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A case for a pragmatic oxygen-based approach to quantifying the biological contribution to the marine carbon sink.

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Abstract. AOU, the 'apparent oxygen utilization', is a widely used concept in ocean biogeochemistry to assess and interpret ocean deoxygenation and changes of the marine carbon cycle. It provides an estimate of oxygen (O_2) used and dissolved inorganic carbon (DIC) released during organic matter degradation in the ocean interior. AOU is calculated from observations of temperature, salinity and O_2. This calculation relies on the assumption that surface water O_2 is in equilibrium with the atmosphere when water masses form and sink into the interior ocean. Using specifically designed idealized model tracers, we here provide an evaluation of the reliability and uncertainty of this approach. Global AOU reliably estimates total oxygen debt, defined as the sum of 'true' oxygen utilization (TOU) since last contact with the atmosphere and biotic oxygen disequilibrium ($O_2^{dis,bio}$). AOU and TOU + $O_2^{dis,bio}$ agree to within about 10%, both for the preindustrial state estimate and the transient climate change situations explored. Taking differences of the biotic components of the O_2 and DIC disequilibrium ($DIC^{dis,bio}$) into account, we find that, for the pre-industrial state estimate, the carbon equivalent of AOU is an about 15% underestimate of the sum of DIC^{remin} and $DIC^{dis,bio}$. For the climate change transient we find that ΔAOU underestimates our estimates of the disequilibrium corrected change in C^{soft} ($DIC^{remin} + DIC^{dis,bio,COU*-BGC*}$) by 25% . In summary, we suggest that AOU in particular can be used to assess causes of ocean deoxygenation, and is a very useful proxy for changes of storage of biologically processed carbon under various climate change scenarios.

1 Introduction

To gain insights into marine biogeochemical cycling and the marine carbon sink, "apparent" oxygen utilization (AOU) is a powerful quantity. It describes the deviation of the observed O_2 concentration (O_2^{obs}) from the saturation state (O_2^{sat}), given the local temperature and salinity. The concept behind this is that temperature and salinity properties are conserved in the ocean interior while O_2 is not. Thus local temperature and salinity provide information about the initial, apparently saturated, O_2 concentrations of waters journeying through the ocean interior. Being one of the oldest concepts in ocean biogeochemistry, dating back to at least the 1930 to 1940 (Redfield, 1934, 1942), AOU provides in particular an estimate of the interior ocean O_2 debt deriving from the O_2 consumed during organic matter degradation. In deoxygenation research, it has been used to distinguish between marine O_2 loss due to surface ocean warming and reduced physical O_2 solubility from that of changes in biotic O_2 usage in the interior ocean (Emerson et al., 2001; Keeling et al., 2010; Takano et al., 2018; Ito et al., 2017; Schmidtko et al. 2017).

More recently, by conversion of O_2 debt to respired carbon, AOU has further been used to quantify the contribution of the biological 'soft tissue' pump to dissolved inorganic carbon stored in the interior ocean (Ogura et al., 1970;

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Doval and Hansell, 2000; Gruber et al., 1996; Sarmiento and Gruber, 2006; Schwinger and Tjiputra, 2018; Wilson et al., 2022). The term soft tissue pump, one of two biological carbon pumps (Volk and Hoffert, 1985), comprises the biological production of organic matter, its transport into the interior ocean and its degradation to dissolved inorganic carbon there. So far, under positive CO_2-emissions, the soft tissue pump has been estimated to contribute little to the marine carbon sink, which is defined as the excess marine carbon since preindustrial times (Koeve et al., 2020; *Wilson et al., 2022*; Frenger et al., 2024). However, it has been projected that dissolved inorganic carbon (DIC) attributable to the soft tissue pump may become an important, even the dominant, sink after temperature overshoot (Koeve et al., 2024). A pragmatic approach - that the AOU concept provides - is needed to quantify this contribution to the marine carbon sink, both in models and future ocean observations.

Despite its value for interpreting ocean changes of oxygen and carbon, and in parallel to the wide usage, a canonical criticism of the AOU concept has been that it is prone to significant uncertainties (e.g. Ito et al.,2004; Sarmiento & Gruber, 2006; Duteil et al., 2013; Wolf et al., 2018; Mackay and Watson, 2021; Carter et al., 2021). The major critique is the assumption of perfect equilibration of surface ocean O_2 with the atmosphere that is built into the computation of AOU (sidenote: here defined as a negative property because consumption reduces O_2, $AOU = O_2 - O_2^{sat}$, where generally $O_2 < O_2^{sat}$). The assumption of perfect equilibration is unrealistic, for example when gas exchange is slowed down due to sea ice cover or when a large atmosphere-ocean O_2-difference is created e.g., when waters with a large O_2 debt upwell into surface water (e.g. Gordon and Huber, 1990, Körtzinger et al., 2004). Under such conditions surface O_2 can remain undersaturated as waters subduct into the ocean interior (Keeling et al., 2010; Ito et al., 2004; Duteil et al., 2013). Beyond the assumption of perfect surface O_2 saturation, other points of critique are that mixing effects and subsurface warming affect local temperature or salinity. This can contribute to uncertainties in the AOU estimate, by introducing biases into O_2^{sat} as an estimate of surface water O_2 characteristics (Dietze and Oschlies, 2005). Estimating, based on AOU, in an additional step, the fraction of DIC which can be attributed to the soft tissue pump (Volk and Hoffert, 1985) comes also with uncertainties, stemming from the carbon-to-oxygen demand of organic matter degradation ($R_{C:O}$) (Körtzinger et al., 2001; Tanioka and Matsumoto, 2020) and differences in O_2 and CO_2 disequilibria (see below).

Despite these caveats of the AOU concept, we argue in this work for its high interpretational value based on a reevaluation of the concept for (a) quantifications of the integrated ocean biotic O_2 utilization and (b) quantifications of the contribution of the biological soft tissue pump to marine carbon storage. Using output from an Earth system model, we compare AOU-based estimates against estimates using several established approaches to directly assess (a) and (b) in models based on idealised model tracers. We apply, for example, a tracer of 'true' oxygen utilization, TOU (Ito et al. 2004; see Methods for details) as well as additional model tracers, such as properties of waters as they subduct to the ocean interior ("preformed" properties, e.g. preformed phosphate, PO_4^{pre}). We also apply idealized model tracers and experimental protocols which allow us to explicitly quantify effects of incomplete air-sea equilibration of oxygen and carbon. We define the usefulness of the AOU approximation for the preindustrial steady state, and decadal to centennial climate change projections.

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2 Methods

We used a modified version of the UVic Earth System Model of intermediate complexity 2.9 (Weaver et al. 2001; Eby et al. 2013), which we ran in ocean-atmosphere-sea-ice configuration (Koeve et al., 2020) . The ocean biogeochemistry used in this model was based on a NPZD model, with phosphate and nitrate as prognostic nutrients and iron limitation prescribed by an iron concentration mask (Keller et al., 2012). The model simulated diazotrophs and ordinary phytoplankton, one zooplankton and one detritus pool. It applied fixed elemental ratios (C:N:P:O_2) for organic matter cycling and the interactions with prognostic O_2, DIC, and alkalinity tracers. Degradation of organic matter was temperature sensitive. For more details on model equations and evaluation against observations see Keller et al. 2012.

We implemented idealized model tracers in order to distinguish contributions from different processes on O_2 , DIC, and phosphate (PO_4) (Ito et al., 2004; Ito and Follows, 2005; Bernardello et al., 2014; Koeve et al., 2020; Koeve et al., 2024). Preformed properties (DIC^{pre}, O_2^{pre}, PO_4^{pre}) represent the fractions of DIC, O_2, and PO_4 which reflects surface water characteristics transported and mixed into the ocean interior, and behave conservatively within the ocean: At the surface DIC^{pre} (O_2^{pre}, PO_4^{pre}) were set to the values of DIC (O_2, PO_4), in the interior ocean (z > 50m) they had no biogeochemical sources or sinks. Remineralized properties (DIC^{remin}, TOU, PO_4^{remin}) represented the impact of organic matter degradation on O_2, DIC and PO_4 in the interior ocean. Below the surface layer (i.e. below z = 50m in this model) TOU and DIC^{remin} (PO_4^{remin}) were subject to source-minus-sink terms associated with organic matter degradation (and production). When organic matter is degraded by oxic metabolism, O_2 is used (the value of TOU becomes more negative) and DIC (PO_4) is released (DIC^{remin} and PO_4^{remin} increase). In the surface layer TOU, DIC^{remin} , and PO_4^{remin} are set to zero at any time step during model runtime. Mass balance applies:

$$O_2 = O_2^{pre} + TOU \quad (1)$$

$$PO_4 = PO_4^{pre} + PO_4^{remin} \quad (2)$$

$$DIC = DIC^{pre} + DIC^{remin} + DIC^{ca}, \quad (3)$$

with DIC^{ca} representing DIC stemming from $CaCO_3$ dissolution in the interior ocean. Idealised tracers have no explicit gas exchange, while bulk tracers (O_2, DIC) have.

As a counterpart of biotically influenced O_2, we further simulate abiotic O_2 (O_2^{abiot}, Oschlies et al., 2019). This tracer has no biotic sinks or source but gas exchange with the atmosphere. A tracer of saturated DIC (DIC^{sat}) is computed in the model surface layer at runtime from surface alkalinity, temperature, salinity, PO_4 and the contemporary atmospheric pCO_2. Within the interior ocean DIC^{sat} is a passive tracer, i.e. has no sources or sinks. All idealized model tracers were transported according to the model physics and could be (further) modified due to mixing of water masses. In the following we reiterate how the idealized tracers relate to infer information about incomplete surface equilibration due to biotic and 'physical' effects, and how those relate to AOU.

The biological contribution to the O_2 disequilibrium is defined as:

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$$O_2^{dis,bio} = O_2^{pre} - O_2^{abiot} \quad (4)$$

Since O_2^{abiot} has no biological sources-or-sinks, it represents the physical conditions at water mass formation, including deviations from equilibration, i.e. $O_2^{abiot} = O_2^{sat} + O_2^{dis,phys}$. The latter, by reordering, provides info about the physical contribution to the O_2 disequilibrium, $O_2^{dis,phys} = O_2^{abiot} - O_2^{sat}$. The superscript 'phys' denotes that the inherent driver of this disequilibrium component is either warming or cooling of the surface water or a change in surface salinity, with thermal effects dominating $O_2^{dis,phys}$ - that is physical processes. Note further, that processes that affect the speed of gas exchange, like wind speed, sea state, sea ice cover, or properties of the surface microlayer (Wanninkhof, 2014; Salter et al., 2011; Gutiérrez-Loza et al., 2022) affect $O_2^{dis,bio}$ and $O_2^{dis,phys}$ alike.

To reflect the meaning of equ. (4), consider the entrainment of water rich in O_2-debt (i.e. TOU) into the surface layer before equilibration. (a) The observed surface O_2 concentration decreases. (b) According to our tracer definitions TOU is set to zero at the surface and O_2^{pre} is set equal to O_2, i.e. decreases as well. (c) Entrainment would affect O_2^{abiot} only, if temperature or salinity of the entrained water differ from those of the surface water (i.e. $O_2^{dis,phys}$). The entrained TOU-signal hence 'hides' in the modified O_2^{pre}, but does not affect O_2^{abiot}. The biotic O_2-disequilibrium is hence given by the difference of O_2^{pre} and O_2^{abiot} (equation 4). Allowing time for equilibration, i.e. flux of O_2 into the ocean for the given example, (and assuming no change in surface temperature and salinity, no biological production or further entrainment), O_2 and O_2^{pre} increase in lockstep, O_2^{abiot} stays constant and $O_2^{dis,bio}$ diminishes. Similarly, biological production in the surface layer will affect O_2 and O_2^{pre}, but not O_2^{abiot}, and hence can give rise to a (positive) $O_2^{dis,bio}$.

The apparent oxygen utilization is quantified as

$$AOU = O_2^{obs} - O_2^{sat} \quad (5)$$

with the observed O_2 concentrations, O_2^{obs} and the O_2 saturation, O_2^{sat}, computed from the model's potential temperature and salinity (Garcia and Gordon, 1992). Note that we use a definition of AOU, which differs from the usually used one (i.e. $AOU = O_2^{sat} - O_2^{obs}$; e.g. Sarmiento and Gruber, 2006), intentionally, by the sign. This is done for consistency with the sign of TOU and the fact that AOU and TOU reflect an O_2 debt, i.e. O_2 missing in the ocean compared with O_2^{sat}. That is, throughout this paper, we use O_2^{sat} as the reference point in all equations. AOU can be rewritten as accumulated sources-minus-sinks (TOU) since last contact with the atmosphere plus surface-set disequilibrium conditions, $O_2^{dis,bio}$ and $O_2^{dis,phys}$:

$$AOU = TOU + O_2^{dis,bio} + O_2^{dis,phys} \quad (6)$$

We note that the computation of O_2^{sat} from temperature and salinity which have been affected by mixing in the interior ocean or by sub-surface warming can cause a low bias (Dietze and Oschlies, 2005). That is, computing O_2^{sat} can give a smaller value compared to O_2^{sat} from an explicit O_2^{sat} tracer which is computed at the surface given surface temperature and salinity and mixed passively in the interior ocean. This effect however, is, globally, much smaller compared to the disequilibria evaluated in this study (Fig. S9) and ignored henceforth.

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For carbon, we will compare the carbon equivalent of AOU against the sum of an explicit tracer of remineralized DIC, DIC^{remin} and an estimate of the biotic contribution to the DIC disequilibrium, $DIC^{dis,bio}$. The carbon equivalent of AOU (the 'AOU approximation') is computed by multiplying AOU with the O_2 demand of organic matter remineralisation applied in the model, $R_{C:O2}$ = -0.66 mol:mol. In the real ocean (or in models with variable stoichiometry) this conversion is complicated by uncertainties and variability of $R_{C:O2}$. Fortunately, this turns out to be a comparatively minor uncertainty, given the relative constancy of this ratio (Körtzinger et al., 2001; Tanioka and Matsumoto, 2020).

To derive $DIC^{dis,bio}$, we proceed as follows: We first compute the total DIC disequilibrium from the difference of idealised model tracers DIC^{pre} and DIC^{sat}:

$$DIC^{dis} = DIC^{pre} - DIC^{sat} \quad (7)$$

Attributing DIC^{dis} to physical versus biological effects is not straightforward as there is no meaningful definition of an abiotic DIC tracer in an Earth system model where atmospheric CO_2 is affected by ocean biology. For O_2 the atmospheric reservoir is large and changes in marine oxygen can be neglected when computing the atmospheric oxygen boundary condition of the ocean; this is very different for carbon - also since carbon affects the climate. Computation of the biotic component of DIC^{dis} , $DIC^{dis,bio}$, is thus based on additional model experiments carried out with two variants of our default model, one with all marine carbon pumps turned on (allPumps) and one in which the impact of biological carbon pumps on alkalinity and DIC is disabled (noBioPumps). Both model variants are run into steady state, conserving the atmosphere+ocean total CO_2 inventory (mass conserving approach). Pre-industrial state estimates presented in this work (Fig. 1b; Tab. S1) are based on this steady state model output.

Following Khatiwala et al. (2019), $DIC^{dis,bio}$ is computed as

$$DIC^{dis,bio} = DIC^{dis,allPumps} - DIC^{dis,noBioPumps} . \quad (8)$$

Starting from the respective steady states, we perform the default transient model experiments by applying CO_2-emissions following the bell shape 1000 Pg C ZECmip (Zero Emission Commitment Model Intercomparison Project) protocol (Jones et al., 2019). In this protocol, CO_2-emissions are restricted to the first 100 years, with net-zero CO_2 emissions thereafter (Fig. S3a). We integrated the model for a total of 800 years. This experiment is performed with the allPumps and the noBioPumps model variants in two setups. In the default setup (COU*) the model is fully coupled, i.e. CO_2-emissions cause global warming and climate and circulation change. In the second setup (BGC*) the climate is kept constant at the preindustrial state.

Applying equation 8 to output from the COU* and BGC* experiment, we derive the climate change component of $DIC^{dis,bio}$ from the respective difference of the fully coupled and the BGC-only coupled model variants.

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$$DIC^{dis,bio,COU^*\text{-}BGC^*} = DIC^{dis,bio,COU^*} - DIC^{dis,bio,BGC^*} \quad (9)$$

Our approach of BGC-only and fully coupled model differs from the standardized approach widely used in climate-feedback research (e.g. Arora et al., 2020) by the usage of CO_2-emissions instead of a prescribed pCO_2^{atm} trajectory in the allPumps experiment (hence COU* and BGC*). In the noBioPumps COU* experiment, we prescribe the climate change trajectory from the allPumps experiment. This approach is chosen in order to derive the climate change component of the biological disequilibrium of the fully coupled model experiment of the allPumps model variant.

We further conducted a series of sensitivity experiments with versions of the default model in which we either change the vertical background diffusivity, or the rate with which the sinking speed increases over depth, always keeping all other model parameters like in the default model. Changing the vertical background diffusivity causes changes in the overturning circulation (Duteil and Oschlies, 2011; Fig. S2b), which, with otherwise constant physical and biogeochemical parameters, causes a considerable range of C^{remin} to establish during the model spinup (Frenger et al., 2024; Fig. S2b). In experiments with modified sinking speed increase over depth, we find larger global C^{soft} in experiments with deeper organic matter penetration and vice versa (Frenger et al., 2024; Fig. S2a). Over all experiments, the AOU spread ranges from -167 to -217 Pmol O_2. The AOU inventory of the World Ocean Atlas (2013, Garcia et al., 2014), regridded to the UVic model grid, is -207 Pmol O_2. Model variants are explored with respect to the steady state relationship of AOU vs. $TOU+O_2^{dis,bio}$ (Fig. 3a) and how these properties respond to a high CO_2-emissions (RCP 8.5) climate change forcing (Fig. 3b).

3 Results and Discussion

3.1 AOU as an estimate of biotic oxygen utilization

The preindustrial state of our default model configuration (Keller et al., 2012) confirms earlier publications (Ito et al., 2004, Duteil et al., 2013), namely that the global integral of AOU (-196.5 Pmol O_2) is larger in magnitude than the global integral of TOU (-160 Pmol O_2) (Fig. 1a, c, e). This is due to systematic O_2 undersaturation of surface waters as they subduct to the ocean interior, causing O_2^{sat} to be a too large estimate for surface ocean O_2 conditions ($O_2^{sat} > O_2^{pre}$; Fig. S1 and see Methods for technical tracer definitions). Globally, most of this difference, about 80%, is explained - rather than by the, primarily, thermal effect of solubility increase due to cooling - by upwelling of undersaturated waters that carry the O_2 debt stemming from organic matter

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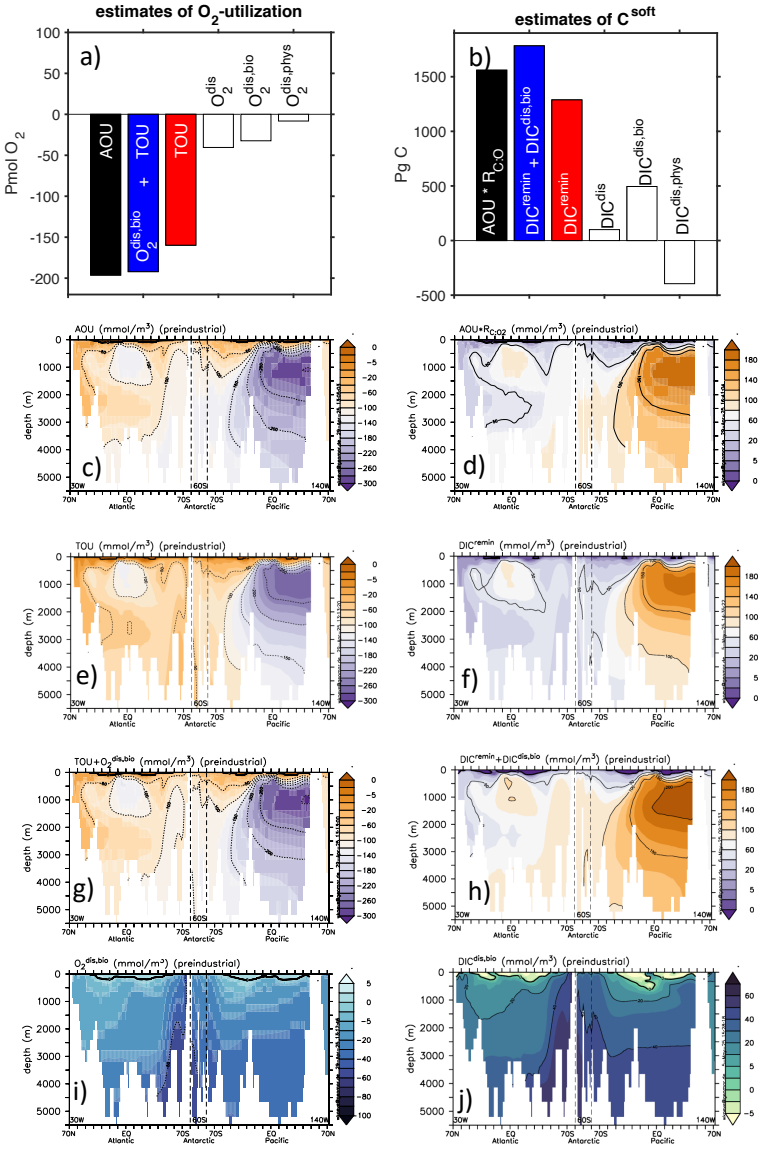

Fig. 1: Preindustrial steady state estimate of estimates of oxygen utilization and soft tissue pump carbon storage from the default UVic model variant. Global estimates of O_2-utilization (a, Pmol O_2) and soft tissue pump carbon storage (b, Pg C). Distribution of O_2-utilization estimates (c, e, g) and C^{remin} estimates (d, f, h) along sections through the Atlantic (30°W, from North to South), the Southern Ocean (60°S), and the Pacific Ocean (140°W, from South to North), showing apparent oxygen utilization, AOU (c, mmol O_2 / m^3), 'true' oxygen utilization, TOU, since last contact with the atmosphere (e, mmol O_2 / m^3), the sum of TOU and the biotic contribution to the O_2 disequilibrium ($O_2^{dis,bio}$), TOU+$O_2^{dis,bio}$ (g, mmol O_2 / m^3), the carbon equivalent of AOU (AOU*$R_{C:O2}$) (d, mmol C / m^3), remineralised DIC, DIC^{remin} (f, mmol C / m^3), the sum of DIC^{remin} and the biotic contribution to the DIC disequilibrium, $DIC^{dis,bio}$ (DIC^{remin} + $DIC^{dis,bio}$) (h, mmol C / m^3. Panels (i) and (j) show Atlantic-SO-Pacific Ocean transects of $O_2^{dis,bio}$ (mmol O_2 / m^3) and $DIC^{dis,bio}$ (mmol C / m^3), respectively. For tracer definitions and details on computation see the Methods.

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degradation in the interior ocean (Fig. 1a, Fig. S2). We refer to this 'biological' contribution to the total O_2 disequilibrium as $O_2^{dis,bio}$ (Fig. 1a, i) and assess it from the difference of our idealised tracers of preformed O_2 (O_2^{pre}) and 'abiotic' O_2 that is unaffected by biology, $O_2^{abiotic}$ (see Methods for technical tracer definitions, rationale and Eq. 4). Under a stable, preindustrial climate, $O_2^{dis,bio}$ is largest in magnitude in waters ventilated in the Southern Ocean (Fig. 1i), consistent with the finding that sea ice cover limits complete O_2 equilibration, in particular in regions where waters with a large O_2 debt from organic matter degradation return to the surface (Ito et al., 2004). The fact that AOU is larger than TOU (Fig. 1a, c, e) in magnitude indicates that, while TOU is an appropriate measure of the accumulated O_2 utilization of interior ocean waters *since last contact with the atmosphere*, it is in fact not a good measure of the total accumulated O_2 debt associated with the degradation of organic matter in the interior ocean. AOU, in turn, adds the information of the effect of biologically induced undersaturation of waters at the beginning of their next journey through the interior ocean. AOU equals TOU+$O_2^{dis,bio}$ (Fig. 1c, g; globally with only 2% uncertainty, Fig. 1a) in our default model setup which had been tuned to represent observations of O_2 and macronutrients (Keller et al., 2012). It hence provides a very reliable global state estimate of the *total* biological effect on O_2, and we will discuss in the following to which extent AOU agrees with TOU+$O_2^{dis,bio}$ in a changing climate and for other variants of our model.

Confronted with an idealised climate change scenario (Fig. S3; Methods), the Earth system model shows that AOU consistently increases in magnitude, and that the change in AOU roughly corresponds to the change in TOU+ $O_2^{dis,bio}$. While the magnitude of ΔAOU is considerably smaller than the magnitude of ΔTOU *(Fig. 2a)*, e.g. by about 30% in year 100, when emissions decrease to net-zero (Fig. S3a), the difference of ΔAOU and Δ(*TOU*+ $O_2^{dis,bio}$) is small. This is so since most, about ⅔, of the former difference is explained by changes in $O_2^{dis,bio}$. The loss in sea ice observed in both high latitudes in particular during the initial 100 year time period of net-positive CO_2 emissions and global warming (see Fig. S3c,d) allows for a more complete O_2 equilibration compared with the preindustrial state (Fig. S4). Globally, the change in AOU underestimates the combined change in TOU+$O_2^{dis,bio}$ by less than 10% until year 100 (Fig. 2a). During the rest of the experiment the relative difference between ΔAOU and ΔTOU+$\Delta O_2^{dis,bio}$ stays in the range of 10 to 13% (Fig. S5), despite diverging ΔAOU and ΔTOU (Fig. 2a), since the magnitude of $O_2^{dis,bio}$ continues to decrease - with an almost stable climate under net-zero CO_2-emissions, sea ice does not return and old waters ventilated at high latitudes gradually adjust (Fig. S3d).

We test the robustness of our findings from a suite of additional model experiments carried out with different variants of the default UVic model (Frenger et al., 2024). We explore variants which are characterized by smaller or larger mixing and Atlantic meridional overturning circulation (AMOC) and identical parameterization of ocean biogeochemistry, and variants with the default mixing and AMOC but modified particle flux attenuation, i.e. shallower or deeper remineralization of organic matter (for details, see Methods, Sensitivity experiments). Running these models into their own climate and biogeochemical steady states allows us to compare the preindustrial globally integrated AOU with the respective sum of TOU and $O_2^{dis,bio}$ (Fig. 3a). The majority of model variants show a small deviation of AOU from TOU+$O_2^{dis,bio}$, consistent with our default model.

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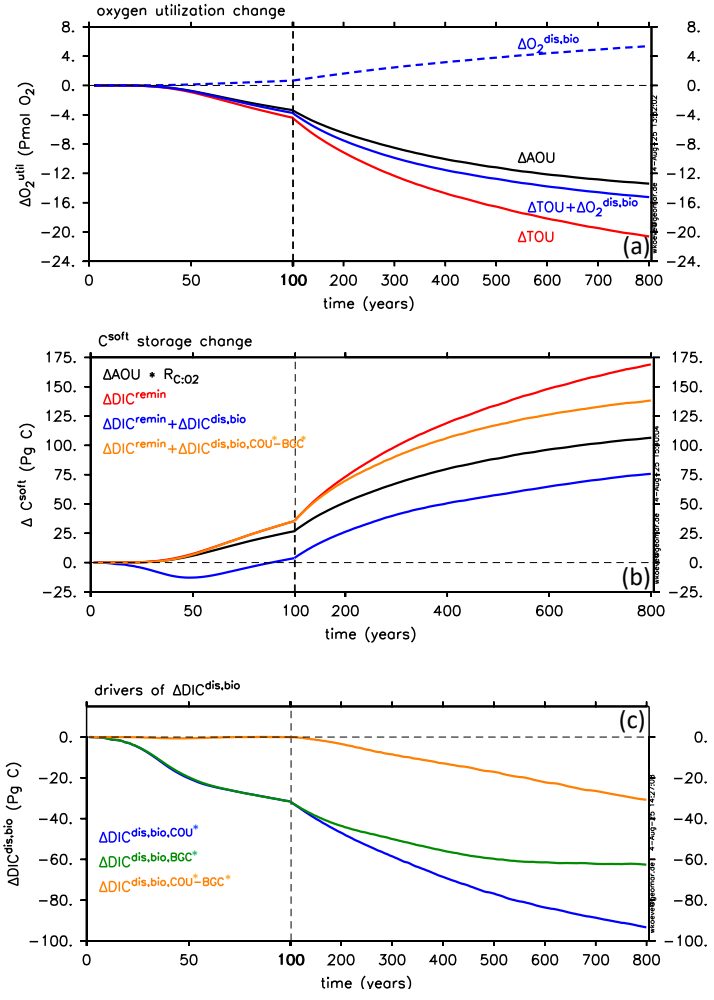

Fig. 2: Temporal development of global integral estimates of oxygen utilization, soft tissue pump carbon storage and drivers of DIC disequilibria under a changing climate. Globally integrated changes in O_2-utilization (a, Pmol O_2), soft tissue pump carbon storage (b, Pg C) and biotic DIC disequilibria (c, Pg C) from the default model variant are shown with split x-axes, with higher resolution of the time period with bell shaped CO_2 emissions following the 1000 Pg ZECmip scenario, compared with the 700 year long period with net-zero emissions. Estimates of O_2-utilization (a): ΔAOU (black solid), ΔTOU (red solid), $\Delta TOU+\Delta O_2^{dis,bio}$ (blue solid), $\Delta O_2^{dis,bio}$ (blue dashed). C^{soft} change estimates (b): carbon equivalent of AOU changes ($\Delta AOU^* R_{C:O2}$, black solid), change in remineralized DIC accumulated since last contact with the atmosphere (ΔDIC^{remin}, red solid; see Fig. S7 for a comparison with additional tracer based estimates), sum of ΔDIC^{remin} and total $\Delta DIC^{dis,bio}$ (blue solid), and sum of ΔDIC^{remin} and the climate change component of $\Delta DIC^{dis,bio}$, $\Delta DIC^{dis,bio,COU^*-BGC^*}$ (orange solid). Drivers of the biotic component of the DIC disequilibrium, $\Delta DIC^{dis,bio}$ (c): experiment COU* - effect of changing atmospheric pCO_2 boundary condition and climate change (blue solid), experiment BGC* - effect of changing atmospheric pCO_2 boundary condition only (green dashed), difference COU* - BGC* - effect of changing climate only (orange solid). Compare Fig. S3 for CO_2-emissions and various climate change indicators of this experiment.

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Confronting the model variants with a high-end CO_2-emissions scenario (Frenger et al., 2024; see Methods), we consistently find for all model variants that ΔAOU underestimates the total change of the O_2 debt due to organic matter degradation ($\Delta TOU+\Delta O_2^{dis,bio}$), as in the default model, by about 10% or less (Fig. 3b). The underestimate is rather small and robust in that it shows no dependence on the initial (preindustrial) mixing and overturning or the imposed variations of particle flux attenuation. That is $\Delta AOU \approx \Delta TOU+\Delta O_2^{dis,bio}$ is generally valid. Finally, we confront our default model with a suite of CO_2 reversibility experiments (Fig. 3c), i.e. experiments which show various degrees of negative emissions after the models had been forced by a 1%pCO_2 increase per year until pCO_2-doubling (Koeve et al., 2024). This causes the models to go through sequences of initial warming and circulation slow down and subsequent cooling and recovery of circulation (Fig. S6). Despite these complex changes of ocean circulation, O_2 equilibration conditions and also biological changes (not shown), ΔAOU is robustly able to estimate $\Delta TOU+\Delta O_2^{dis,bio}$ to within about 10% uncertainty (Fig. 3c).

We conclude that globally integrated AOU provides a very reliable estimate of the total O_2 debt from organic matter degradation, which, based on our additional tracers, we describe by the sum of $TOU+O_2^{dis,bio}$. This is the case for the state estimate and the transient situations explored, with deviations of around 10% (or less). We suggest AOU hence to be a suitable metric to quantify changes in biotic O_2 usage in the interior ocean in the framework of ocean deoxygenation research.

3.2 AOU as estimate of soft tissue pump carbon

In this section we explore whether AOU, beyond attributing changes of oxygen to biology, can also be used to estimate changes of carbon due to biology. We refer to the fraction in DIC which can be attributed to the soft tissue pump as 'soft tissue pump carbon', C^{soft}. In analogy to our findings above, we consider C^{soft} to be a composite of (a) C^{soft} accumulated since last contact with the atmosphere and (b) a recirculated biotic component of the carbon disequilibrium. We trace the former by an idealised model tracer, DIC^{remin} (Methods for details). The estimation of the biotic fraction of the DIC disequilibrium, $DIC^{dis,bio}$, is technically more complex as it is based on a comparison between our default model and a model which lacks the impact of both biological carbon pumps ('biology') on DIC and alkalinity, similar to Khatiwala et al., 2019 and Tjiputra et al., 2025. Deriving DIC^{dis} from the differences of idealised tracers of preformed DIC and saturated DIC (Methods, Eq. 7), we quantify $DIC^{dis,bio}$ from the difference of the runs with and without biology (Methods, Eq. 8). This indirect approach is needed since there is no meaningful definition of an abiotic DIC tracer in an Earth system model where atmospheric CO_2 is affected by ocean biology, where atmospheric pCO_2 affects climate, and where climate in turn affects ocean circulation and ocean biology.

In the following we evaluate AOU converted to carbon units (the 'AOU approximation') against the sum DIC^{remin} + $DIC^{dis,bio}$. We estimate a preindustrial global value of $DIC^{dis,bio}$ of 520 Pg C and a global inventory of DIC^{remin} of 1290 PgC (Fig. 1b; Tab. S1). The sum of DIC^{remin} and $DIC^{dis,bio}$ (1810 Pg C) suggests that the AOU-approximation (1562 Pg C) is a modest underestimate of the preindustrial carbon attributable to the soft tissue pump, i.e. by about 15% smaller than DIC^{remin} + $DIC^{dis,bio}$ (Fig. 1b; Tab. S1).

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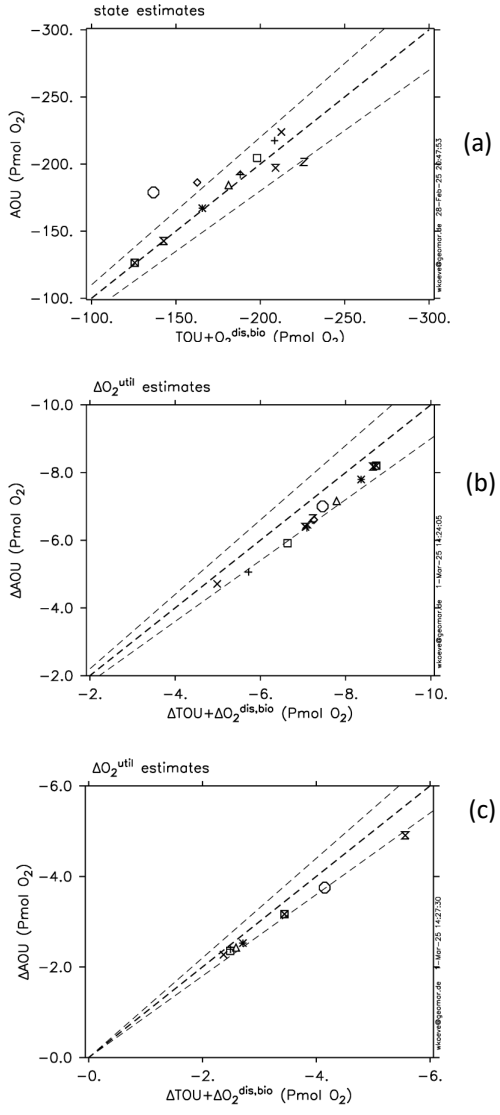

Fig. 3: AOU robustly estimates global inventories of TOU+$O_2^{dis,bio}$. (a) AOU and TOU+$O_2^{dis,bio}$ inventories (Pmol O_2) from model experiments conducted with variants of our UVic model which have been run to steady state (6000 model years) with either modified mixing and AMOC (and identical biogeochemical parameters) or identical physical parameters but differing particle flux attenuation. Thick dashed line is the 1:1 line and thin dashed lines represent the ±10% space around the 1:1 line. Data are from Frenger et al. 2024. (b) Changes in global inventories of AOU and TOU+$O_2^{dis,bio}$ in RCP 8.5 CO_2-emission forced experiments carried out with the model variants used in (a). The change of global inventories by year 2100 relative to the preindustrial initial state is shown. (c) Changes in global inventories of AOU and TOU+$O_2^{dis,bio}$ from model experiments with our default model variant forced with a suit of CO_2 and climate reversibility forcings (Koeve et al., 2024). The difference of inventories between yr 500 and the initial start year is shown. Compare Fig. S6 for transient atmospheric temperatures (ΔSAT, °C) and transient overturning (ΔAMOC, Sv) in model experiments explored in (c).

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Turning to conditions of a changing climate, we have to consider that, in contrast to atmospheric O_2, the atmospheric CO_2-boundary condition also changes considerably. This will affect the extent that reemerging respired CO_2 will outgas to the atmosphere and might make the carbon equivalent of AOU differ from DIC^{remin}+$DIC^{dic,bio}$, an aspect that we will test in the following. Indeed, considering the change in the equilibration of carbon based on our estimate of $\Delta DIC^{dis,bio}$ together with the change in the DIC^{remin} model tracer (Fig. 2b), suggests that the ΔAOU-approximation is not a satisfying estimate, with an error of at least 40% compared with ΔDIC^{remin} + $\Delta DIC^{dis,bio}$. Moreover, during the first 100 years the AOU approximation appears to be unreliable. Since, in our constant stoichiometry model, ΔDIC^{remin} and $\Delta TOU^{*}R_{C:O2}$ agree to within a few percent (Fig. S7) we urge to understand what drives $\Delta DIC^{dis,bio}$. Specifically, we need to quantify the component of $\Delta DIC^{dis,bio}$ which is associated with climate change, similar to that $\Delta O_2^{dis,bio}$ is affected by climate change, and the component which is a mere response to the changing atmospheric CO_2-boundary condition. This needs another technical step: We explore the behaviour of $DIC^{dis,bio}$ in our default "fully coupled" simulation (COU*) and an additional simulation, namely a merely "biogeochemically coupled" model experiment (BGC*) (Fig. 2c). The combination of fully coupled and biogeochemically-only coupled experiments is a standard approach in Earth system modelling to distinguish carbon-concentration feedbacks and carbon-climate feedbacks on atmospheric CO_2 (e.g., Arora et al, 2020). BGC* experiments "feel" CO_2 emissions like the default (COU*) model does, but the resultant climate change is suppressed (technically the atmospheric CO_2 increase is neglected as radiative forcing in our model). This means that there are no climate feedbacks in BGC* simulations, and the change in DIC reflects purely "carbon-concentration effects", in particular the marine uptake of anthropogenic CO_2 (C^{anth}). We adopt this approach here, and obtain, by difference of the two experimental set ups, "$\Delta DIC^{dis,bio,COU*-BGC*}$", the evolution of $\Delta DIC^{dis,bio}$ under changing ocean circulation. $\Delta DIC^{dis,bio,COU*-BGC*}$ intentionally disregards the physico-chemical effect of increasing atmospheric CO_2 on $\Delta DIC^{dis,bio}$, $\Delta DIC^{dis,bio,BGC*}$.

We find that over the entire experiment, $\Delta DIC^{dis,bio}$ is dominated by the effect of a changing atmospheric pCO_2-boundary condition under constant climate (BGC*). Under a constant climate, circulation, sea ice, surface ocean productivity and particle export (Fig. S8), as well as DIC^{remin} (Fig. S7, dashed lines) are in steady-state and do not change over time. The change of $DIC^{dis,bio}$ in this experiment can neither be related to biology itself and its impact on carbon storage ('gain side' effects on C^{soft}, Frenger et al., 2024), nor to the circulation and ice cover which could also affect storage attributable to the soft tissue pump if changed ('loss side' effects on C^{soft}, Frenger et al., 2024), as either remain unchanged. Instead, the change in $DIC^{dis,bio}$ in the BGC*-experiment is a response to the transient increase of atmospheric pCO_2 (Fig. S8b), hence rather related to the physical-chemical invasion of C^{anth}. Since oxygen does not have a respective ('O_2^{anth}') effect, an AOU based estimate of C^{soft} is blind against the C^{anth}-effect. In contrast, the difference of COU* and BGC* experiments of $DIC^{dis,bio}$ reflects climate change impacts such as changes in sea ice cover, circulation and biology on $DIC^{dis,bio}$.

It is a philosophical question if one wants to consider the BGC-effect or not. In most cases, however, like observations from the ocean, and most climate climate models, it is either impossible or at least practically difficult, demanding no-biology model setups and costly model spinup, to do so. Getting back to our motivation to assess how well we can estimate effects of changes of the soft tissue pump based on AOU, in conclusion, we

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find that the sum of our tracer based estimate of C^{soft} and $\Delta DIC^{dis,bio,COU\text{-}BGC*}$ is larger than the AOU-approximation on average by about 25%.

4 Conclusion

The computation of AOU is a pragmatic method which allows quantifying the O_2 debt stemming from organic matter degradation in the ocean and its carbon equivalent. This method can be applied to available historical observations, like global ocean data basis (Garcia et al., 2024), upcoming sensor based observations with potentially high temporal and regional coverage, like those from the BGC-Argo program (Sharp et al., 2023), and output from basically any ocean model that includes marine biogeochemistry (Wilson et al., 2022). As such it provides a powerful tool to evaluate models, observe the signal of change in the real ocean and quantify the contribution of carbon attributable to the soft tissue pump to the marine carbon sink under various potential futures (Koeve et al., 2020; 2024; Wilson et al., 2022; Frenger et al., 2024).

This advantage comes with the need to state inherent assumptions of the AOU approach, understand how we can interpret it, and the need of quantifying related uncertainties. As shown above, the AOU method includes contributions in particular from an undersaturation of surface ocean waters with respect to atmospheric O_2. Hence, it overestimates the O_2 debt due to accumulated respiration of organic matter since last contact with the atmosphere (so called 'true' oxygen utilisation; Ito et al., 2004: Duteil et al., 2013). Given that, as shown above, most of this overestimate is attributable to the *biotic* O_2 disequilibrium, i.e., that the O_2 debt of upwelled waters, stemming from former organic matter degradation, tends to not fully get replenished with atmospheric O_2 before re-subduction of waters, AOU provides a reasonable estimate of the *total* accumulated O_2 debt due to oxic organic matter degradation, which globally is correct to within about 10% error for most of the preindustrial state estimate and the transient climate change scenarios studied here.

The fraction of total DIC attributable of the soft tissue pump has been estimated to about 1300 ± 230 Pg C (Carter et al., 2021; Nowicki et al., 2022), or about 3.5% of the total DIC inventory (37,300 Pg C; DeVries 2022). By definition of the chosen approaches in the respective studies, the estimate of 1300 ± 230 Pg C is a state estimate of the DIC attributable to the marine soft tissue pumps accumulated *since last contact with the atmosphere*. The respective DIC^{remin} inventory state estimate in our model, within uncertainty, is the same (1290 Pg C). In the real ocean, C^{soft} can not be distinguished by chemical analysis from the large background inventory of DIC, but AOU provides this insight/information. Given that, as outlined above, AOU considers the accumulated O_2 debt due to oxic organic matter degradation, this is the case also for the AOU-based estimate of respired carbon: it includes the effect from incomplete equilibration of re-surfacing old waters that are enriched with carbon. We here assess technical uncertainties of using AOU to estimate remineralized carbon and find that for the preindustrial state estimate the AOU-approximation (1562 Pg C) is an about 15% underestimate of the sum of the DIC^{remin} and $DIC^{dis,bio}$.

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For the climate change transient we find that ΔAOU underestimates the disequilibrium 'corrected' change in C^{soft} ($DIC^{remin} + DIC^{dis,bio,COU^*-BGC^*}$) by 25%. An additional aspect, that we do not have for O_2, is that atmospheric CO_2 changes (increases; while atmospheric O_2 remains quasi-constant). The transient increase of atmospheric CO_2 itself, everything else unchanged, brings CO_2-oversaturated surface ocean waters closer to equilibration. Since this applies to the experiments with and without biology alike, it reduces the biotic component of incomplete equilibration ($DIC^{dis,bio}$) which is computed by the difference of these experiments.
Importantly, quantifying $DIC^{dis,bio}$ requires additional no-biology model variants, spinups and transient experiments and therefore is computationally very demanding.

Quantifying explicitly the climate change effect on $DIC^{dis,bio}$ is even more demanding, requiring fully coupled and biogeochemically coupled transient experiments carried out with both model variants . Assessing $DIC^{dis,bio,\ COU^*-BGC^*}$ in climate models is hence technically very challenging and costly. Said that, we suggest that ΔAOU provides, while not perfect, a quite satisfying metric for the change of marine excess carbon from the soft tissue pump under anthropogenic climate change.

Code and data availability

Model code, forcing files and output are available from GEOMAR at the following data archives: https://hdl.handle.net/20.500.12085/209f14f8-4c41-4e93-abe4-65a0af271fa6; https://hdl.handle.net/20.500.12085/74a83d93-c755-44c1-a615-2cfa4197f016 and https://hdl.handle.net/20.500.12085/959a266e-d785-4d57-87bb-103b28d2bb25.

Author contributions

W.K. and I.F. designed the research
W.K. performed the model experiments
W.K. analysed model output
W.K. and I.F. wrote the manuscript

Competing interest

The authors declare that they have no conflict of interest

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