AOU from high-quality data of temperature, salinity and oxygen is a more straight-forward task [*García and 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 [*Garcia et al.*, 2005] and further allow to quantify its change over the last 50 yrs [*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 (Fig. S5), though ΔAOU tends to underestimate ΔTOU 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 sea water with the atmosphere, a major reason identified for O_2^{sat} (AOU) to overestimate O_2^{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) (Fig. S6), which should have the effect to make AOU (O_2^{sat}) a more reliable estimate of TOU (O_2^{pre}) over the course of our model experiments. The smaller change in AOU compared to TOU in our experiments is hence an artefact of the default procedure to compute AOU (the O_2^{sat} assumption; Fig. S7). Improved procedures, e.g. the evaluated oxygen utilization, EOU [*Duteil et al.*, 2013], may be used instead. The strong correlation between ΔTOU and ΔF_{O2}^{biotic} (Fig. 3a) as well the correlation between ΔAOU and ΔTOU (Fig. 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.

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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 directly related to that DIC gradient and easily measured in the ocean. In contrast, we found that changes of export production show no clear relationship with the biogenic O_2-flux between atmosphere and ocean and hence has no predictive capacity to quantify relevant changes of the biological pump.

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

298 the biogenic oxygen flux by the ocean mean oxygen-to-carbon ratio (the oxygen demand of
299 organic matter degradation, $r_{-O2:C}$=1.4; [*Anderson and Sarmiento*, 1994]). The true CO_2 flux
300 attributable to changes of the biological-physical pump, will, however, be considerably
301 different. This is due to the buffering effect of surface ocean seawater [*Ito and Follows*,
302 2005]. In steady state, the true CO_2-flux from biological pump changes may be only 10-20%
303 of the potential CO_2-flux [*Gruber et al.*, 2004].
304
305 We derive a first-order estimate of the steady-state CO_2-flux attributable to biological
306 carbon pump changes from the observed rate of ocean deoxygenation [*Schmidtko et al.*,
307 2017]. Over the recent 50 years the rate of ocean deoxygenation (961 Tmol per decade,
308 [*Schmidtko et al.*, 2017]) is mainly due to an increase in AOU (831 Tmol per decade), which is
309 equivalent to a potential CO_2-flux into the ocean of +594 Tmol C per decade. Using the
310 steady-state buffer correction of this flux taken from [*Gruber et al.*, 2004] this translates into
311 an ultimate true CO_2-flux into the ocean attributable to the biological pump of 0.7 to 1.4 Gt
312 C per decade, or 0.07 to 0.14 Gt C/yr. Compared with the mean total marine uptake for 2006
313 to 2015 (2.6 ± 0.5 GtC/yr, [*Le Quéré et al.*, 2016]) this estimate of the CO_2-flux attributable to
314 changes of the biological carbon pump (soft tissue pump) appears negligible.
315
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318
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325

326 ## 8. Data availability

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328 Model output is available from data.geomar.de (http://hdl.handle.net/20.500.12085/396970fe-
329 3529-430c-a774-55ccc681795e).
330

9. Author contributions

W.K. designed the study, carried out the model experiments and analysis, and wrote the original manuscript . All authors contributed to discussion and writing of the final publication.

10. References

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11. Figures (captions):

Fig. 1. Theoretical and simulated cumulative global oxygen fluxes (Pmol O_2) in UVic model experiment COUPLED_SST (solid lines) and COUPLED (dashed lines) between 1770 and 2100. Simulated air-sea oxygen flux (ΔF_{O2}^{biotic} , black solid line), theoretical cumulative flux (green lines) derived from cumulative export-production change **(Fig. S3b**), and theoretical air-sea flux derived from TOU inventory change (red lines, **Fig. S3b**). Theoretical fluxes are computed assuming that the changes in cumulative export or TOU, respectively, result in an immediate flux at the air-sea boundary. Following conventions, a flux into the ocean is positive. TOU is integrated below z=130m, export production is quantified at z=130m.

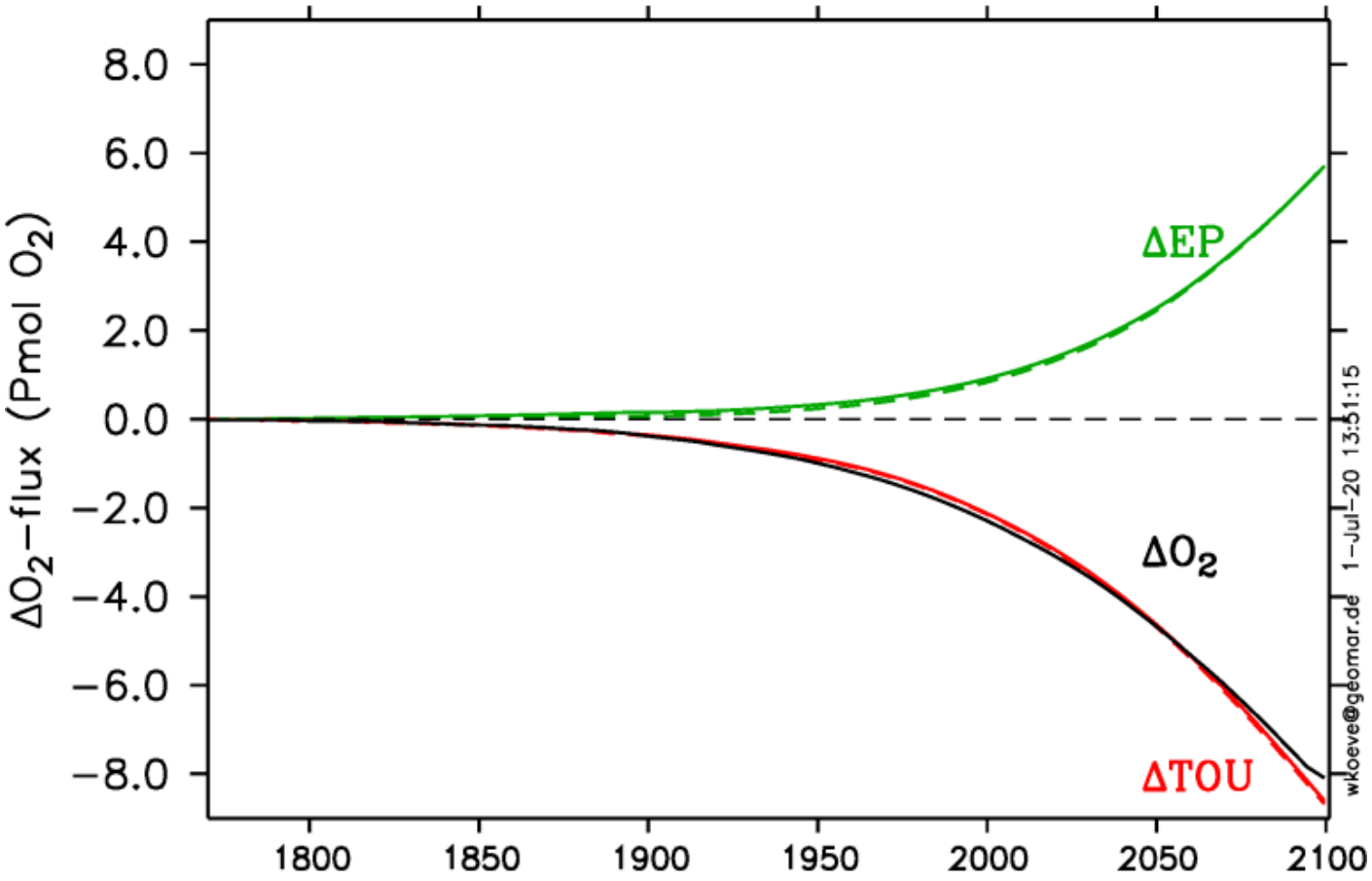
Fig 2. Disentangling direct and indirect effects of the biological-physical carbon pump changes on oxygen and TOU inventory as well as oxygen fluxes. All numbers are presented in units of oxygen flux at the air sea boundary. **(a)** Experiment CTRL_IMPOSE (no circulation change, but with imposed changes of biological rates affecting O_2-sms like in the COUPLED, compare Fig. S4a): simulated oxygen air-sea flux ΔF_{O2}^{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 O2-flux (orange) derived from cumulative change of respiration below 1000m (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 Fig. S4b). Theoretical fluxes are computed assuming that the changes in cumulative export, sequestration flux, or TOU, respectively, result in a flux at the air-sea boundary without any time delay. 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=130m.

Fig. 3. Time integrated (yr 1765 to 2100) change of **(a)** TOU and **(b)** export production (in oxygen equivalents) vs. the cumulative biogenic air-sea oxygen flux.
Dashed lines indicate the respective equivalence points (1:1 relationship) of (a) ΔTOU vs ΔF_{O2}^{biotic} and (b) ΔEP and ΔF_{O2}^{biotic}, assuming that changes in TOU or EP would translate completely and immediately into a O_2- flux at the sea surface. The hatched area indicates

where the signs of change of ΔEP and ΔF_{O2}^{biotic} are inconsistent. Compare **Tab. S1** for symbol legend.

Figure.

Fig. 1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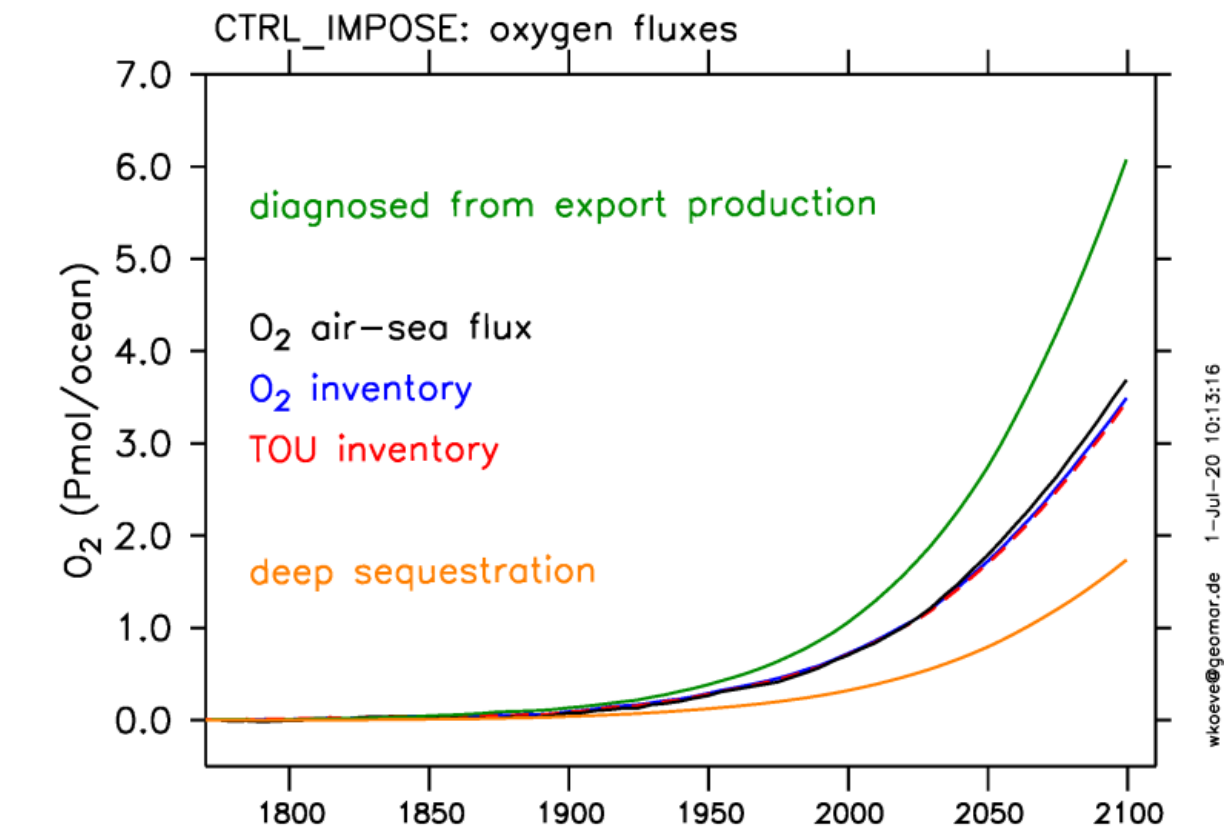
−8.0
ΔO2−flux (Pmol O2)
1800
1850
1900
1950
2000
2050
2100
ΔEP
ΔO2
ΔTOU
wkoeve@geomar.de 1-Jul-20 13:51:15

Figure.

Fig. 2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diagnosed from export production
O_2 air–sea flux
O_2 inventory
TOU inventory
deep sequestration
O_2 (Pmol/ocean)
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6.0
5.0
4.0
3.0
2.0
1.0
0.0
1800
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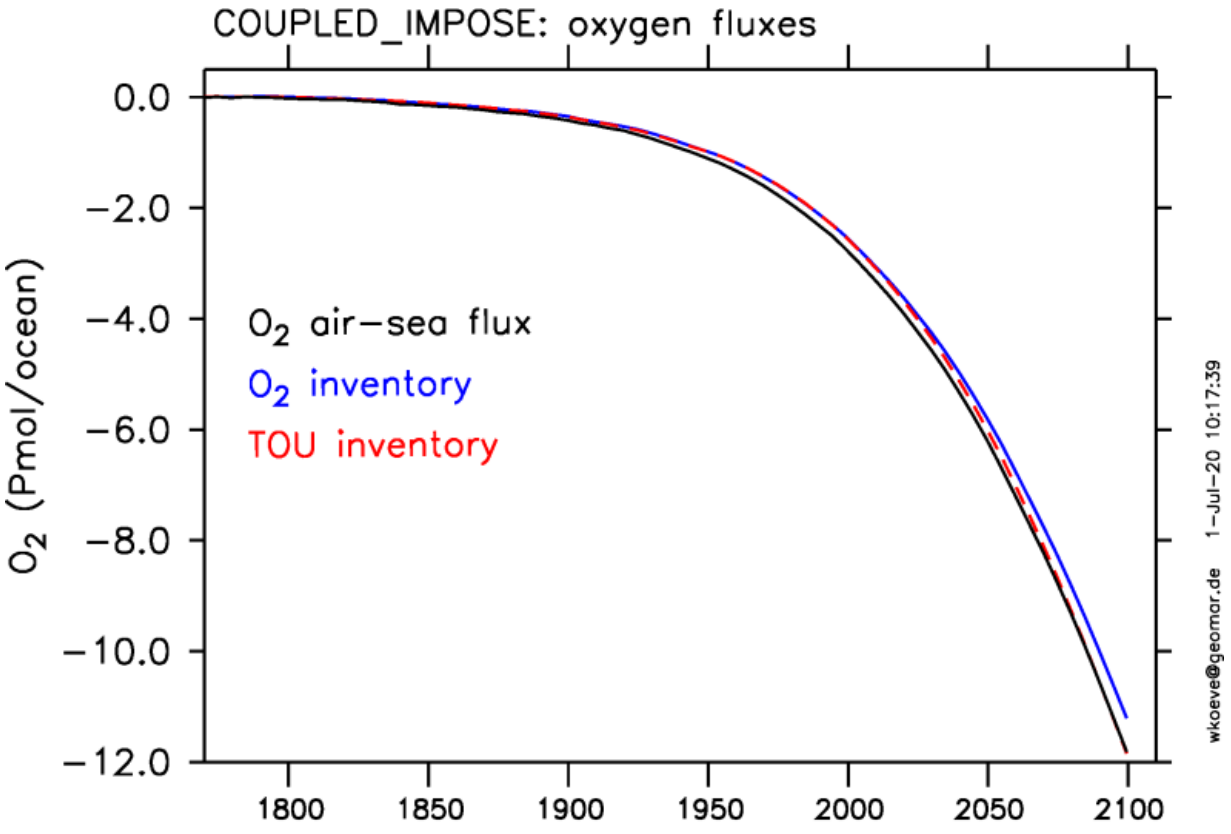
COUPLED_IMPOSE: oxygen fluxes
O_2 air–sea flux
O_2 inventory
TOU inventory
O_2 (Pmol/ocean)
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−2.0
−4.0
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−10.0
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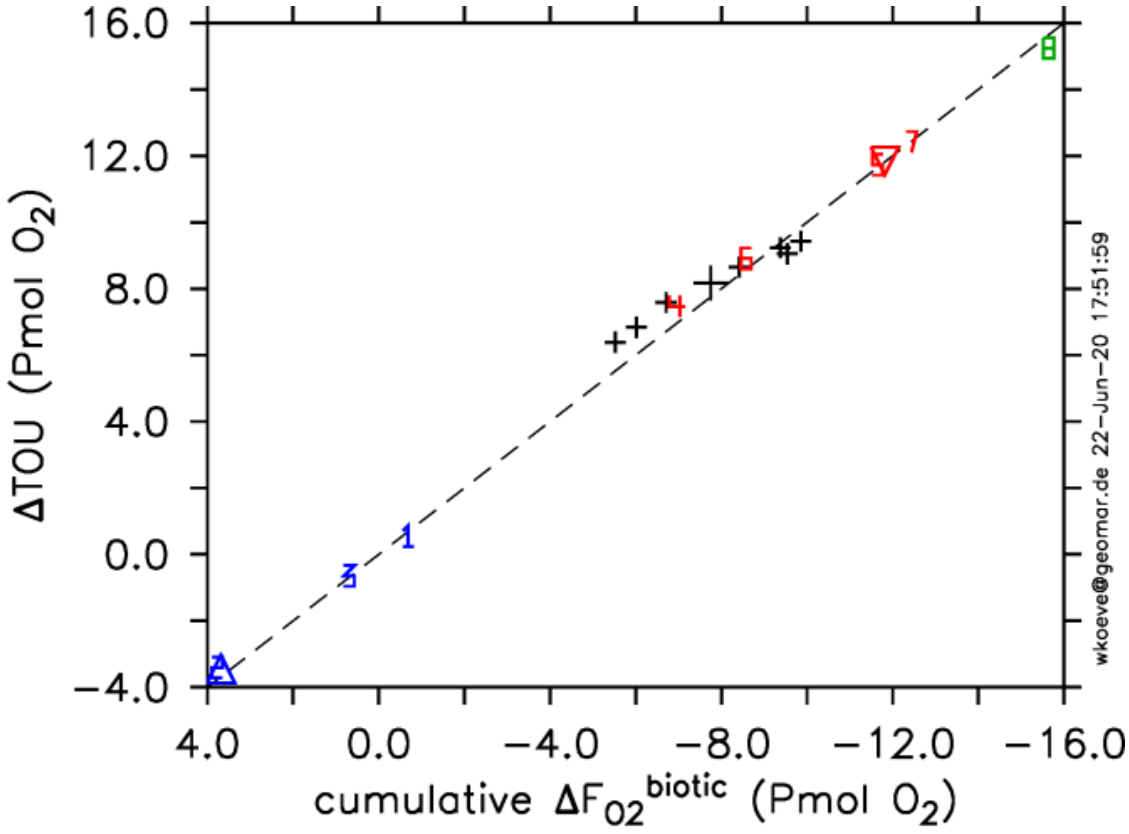
Figure.

Fig. 3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8.0
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0.0
−4.0
ΔTOU (Pmol O2)
4.0
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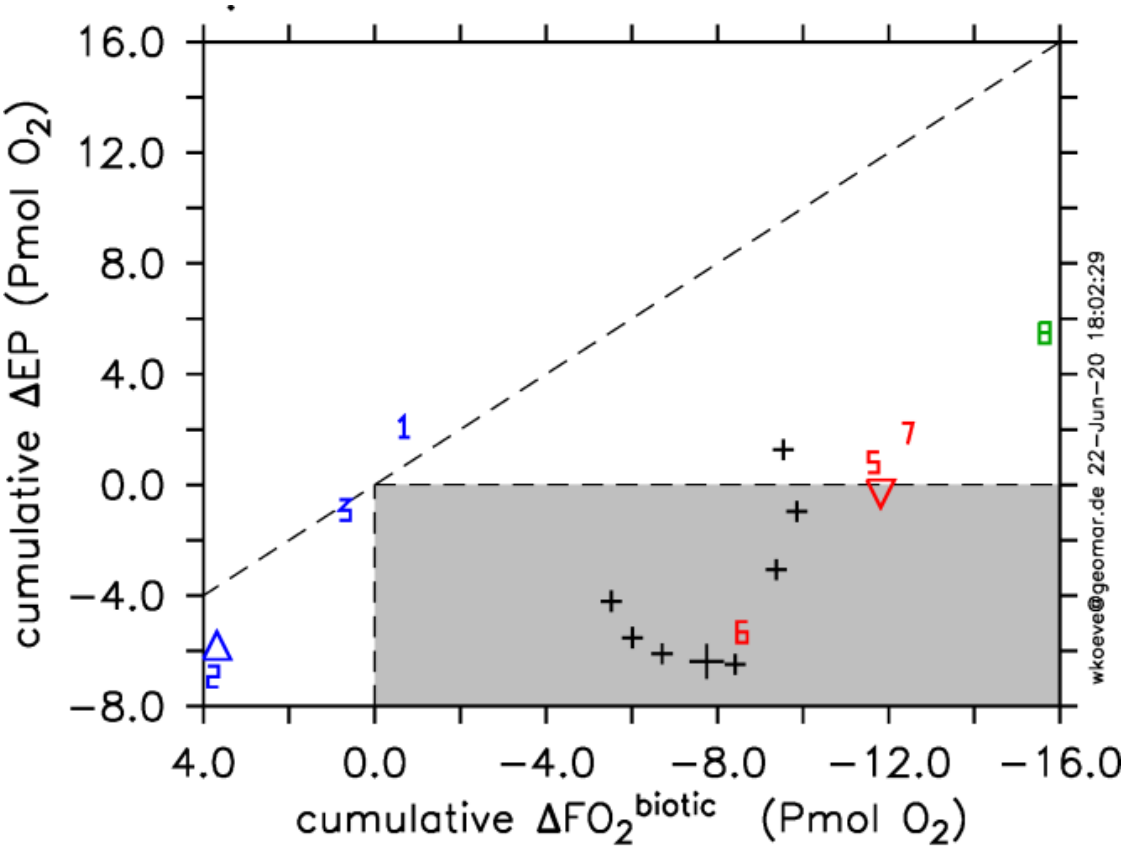
cumulative ΔF02biotic (Pmol O2)
wkoeve@geomar.de 22-Jun-20 17:51:59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