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Mechanisms Underpinning the Net Removal Rates of Dissolved Organic Carbon in the Global Ocean

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Key Points:

- A model to reconcile millennial-scale bulk dissolved organic carbon degradation rates and short-term microbial turnover times is presented
- Macronutrient colimitation can explain observed concentration patterns of dissolved organic carbon in the surface ocean
- Continuous microbial reworking suggests a higher temporal variability of the marine dissolved organic matter inventory than previously thought

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract With almost 700 Pg of carbon, marine dissolved organic carbon (DOC) stores more carbon than all living biomass on Earth combined. However, the controls behind the persistence and the spatial patterns of DOC concentrations on the basin scale remain largely unknown, precluding quantitative assessments of the fate of this large carbon pool in a changing climate. Net removal rates of DOC along the overturning circulation suggest lifetimes of millennia. These net removal rates are in stark contrast to the turnover times of days to weeks of heterotrophic microorganisms, which are the main consumers of organic carbon in the ocean. Here, we present a dynamic "MICrobial DOC" model (MICDOC) with an explicit representation of picoheterotrophs to test whether ecological mechanisms may lead to observed decadal to millennial net removal rates. MICDOC is in line with >40,000 DOC observations. Contrary to other global models, the reactivity of DOC fractions is not prescribed, but emerges from a dynamic feedback between microbes and DOC governed by carbon and macronutrient availability. A colimitation of macronutrients and organic carbon on microbial DOC uptake explains >70% of the global variation of DOC concentrations, and governs characteristic features of its distribution. Here, decadal to millennial net removal rates emerge from microbial processes acting on time scales of days to weeks, suggesting that the temporal variability of the marine DOC inventory may be larger than previously thought. With MICDOC, we provide a foundation for assessing global effects on DOC related to changes in heterotrophic microbial communities in a future ocean.

Plain Language Summary The ocean stores more carbon as dissolved organic compounds (DOC) than all animals and plants on land and the oceans combined. However, numerical models used for future climate scenarios lack an implementation of processes transforming DOC back to CO_2 by marine microorganisms. Here, we present a global dynamical ocean model that explicitly considers the processes of DOC degradation by marine microorganisms. In the present ocean, the availability of organic carbon but also nitrogen and phosphorus control the amount of carbon stored as DOC, as the lack of these nutrients inhibits its degradation by bacteria. The identification of these ecological controls allows a quantitative assessment of the fate of this large carbon reservoir in the future. The findings indicate that the marine DOC reservoir is potentially more dynamic than previously thought, since decadal to millennial scale net removal rates might be a result of microbial processes acting on shorter time scales.

1. Introduction

The marine dissolved organic carbon (DOC) pool is a major carbon reservoir (~662 Pg C, Hansell et al., 2012) and a central part of all major element cycles, because it is tightly connected to the flow of energy and matter through marine ecosystems. Most of the DOC originates from marine phytoplankton and is respired back to CO_2 or transformed and diversified by heterotrophic microorganisms (Azam, 1998; Fry et al., 1998; Moran et al., 2016). Both, organic carbon compounds and heterotrophic microorganisms, are characterized by an enormous molecular and microbial diversity (Moran et al., 2016). The complex interactions between microorganisms and organic compounds, mediated by physicochemical parameters in the ocean, have the potential to result in climate feedbacks (Jiao et al., 2014; Legendre et al., 2015; Roshan & DeVries, 2017). Current Earth System Models mainly focus on impacts related to carbon fixation (Anderson et al., 2015), that is, the phytoplankton component. However, the time scales of variability of marine carbon reservoirs also depend on the ability of the heterotrophic microbial community to transform organic carbon back to CO_2. Identification of the processes underlying organic carbon remineralization and their influence on the global DOC distribution is

therefore important but remains a challenge to date (Legendre et al., 2015; Lønborg et al., 2020; Wagner et al., 2020). This uncertainty directly translates into an inability to project how the DOC inventory may change in future climate scenarios (Legendre et al., 2015; Lønborg et al., 2020; Wagner et al., 2020).

At present, DOC concentrations are highest in the surface ocean with an additional accumulation in subtropical gyres, and decrease toward a concentration of ∼35 μM in the deep sea along the overturning circulation (Hansell et al., 2009). In contrast to substantial variations in the upper-ocean gradients, DOC concentrations in the deep ocean are remarkably homogeneous. The fact that the marine DOM pool with ^{14}C derived ages of up to thousands of years (Beaupré & Druffel, 2009; Druffel et al., 2016; Williams et al., 1969) exists in the presence of microbial heterotrophic consumers has been termed the "DOM paradox" (Dittmar, 2015; Dittmar et al., 2021). A dynamic model that is suitable for future climate projections of DOC must be capable to reproduce today's distribution of DOC at basin-scales and relate these spatiotemporal patterns to environmental conditions.

Current state-of-the-art models of marine DOC typically prescribe the net removal of one or more reactivity fractions of the DOC pool (Anderson et al., 2015). In these models, DOC produced by phytoplankton is channeled in fixed ratios into reactivity classes of different lability, which each decay with a specific prescribed first-order degradation rate. In a seminal study by Hansell et al. (2012), net removal rates of a semi-labile, semi-refractory and refractory DOC pool have been derived from observational data. The resulting dynamic model based on these three reactivity pools achieved excellent agreement with DOC measurements in the deep ocean ("prescribed reactivity" in the following). In that study, net removal rates for semi-labile (2–9 mmol C m^{-3} yr^{-1}), semi-refractory (0.2–0.9 mmol C m^{-3} yr^{-1}) and refractory (0.0024–0.004 mmol C m^{-3} yr^{-1}) were derived by both linking observed DOC concentrations to water mass age proxies, as well as using a model with prescribed reactivity classes. While modeling net removal rates is an elegant way to reproduce observed concentrations in the oceans today, the millennial time scales of DOC net degradation contrast the time scales on which the major microbial consumers act, which have growth rates on the order of days to weeks (Kirchman, 2016). Hence, focusing on net removal rates for future climate projections may result in a biased view, as underlying microbial processes and their dependency on changing environmental conditions are not explicitly resolved. Efforts have been undertaken to include a dynamic representation of heterotrophic microorganisms in global numerical models. However, global scale models that include heterotrophic microorganisms have produced concentration patterns that differ markedly from observed concentration patterns (Bendtsen et al., 2002; Hasumi & Nagata, 2014; Yamanaka & Tajika, 1997), partly because the mechanisms behind both the basin-scale distribution of DOC as well as its longterm persistence are not sufficiently understood.

The reasons behind the basinscale distribution of DOC concentrations are quantitatively not well constrained. This is reflected by the fact that no dynamic model sufficiently reproduces observed surface patterns of DOC: Those models that include microbial consumers cannot reproduce patterns, and the net removal rate models rely on a square root dependence of net primary production for DOC production without biological meaning or result from machine learning approaches without dynamically resolving underlying processes (Hansell et al., 2009; Matsumoto et al., 2022; Roshan & DeVries, 2017). The role of new nutrients in the basin-scale concentration pattern in the North Atlantic has been assessed in a correlative study by Romera-Castillo et al. (2016). Although the DOC accumulation in the North Atlantic gyre could not be explained satisfactorily with this approach, it highlights the tight connection between nutrients and DOC concentrations. Still, an implementation of a connection between DOC and macronutrients into a dynamic model that is suited for simulating climate scenarios is lacking.

The second issue for modeling global marine DOC concentrations in a dynamic way is the mechanism behind the longterm persistence of the DOC pool in the presence of carbon-limited microorganisms in the deep sea. The apparent radiocarbon (^{14}C) age of bulk DOC exceeds 5,000 years in the deep ocean, indicating that the lifetime of the DOC pool as a whole exceeds the timescale of the overturning circulation (Beaupré & Druffel, 2009; Druffel et al., 2016; Williams et al., 1969). The mechanisms behind the long-term persistence of DOC have so far been described by three hypotheses that are not mutually exclusive (Dittmar, 2015): (a) the environmental hypothesis, stating that environmental conditions hamper the decay of DOC, (b) the intrinsic recalcitrance hypothesis, stating that molecular properties make compounds persistent in the ocean for thousands of years, and (c) the dilution hypothesis, stating that low concentrations of individual compounds in the diverse mixture of DOC slow down microbial uptake. The role of microorganisms in increasing the stability of DOC is generally acknowledged ("microbial carbon pump," Jiao et al., 2010). However, the extent to which these mechanisms control global DOC

turnover remains unresolved (Arrieta et al., 2015; Dittmar, 2015; Jiao et al., 2011, 2014), as microorganisms alter both the chemical structure and the diversity of DOM. The relative roles of these hypothetic mechanisms remain uncertain (Dittmar et al., 2021; Lennartz & Dittmar, 2022; Shen & Benner, 2020). Reactivity of DOM has been related to molecular properties such as molecular size ("size-reactivity-continuum," Benner & Amon, 2015), and the fact that high molecular weight DOM usually has a younger radiocarbon age than low molecular weight DOM (Walker et al., 2016). This observation may result from different feeding strategies of bacteria (Arnosti et al., 2018), highlighting the importance to consider the interactions between microorganisms and DOC compounds in order to move toward causative relationships. While molecular substrate properties shape bacterial succession and therefore degradation rates on short time scales, for example, during blooms (Teeling et al., 2012), the role of molecular properties as a cause for DOM persistence on much longer time scales is not clear (Dittmar et al., 2021).

The intrinsic recalcitrance hypothesis in which properties of the DOC pool (i.e., the degradation rate constant) define its reactivity has been applied in the majority of DOC modeling approaches (Anderson et al., 2015). In contrast, the dilution hypothesis has so far been assessed on a conceptual level (Wilson & Arndt, 2017). In order to represent the mechanisms of the dilution hypothesis in models, both a dynamic feedback with a microbial community and the high molecular and microbial biodiversity need to be considered. Hence, recent efforts call for assessing DOC turnover with a dynamical heterotrophic microbial component (Dittmar et al., 2021; Zakem et al., 2021). Such approaches are beginning to be addressed in theoretic frameworks (Mentges et al., 2019; Zakem et al., 2021) but not yet on a global scale. It is important to emphasize that these hypotheses are not mutually exclusive. Rather, their juxtaposition serves the pragmatic purpose of hypothesis testing. Together they represent the extremes within the spectrum of potential mechanisms contributing to the long-term persistence of DOM, and they do not cover all proposed mechanisms.

Here, we address the fundamental shortcoming of an adequate dynamical representation of remineralization in models by assessing the mechanisms underpinning the seemingly decadal to millennial scale degradation rates of marine DOC. We developed a process-oriented model, which is still sufficiently simple to be implemented in global model approaches, and in which heterotrophic communities (mainly bacteria and archaea, picoheterotrophs in the following) are explicitly included (model of MICrobial-DOC interactions, MICDOC). We hypothesize that environmentally controlled processes on short time scales (days to months) lead to millennial-scale net removal rates. The aim here is to explore why a certain part of DOM is processed quickly, while other fractions are processed more slowly, corresponding to the semi-labile, semi-refractory and refractory reactivity classes as presented in Hansell et al. (2012). We aim to identify microbial mechanisms that shape concentration patterns of DOC on basin-scales, and derive corresponding net removal rates. First, we systematically assess which environmental controls on microbial DOC uptake and transformation may explain the observed surface patterns of DOC in an analytical approach. We then implemented the most promising process in a 3D ocean model of the University of Victoria Earth System Model of Intermediate Complexity (UVic, Keller et al., 2012; Weaver et al., 2001) and compared the results with an extensive set of observational data consisting of more than 40,000 DOC concentrations in the world ocean (Hansell et al., 2021).

2. Materials and Methods

2.1. The MICDOC Model

The MICDOC model is based on an aggregated version (Mentges et al., 2020) of a more detailed interaction network model (Mentges et al., 2019). The detailed interaction network with 100 DOC compounds and 35 bacterial groups has been summarized to state variables for bulk DOC and bulk microbial biomass (Mentges et al., 2020). According to the approach of complex systems theory in the original model, these 100 DOM compounds and bacterial units are theoretical representations of DOM fractions. Similar to the three reactivity fractions in Hansell et al. (2012), they are not directly related to chemical structures. The exact number of compounds (100 in the original model) is irrelevant to the overall behavior of the model in which a persistent DOM pool emerges on a system's level (see Lennartz and Dittmar (2022) for a detailed discussion on this). Both the detailed network model and the aggregated model consider the following processes: uptake of DOC by microorganisms, release of DOC during growth and lysis, as well as transformation to inorganic carbon by respiration. The DOC taken up by microorganisms is partitioned into three routes, that is, incorporation into biomass (η), release as DOC ($\beta(1-\eta)$) and respiration to CO_2 $(1-\beta)$ $(1-\eta)$. The differential equations for DOC and heterotrophic microorganisms result from the aggregation of a detailed network model of microbial DOC

interactions (Mentges et al., 2019) and are derived from Mentges et al. (2020). Their rates are calculated as follows:

$$\frac{d\mathrm{DOC}}{dt} = -\alpha(f)\, B\ \mathrm{DOC} + \mu B + \beta(1-\eta)\alpha(f)\, B\ \mathrm{DOC} + s \tag{1}$$

$$\frac{dB}{dt} = +\eta\alpha(f)\, B\ \mathrm{DOC} - \mu B \tag{2}$$

with α the apparent DOC uptake rate as a function of the factor for inorganic nutrient limitation f (Equation 3), μ the microbial mortality rate (lysis), η the bacterial growth efficiency (so that the growth rate becomes $\alpha \cdot \eta$), β $(1-\eta)$ the fraction of DOC uptake that is released during growth, and s the supply rate of DOC from other sources. The fraction $(1-\beta)\,(1-\eta)$ is respired to CO_2 (equation not shown here but in Mentges et al. (2019)). The apparent uptake rate α is calculated as in the original description of the box model in Mentges et al. (2019)

$$\alpha(f) = f \cdot \frac{\rho}{\kappa}\frac{n_u}{\mathrm{n}} \tag{3}$$

with DOC uptake rate constant ρ, microbial substrate specificity κ (half-saturation constant of the Monod-equation, here the slope of the linearized form, see derivation in Mentges et al. (2020)), and $\frac{n_u}{n}$ as a measure of the fraction of DOC compounds available to an average bacterium (with n the total number of molecules and n_u the number of molecules the average bacterium can take up, see also (Mentges et al., 2020). This parameter reflects observations, that is, that bacteria have a specific substrate spectrum and cannot take up all compounds present. By introducing this parameter, the overall uptake rate of DOC in the aggregated model is effectively reduced. This reduced uptake rate accounts for the fact that each microbe can only take up a subset of DOM compounds present. This step is necessary in order to retain model behavior when aggregating from the model that resolves uptake and release of individual compounds by specific bacterial groups as in Mentges et al. (2019) to the aggregated version suitable for global scale modeling approaches employed here. Factor f is applied to describe environmental controls on the uptake rate, as described below. Here, α is parameterized to match observations of global DOC and bacterial biomass (see below, Buitenhuis et al., 2012; Hansell et al., 2021) and slightly deviates from the original model set-up in Mentges et al. (2020). The model parameters and their values are listed in Supporting Information S1 (Table S2). The parameterization is intentionally kept structurally simple to allow implementation in Earth System Models. By aggregating the DOC compounds into one bulk pool without further specifying molecular properties like reactivities or molecular weight, we can derive primary environmental controls that shape the patterns of bulk DOC. Moreover, MICDOC is a suitable platform to implement varying bacterial uptake strategies or DOM pools in future studies.

2.2. Analytical Solutions

Analytical solutions for the spatial variations of several parameters of the microbial DOC model were determined by setting $\frac{d\mathrm{DOC}}{dt} = \frac{dB}{dt} = 0$ and solving for DOC and B. In total, we tested 13 scenarios in which parameters of the model are influenced by environmental conditions, for example, growth rate by temperature or nutrient concentrations, etc. These analytical solutions have been used to screen for potential environmental controls that result in observed patterns (see supplements for detailed results, Text S2, Figures S1–S15 in Supporting Information S1). The analytical solutions for the differential equations as in Equations 1 and 2 are the following.

$$\mathrm{DOC}^* = \frac{\mu}{\alpha(f)\eta} = \frac{\mu}{\eta}\frac{\kappa}{f\cdot\rho}\frac{n}{n_u} \tag{4}$$

$$B^* = \frac{\eta s}{\mu(1-\beta)(1-\eta)} \tag{5}$$

Note that (as in classical consumer-resource theory (Tilman, 1982)), only the steady-state concentration of bacterial biomass B^* Equation 6 depends on the production rate of DOC, s, opposite to the steady-state concentration of DOC* Equation 5. For a derivation of the analytical solution, we refer the reader to the Supporting Information S1.

The steady-state DOC surface concentration and bacterial biomass were then calculated for each model grid point using environmental factors such as surface temperature, nutrient concentration, external DOC supply etc. from the remineralization rate of the standard NPZD component in the UVic model in a monthly resolution. The analytical solution was then subsampled at month and location of the observations in the reference data sets. The reference data set for DOC was compiled from individual cruises obtained from https://cchdo.ucsd.edu; details on the cruises can be found in Table S3 of the Supporting Information S1. The reference data set for picoheterotrophic biomass was obtained from https://doi.pangaea.de/10.1594/PANGAEA.779142 (Buitenhuis et al., 2012), with data sets from additional studies (Clarke & Leakey, 1996; Lara et al., 2017; Rivkin, 1991; Simon et al., 1999; Smetacek et al., 1997; Wigington et al., 2016).

2.3. MICDOC: A DOC-Microbial Component for the 3D Ocean Model in UVic

The University of Victoria Earth System Model of intermediate complexity (UVic) (Keller et al., 2012; Weaver et al., 2001) is an Earth System Model with a focus on the ocean. The UVic version 2.9 contains a general ocean circulation model (MOM2) and a biogeochemical (Nutrient-Phytoplankton-Zooplankton-Detritus) NPZD model, as described in Keller et al. (2012). The default NPZD model does not include a DOC pool, so that DOC cycling is not explicitly involved in the remineralization but implicitly included (see below). The model environment of UVic was chosen as it provides the possibility of performing computationally efficient global simulations while simulating other biogeochemical properties in a reasonable manner. The state variables for DOC and bacterial biomass as in Equations 1 and 2 have been implemented.

The macronutrient (co-)limitation of DOC utilization is realized by making the bacterial DOC uptake rate a function of a nutrient-dependent reduction factor f in the range [0,1]. Here, we only consider phosphate as the limitating nutrient, but future studies can explore the effect of other limitations in a similar manner. We assume that the nutrient limitation basically follows a Monod-kinetics, but that the local microbial community instantly shifts toward optimal values along a gleaner-opportunist trade-off (Figure 1b). Summarizing these kinetics into a trade-off-line is an established procedure (Litchman et al., 2007). This effectively allows us to model the limitation by a linear increase of the factor f with the macronutrient, in our case the phosphate concentration:

$$f = \min\left(a \cdot \left[PO_4^{2-}\right] + b, 1\right) \tag{6}$$

The linear dependency is characterized by the slope a and intercept b and it saturates at the maximal value $f = 1$ for high phosphate concentrations, representing the fact that the overall uptake rate α then is no longer limited by phosphate but only by the DOC concentration.

Slope a and intercept b (Equation 7) of this trade-off-line have been manually tuned to achieve best agreement with the DOC surface concentration (shallower than 50 m) of the reference data set, as nutrient limitation is most pronounced in surface waters (Rivkin & Anderson, 1997).

The MICDOC model uses the UVic model as a host model, that is, the MICDOC model is fueled by the default NPZD model and is subjected to the same advection and diffusion, but processes in MICDOC such as DOC supply and nutrient limitation do not affect the NPZD model. As such, the MICDOC model represents a more detailed description of the simplified remineralization of detritus in the original NPZD model. The coupling also includes a Redfield conversion of remineralization rate from nitrogen units of the NPZD model to carbon units of the MICDOC model. To make the simulation consistent, the DOC supply s in Equation 1 is thus set to the remineralization of detritus of the original NPZD model. Additional tests varying the DOC supply based on primary production or particle concentration did not significantly alter the results (Text S2 in Supporting Information S1), as the equilibrium DOC concentration in this model is independent from s (Mentges et al., 2020). The unidirectional coupling allows us to include the effects of physical transport, nutrient concentration and DOC supply on the modeled spatial patterns of DOC.

The model is initialized with a globally uniform DOC concentration of 40 μmol L^{-1} representing the background concentration (Roshan & DeVries, 2017) and a microbial biomass of 1 mmol carbon m^{-3} reflecting surface values (Buitenhuis et al., 2012) and a fully spun up ocean physics (10,000 years starting from World Ocean Atlas conditions). The full model is then run for 5,000 years, repeating the forcing of year 1850, until the model

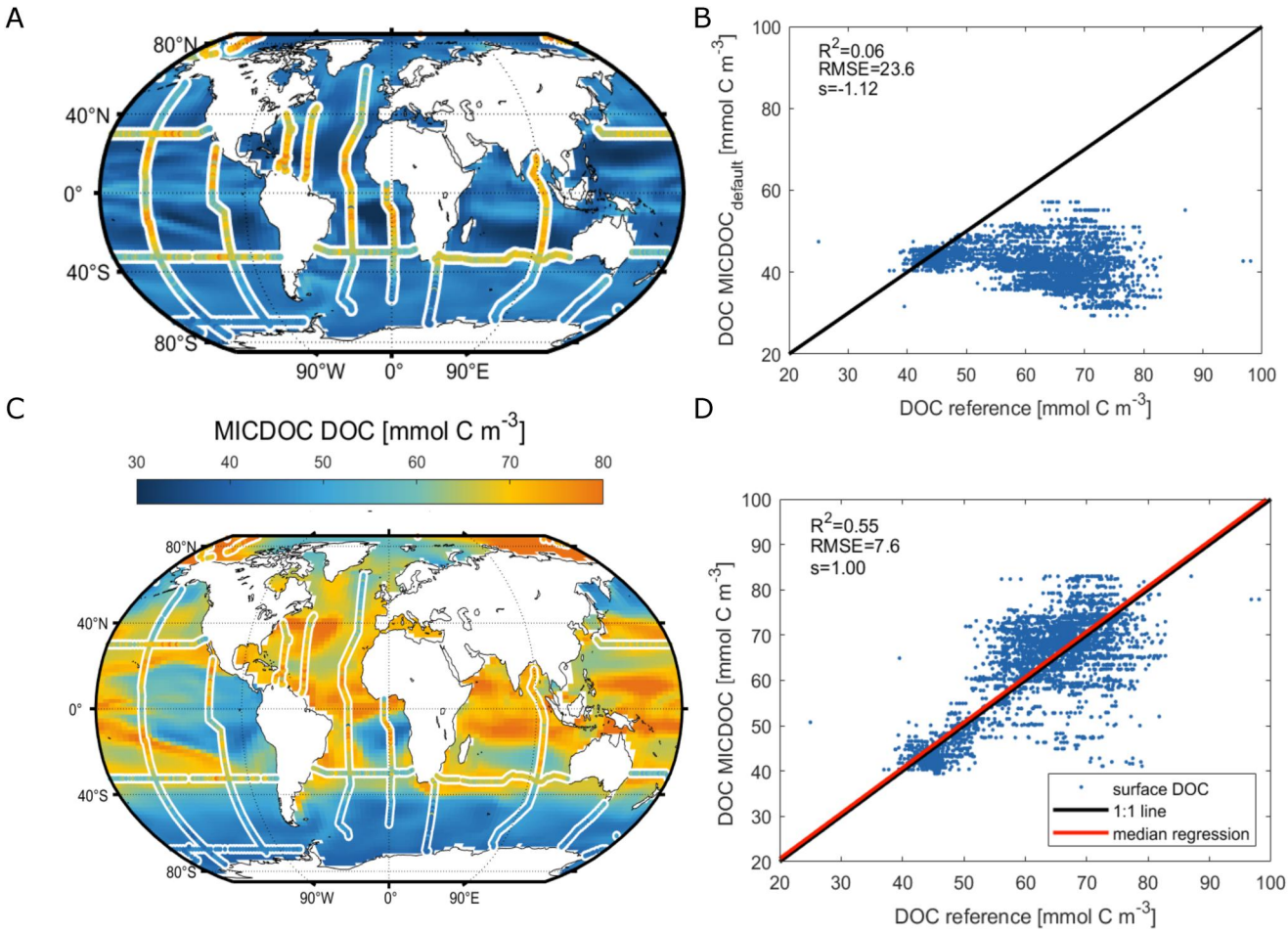

Figure 1. DOC surface concentration in model simulation. (a) Surface DOC concentration in the UVic-MICDOC model with globally constant parameters, that is, no environmental control on microbial DOC interactions (default version). DOC measurements along cruise transects of the reference data set are shown in the same color scale. (b) 1:1 comparison of the same simulation subsampled at locations of the reference data set (see Section 2). Black line indicates the 1:1 line. (c) Same as (a) but with nutrient colimitation implemented. (d) Same as (b) but with nutrient colimitation implemented. RMSE = root mean square error, s = slope of median regression.

stabilizes (i.e., average DOC concentration changes less than 1 μmol L^{-1} in 100 years). Then, the time span 1850 to 2000 is simulated using CMIP5 forcing and an average of year 2000 is used for comparison with the observational data.

2.4. Net Removal Rates

Net removal rates of DOC were calculated and compared in three different ways. As the model allows to directly calculate net removal rates from the gross rates in the model, we computed net removal rates as the DOC supply rate minus the uptake rate plus the release rate, that is, the amount of carbon that is neither respired nor incorporated into biomass:

$$R_{\text{net}} = R_{\text{supply}} - R_{\text{uptake}} + R_{\text{release}} \quad (7)$$

Although this is the most accurate method for our model output and can be compared to the model output in Hansell et al. (2012), it is not exactly comparable to the net removal rates of the semi-refractory and refractory pools derived from observed age proxies in that study. In order to ensure comparability with these net removal rates, we additionally subsampled model output at the location of the measurements used in that study and performed a linear regression of modeled DOC with observed age proxies of Chlorofluorocarbons and radiocarbon as in Hansell et al. (2012). We also took advantage of the model's capability to compute ideal water mass

age at each grid point, so as to obtain a comprehensive data set of modeled DOC and an age tracer. Ideal age is calculated as the time since the last contact with the atmosphere, that is, surface layer, in the model, and is therefore by definition zero at the surface.

3. Results and Discussion

3.1. Spatial Patterns of Surface DOC in a Scenario of Carbon Limitation Only

The default model in which microorganisms are only carbon limited everywhere in the ocean results in a rather homogeneous DOC concentration (Figures 1a and 1b). This homogeneous distribution reflects the subsistence concentration resulting from picoheterotrophic DOC interactions. The emergence of such a stable steady-state concentration is known as Tilman's R^* concentration from ecological theory, that is, consumer-resource theory (Tilman, 1982). In line with the original network model (Mentges et al., 2019, 2020), the persistence of the DOC pool emerges in this model from microbial DOC interactions despite individual constituents of bulk DOC being bioavailable on short time scales (maximum turnover rates of days). The size of the emergent DOC pool is defined by microbial properties (Equation 5) rather than chemical properties of DOC. There is no explicit representation of subsistence concentration in the sense of a threshold value (Wilson & Arndt, 2017), but any system with a feedback between a consumer and a resource will lead to a subsistence concentration, as this results from first principles (Tilman's R^*, Tilman, 1982). The mechanism behind this stability is the coupling of production and consumption rates: low supply rates of fresh DOC result in low bacterial biomass (Equation 5) and hence cause low degradation rates, and vice versa. This mechanism is in line with the dilution hypothesis of DOC persistence: A diverse microbial community will decrease the concentration of individual substrates to low concentrations, which add up to a large DOC pool (Arrieta et al., 2015). In order to mimic this model behavior in the aggregated model, in which individual compound groups are not resolved, the molecular diversity is reflected by an additional parameter (n_u/n, Equation 5), which lowers the overall bulk DOC uptake rate and therefore increases the bulk DOC R^* concentration (Mentges et al., 2020).

3.2. Spatial Patterns of Surface DOC in Scenarios of Environmental Controls

To determine the factors that explain surface DOC patterns, we systematically tested environmental controls on each model parameter (Text S2 in Supporting Information S1) in 12 separate and 2 combined parameterizations for analytical steady-state solutions. Among others, we tested environmental controls by a temperature dependence of bacterial DOC uptake (Blackford et al., 2004), controls on mortality by viruses (density-dependent mortality) and grazing (mortality correlated to zooplankton abundance in the host model), photochemistry and an opportunist-gleaner trade-off (copiotroph-oligotroph) for macronutrient limitation (Litchman et al., 2015; Rivkin & Anderson, 1997). We compared model output to reference data sets, including a compilation of more than 30 cruises with DOC measurements (see Section 2), and a database on picoheterotrophic biomass (Buitenhuis et al., 2012). We then implemented the most promising solution into the dynamic MICDOC model.

Among all tested parameterizations in the analytical set-up, two achieved good agreement with observations data in terms of explained variance (>60%) and root mean square error (RMSE, <10 mmol C m^{-3}): a tuned temperature dependency of the bacterial growth efficiency η (Rivkin & Legendre, 2001) (steady-state solution 3 in Figure S3 of the Supporting Information S1), and a macronutrient colimitation on DOC uptake (Hale et al., 2017) (steady-state solution 7 in Figure S9 of the Supporting Information S1). Macronutrient control on bacterial growth efficiency (del Giorgio & Cole, 1998) led to qualitatively similar results as macronutrient colimitation (steady-state solution 4 in Figure S4 of the Supporting Information S1), while macronutrient control on the release efficiency β had a neutral effect (steady-state solution 10, Figure S12 in Supporting Information S1). The effect of the temperature-dependent growth efficiency η, however, was canceled out by the effect of a temperature dependent growth rate (Figures S7 and S8 in Supporting Information S1), as they work in opposite directions. Our arguments for selecting macronutrient colimitation as a primary control on surface patterns are (a) widespread experimental evidence for this process on a community level from nutrient amendment experiments, and (b) emerging DOC concentration patterns that agree with observations. We do not exclude other factors like chemical properties or temperatures as important controls for DOC concentrations, but they did not produce observed patterns when tested individually in our model, and we therefore decided to keep bacterial growth rate α and growth efficiency η temperature independent.

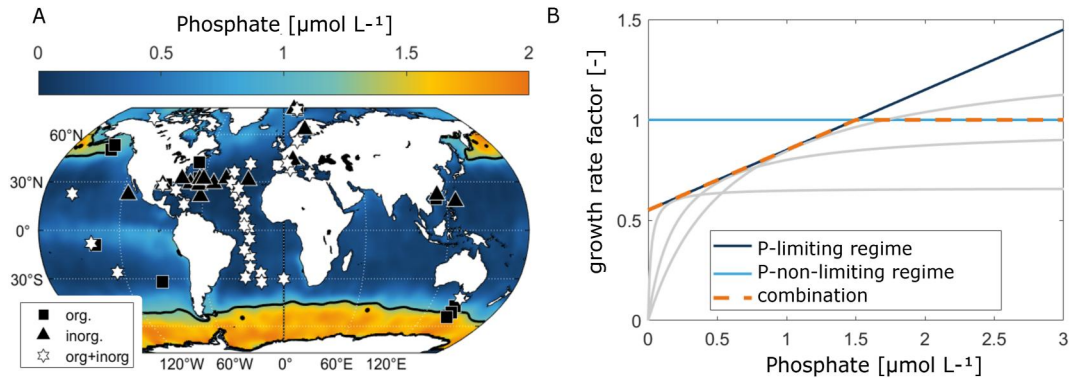

Figure 2. Impact of nutrient limitation on DOC uptake. (a) Global map of observed phosphate concentration from World Ocean Atlas (Boyer et al., 2018), with locations and results of nutrient addition experiments collected from the literature (Carlson & Ducklow, 1996; Caron et al., 2000; Chin-Leo & Benner, 1992; Church et al., 2000; Cotner et al., 1997, 2000; Donachie et al., 2001; Hale et al., 2017; Hoch & Bronk, 2007; Joint et al., 2002; Kirchman, 1990; Kuparinen & Heinänen, 1993; Liu et al., 2014; Martínez-García, Fernández, Álvarez-Salgado, et al., 2010; Martínez-García, Fernández, Calvo-Díaz, et al., 2010; Mills et al., 2008; Obernosterer et al., 2003; Ortega-Retuerta et al., 2012; Pinhassi et al., 2006; Pomeroy et al., 1995; Rivkin & Anderson, 1997; Shiah & Ducklow, 1993; Vadstein, 2011; Yuan et al., 2011; Zweifel et al., 1993). According to the experiments, the heterotrophic microbial community was limited by organic compounds (square), inorganic compounds (nitrate, phosphate or both, triangles), or colimited by both (stars). (b) The colimitation by DOC and macronutrients was implemented as a linear trade-off line (resulting from ecological trade-offs between substrate affinity and maximum uptake rate as in the classical opportunist-gleaner-trade-off, exemplatory indicated by gray lines, see text). The dashed orange line indicates the resulting parameterization for f (Equation 7) in the model, that is, a decreased DOC uptake at low phosphate concentrations, and a DOC uptake rate not influenced by phosphate concentrations above ca. 1.5 µmol P L^{-1}.

Oligotrophic conditions as a cause for DOC accumulation have been suggested before in theoretical (Polimene et al., 2006) and regional modeling studies (Polimene et al., 2007). In MICDOC, we implemented the control of macronutrients on DOC uptake as a colimitation into the global ocean model, which resolves the physical transport in addition to the biogeochemical control. The colimitation was realized by decreasing the overall DOC uptake rate according to the macronutrient concentration along a linear trade-off line (Litchman et al., 2015) (Figure 2b). This setup represents the established relationship of a "gleaner" or oligotroph that has a high substrate affinity but only low growth rates and "opportunists" (copiotrophs) vice versa (Litchman et al., 2015).

In our model, the degradation of DOC is hampered in regions with low nutrient concentrations, leading to the observed patterns of DOC concentrations, such as the concentration gradient with depth and the accumulation in the surface layer of the subtropical gyres (Figure 1b). The explicit consideration of this nutrient trade-off explains a major part of the variance of surface DOC concentrations (depth < 50 m, Pearson's $R^2 = 0.55$, Figure 1). With a RMSE for DOC surface concentrations of 7.6 mmol C m^{-3}, our model performs slightly better than traditional net prescribed reactivity models with RMSE >10 mmol C m^{-3} at the surface (Hansell et al., 2012). Residual analysis shows that the model reduces systematic bias compared to the version with carbon limitation alone (Figure S16 in Supporting Information S1). The remaining residuals are to some extent "wrong for the right reasons," as DOC is overestimated at locations where phosphate concentration is underestimated in the host model UVic, and vice versa (Figure S18 in Supporting Information S1).

The general importance of macronutrients for DOC patterns at the ocean's surface has been described previously (Carlson et al., 2002; Rivkin & Anderson, 1997; Romera-Castillo et al., 2016; Roshan & DeVries, 2017). Nutrient amendment experiments from almost all major ocean basins have repeatedly reported (co-)limitation of the heterotrophic community by macronutrients in the majority of the nutrient depleted surface ocean (Figure 2a) (Hale et al., 2017; Pomeroy et al., 1995; Rivkin & Anderson, 1997). The majority of these studies shows that the heterotrophic community production increases upon the addition of either macronutrients (N, P, N + P) alone or in combination with DOC (Figure 2a). Pure carbon limitation prevails in regions with high macronutrient concentrations (Southern Ocean, coastal regions, Figure 2a). Macronutrient limitation of heterotrophic bacteria by phosphorus or nitrogen has also been experimentally demonstrated (Trautwein et al., 2017). The colimitation in

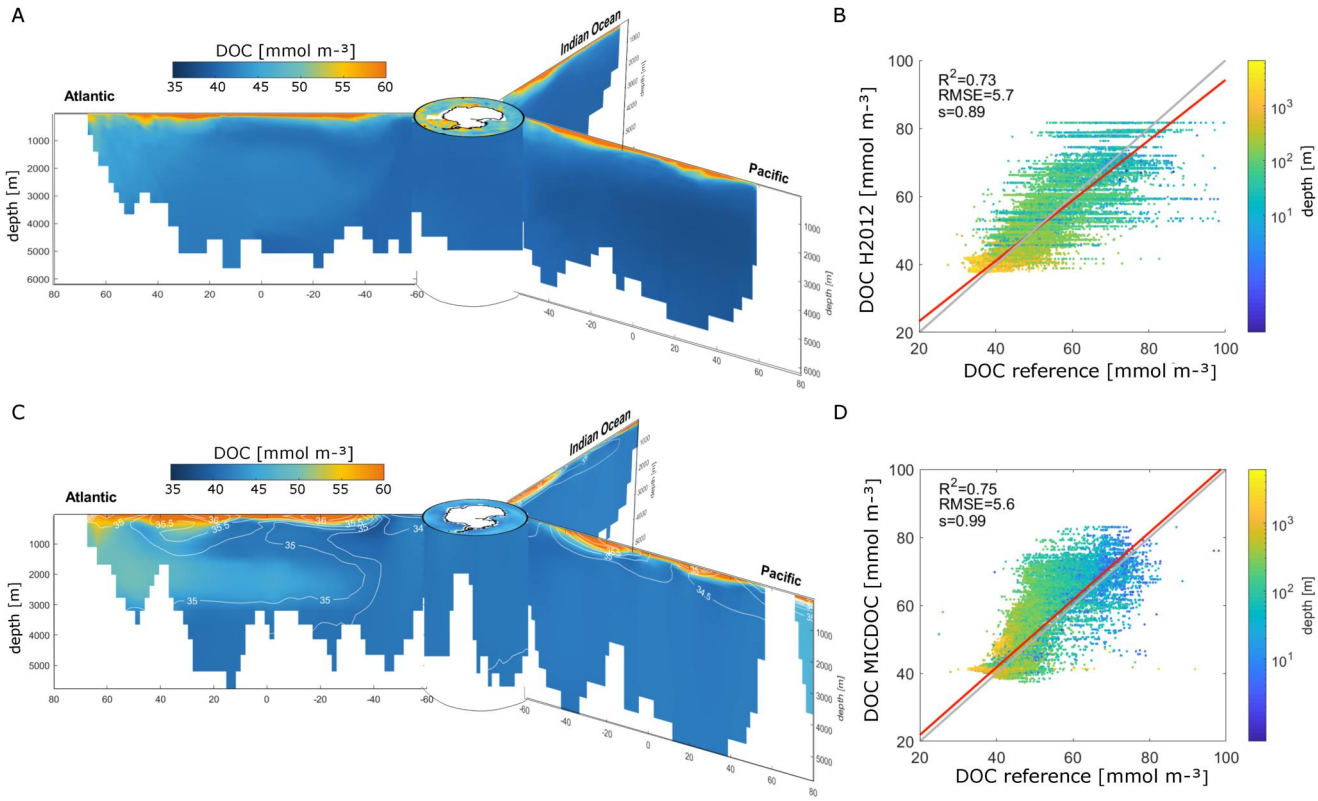

Figure 3. Comparison of model results of Hansell et al. (2012) based on net removal rates (prescribed reactivity) and MICDOC (emergent reactivity) with observations in the global ocean. Cross sections along the three major ocean basins (150°W, 30°W, 70°E) showing the DOC concentration in the net removal rate model as in (a) Hansell et al., 2012 (H2012) and (c) in MICDOC simulated with the nutrient (co-)limitation trade-off, white lines indicate salinity. (b) Model output subsampled for locations of the reference data set across the whole water column for the net removal rate model, 1:1 comparison of modeled DOC from panels (a) and (c) with the reference data set (gray line, n = 42,340), red line is a median regression of the median (note that the 95% confidence intervals are too narrow to be discernible). RMSE = root mean square error in mmol C m^{-3}, s = slope of quantile regression, R^2 = Pearson's R. (d) Same for the MICDOC model.

nutrient depleted areas and the pure carbon limitation in high-nutrient regions is completely in line with our parameterization, which only lowers the DOC uptake rate at nutrient concentrations below 1.5 μmol P L^{-1} (Figure 2b). The resulting implementation of this process is efficient yet reproduces observations, and is therefore well suited to improve the representation of DOC in large-scale biogeochemical ocean and Earth System Models compared to the previous state of net-removal rate models. These results are qualitatively robust, regardless of whether the limitation results from organic or inorganic phosphorus, although we cannot differentiate between these limitations in our model at this point.

3.3. Subsurface Patterns of DOC Resulting From Macronutrient Colimitation

Surprisingly, implementing macronutrient colimitation also led to an improvement in reproducing spatial patterns of DOC in the deep ocean. As suggested by prescribed reactivity models and observations, DOC concentrations decline along the main pathways of the overturning circulation, and from surface to depths, most prominently following deep water formation and transport in the North Atlantic (Hansell et al., 2009). In models in which DOC net removal rates are prescribed as millennial time scales, these surface patterns are largely controlled by the surface concentrations (Matsumoto et al., 2022) (Figure 3a). In MICDOC, this pattern is surprising, because DOC can be degraded on much shorter time scales due to the explicitly described microbial degradation, which acts on time scales of days to years. Here, these patterns naturally emerge in MICDOC due to nutrient availability limiting DOC uptake at the surface (Figure 3c). With subducting waters in the North Atlantic, macronutrient limitation transitions toward pure carbon limitation at a steady-state DOC concentration in the deep ocean that is constrained by microbial properties and molecular diversity (see analytical solution in Equation 5). Macronutrient concentrations gradually increase along the path of North Atlantic deep waters as they are replenished during organic matter remineralization, so that the DOC degradation becomes gradually less nutrient limited (discussed below).

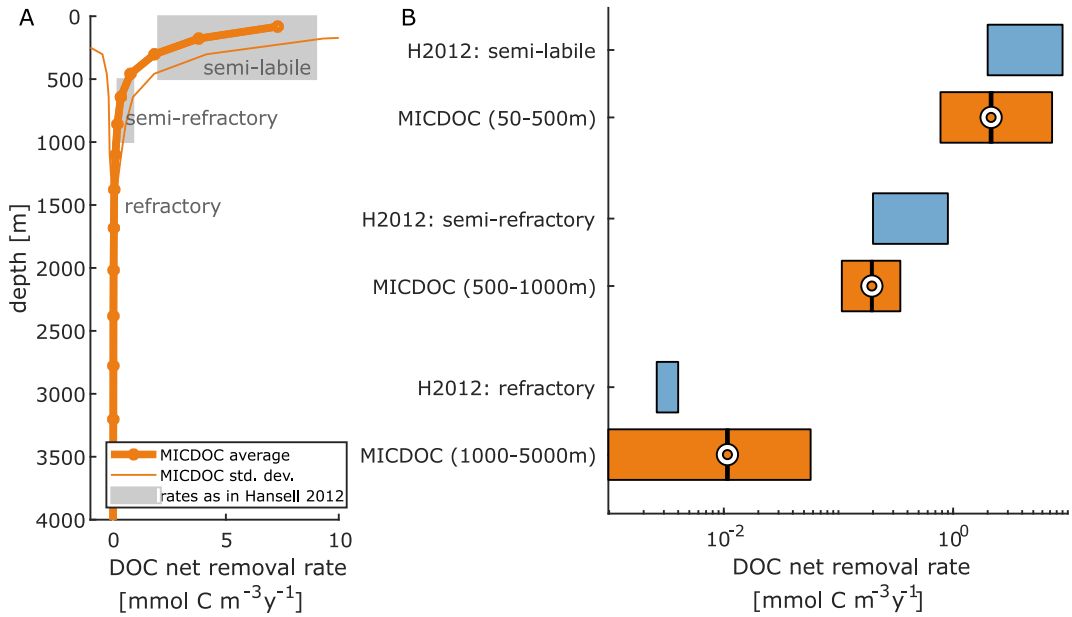

Figure 4. Comparison of net removal rates in MICDOC and Hansell et al. (2012, H2012). (a) Profile of net removal rates of bulk DOC in MICDOC. Area-weighted average and standard deviation for net removal rates of bulk DOC in MICDOC, calculated from the model's supply, uptake and release rates. Gray boxes show net removal rate ranges from Hansell et al. (2012), that is, the horizontal extent is the range of net removal rates for the corresponding depth, which is shown here by the vertical extent. (b) Range of net removal rates of reactivity fractions of Hansell et al. (2012) and corresponding area-weighted averaged for respective MICDOC depths. Markers indicate average over depth interval. Note the logarithmic scale of *x*-axis.

Because bacterial abundance is lower at depths compared to the surface, degrading the remaining DOC after the release of macronutrient limitation takes comparably longer, that is, several years in our model. This time lag leads to a further expansion of the elevated DOC concentration along the North Atlantic Deep Water trajectory in the model (Figure 3). In situ incubation studies from this region and depth would serve as a ground truth for our study in the macronutrient-limited part (Figure 5), but would require to take into account the low bacterial abundance as an additional factor for elevated DOC concentrations. As MICDOC may underestimate bacterial biomass in the deep sea (see below), the elevated DOC concentrations outside the P-limited area, downstream of the deep water formation site (Figures 3c and 5) may be overestimated in the model.

Comparison between the model results based on net removal rates by Hansell et al. (2012) and the MICDOC results shows excellent agreement (Figure 3c). Both models explain a comparable amount of the overall DOC variability in the reference data set (73% in the model based on net removal rates, 75% in MICDOC with nutrient colimitation), and a very similar overall RMSE (5.7 mmol C m^{-3} in the net removal rate model, 5.4 mmol C m^{-3} in MICDOC). The version with nutrient colimitation also reduces systematic bias compared to the default MICDOC version without nutrient colimitation (Figure S17 in Supporting Information S1).

3.4. Net Removal Rates

Net removal rates were calculated for the MICDOC model and show excellent agreement with those in Hansell et al. (2012) (Figure 4). As we are not calculating the DOC pools separately, a comparison is only possible with respect to the depths or water mass ages given in Hansell et al. (2012). We have therefore followed a three-pronged approach. (a) Net removal rates in the model were calculated by subsampling at locations of observations for exact comparison, (b) by using a model's internal age tracer (ideal water mass age), and (c) net removal rates were calculated from the model's gross rates. Calculated rates for the surface and mesopelagic ocean lie within the same range as those reported in Hansell et al. (2012) (Figure 4, Table S1 in Supporting Information S1). The average net removal rates in MICDOC in the upper ocean, comparable to the semi-labile reactivity fraction, are on average 2.8 μmol C L^{-3} y^{-1}, 0.21–0.35 μmol C L^{-3} y^{-1} for the semi-refractory, and 0.0017–0.01 μmol C L^{-3} y^{-1} for the refractory fractions (Text S3, Figures S21 and S22, Table S1 in Supporting

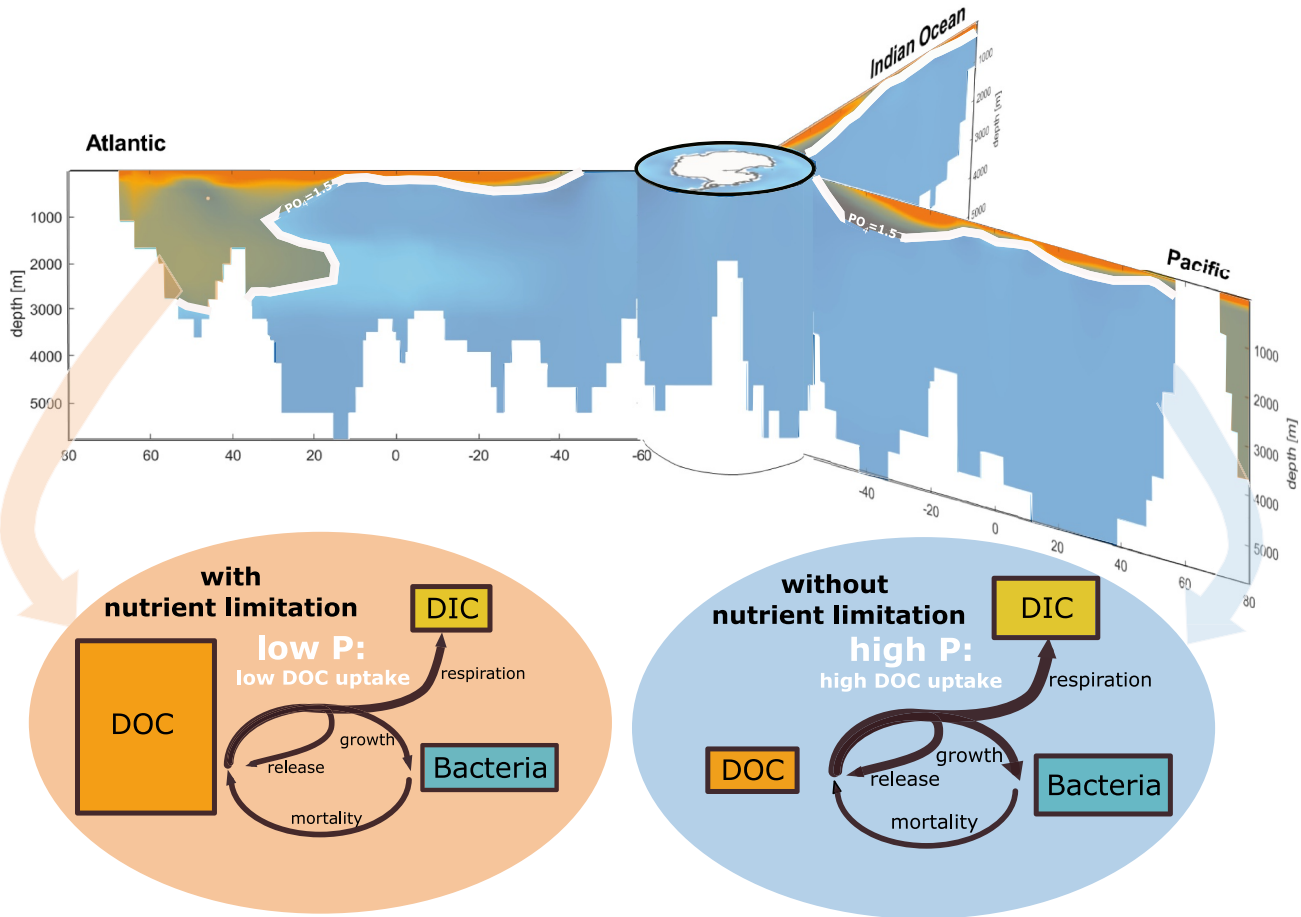

Figure 5. Geography of limitation regimes for DOC uptake by heterotrophic microorganisms. Regions where nutrient limitation decreases DOC uptake and leads to an accumulation of DOC are shaded in orange, and regions where diversity of compounds becomes the limiting factor are shaded in blue. The threshold (=white line) for the limitation regime is set by the trade-off line in Figure 2, that is, here at 1.5 μmol P L^{-1}. The background of figure is DOC concentration as in Figure 3c for MICDOC.

Information S1). Net removal rates of the refractory pool are very sensitive to the reference frame, that is, water mass age or depth. Net removal rates calculated with the model's gross rates result in slightly larger net removal rates, whereas those calculated by relating DOC concentration to water mass age proxies result in slightly lower net removal rates than in Hansell et al. (2012) (Table S1 in Supporting Information S1). While the overall agreement is very good, these deviations also indicate that deep sea microbial processes with respect to DOC are not yet well understood. For example, a systematic difference remains in the very old water mass ages >1,000 radiocarbon years (Figure S21c in Supporting Information S1), where the MICDOC model converges toward a stable background concentration of ca. 40 μM. Observed values still slightly decline until ca. 35 μM. The background value in MICDOC emerges in the model simulations after microbial properties have been fitted to the surface, indicating that the properties of the deep sea microbial communities are not fully captured by the model. The physiology and metabolic capabilities of deep-sea microbial communities are only beginning to be unraveled (Acinas et al., 2021; Moran, 2015). Deep-sea microbial communities may cope better with molecular diversity than surface communities (Sebastián et al., 2020), which affects parameter n_u/n in MICDOC and potentially enhances DOC degradation in the deep sea. On the other hand, the high pressure in the deep sea reduces microbial activity (Amano et al., 2022), which is also not yet considered in MICDOC, impacting parameter α and reducing DOC uptake rates in the deep sea. Furthermore, abiotic mechanisms such as interactions between DOC and particles (Baltar et al., 2010; Verdugo et al., 2004, 2008) are not yet considered in MICDOC, and might play a relatively larger role in deep waters compared to the surface. Although the overall agreement between modeled and observed DOC is good, some systematic deviations remain that point to additional processes governing the DOC distribution in the deep sea.

The constant recycling of carbon compounds is in line with the high radiocarbon age observed for DOC, as has been shown with the detailed network model that MICDOC is based on (Mentges et al., 2019). In the bulk model, however, it is not possible to resolve the spectrum of uptake of individual compounds that leads to the old radiocarbon age. Hence, no age information can be obtained. The concentration and ^{14}C profiles of DOC in the global ocean provide evidence of the presence of a variable amount of young, semi-labile DOM cycling primarily in the upper ocean (<1,000 m). This occurs alongside a widespread background of old, refractory DOC (Druffel & Griffin, 2015; Loh et al., 2004; Walker et al., 2016). But also in the deep ocean, there is isotopic diversity in DOC, indicating various sources and cycling times. While some components are modern, others surpass 10,000 years in age (Follett et al., 2014). Consequently, even the seemingly long-lasting "refractory" DOM in the deep ocean exhibits diversity and undergoes active cycling. Our model is in line with these results, as MICDOC—in contrast to most prescribed reactivity models—considers deep sea DOC as a steady-state concentration with ongoing production, recycling and consumption.

The results are also in line with the microbial carbon pump concept, which states that microbial processes enhance the stability of DOM (Jiao et al., 2011). The underlying rationale in MICDOC is the diversification of compounds by microorganisms that lowers the concentration of individual substrates and therefore decreases the uptake rate, which is formulated in detail in the interaction network model by Mentges et al. (2019) and represented here in the apparent growth rate (see Section 2).

3.5. Uncertainties in MICDOC

While the MICDOC model achieves good agreement with observations on the same order of magnitude as net removal rate models with prescribed reactivities, large uncertainties inherent to the simplifications of a global model approach remain. In 10 additional sensitivity simulations, we have altered the parameters for the nutrient trade-off line, that is, slope and intercept in Figure 2b (a and b in Equation 4), randomly by 25% using a Latin-Hypercube sampling design. The modeled DOC concentrations are most sensitive toward the y-intercept of the nutrient trade-off line (b in Equation 4) (Figures S19 and S20 in Supporting Information S1). Error metrics, that is, slope of the 1:1 line and RMSE, decrease for changes in parameter values for both a and b, indicating the robustness of the fit obtained in this study.

While the model allows for the conclusion that DOC uptake is limited by nutrients other than carbon in the surface ocean, it does not allow conclusions on the nature of this limitation. The host model simulates a static stoichiometric ratio, as typical for Earth System Models of Intermediate Complexity. Hence, we cannot differentiate whether organic or inorganic forms of N or P, or other co-limitations, are limiting DOC uptake, as they covariate at basin scales. For example, experiments show that iron can be limiting for bacterial growth in the surface ocean (Church et al., 2000) and potentially in the mesopelagic (Baltar et al., 2018), although a global modeling study found it to be not the main limiting factor (Pham et al., 2022). Similarly, community-aspects of co-limitations have not been included here (Bannon et al., 2022). Global models intentionally generalize and simplify, and assessing such microbial community effects on global scales using Earth System Models is currently out of reach, because the huge diversity of compounds and microorganisms still poses a huge challenge to models, and heterotrophic microorganisms are usually not even included. With our model here, we are paving the way toward such studies by implementing a trait-based modeling approach for heterotrophic microorganisms. In addition, this approach presents a way to cope with diversity by applying an aggregated version of a complex-system's approach (the original model by Mentges et al. (2019)).

3.6. Modeled Bulk Picoheterotrophic Biomass

The model reproduces picoheterotroph biomass of a reference data set in the range of 0.1–3.7 mmol C m^{-3} at the surface (Figure S23 in Supporting Information S1), as well as the overall gradient of biomass declining with water depth, but moderately underestimates bacterial biomass in the deep ocean (Figure S24 in Supporting Information S1). Although the simulated biomass range agrees well with observations, the spatial variation at the surface is not well reproduced (Figure S23 in Supporting Information S1). This mismatch is not surprising given the higher spatiotemporal variability for picoheterotrophic biomass compared with DOC. However, biomass impacts the local steady-state DOC concentration only marginally (Equation 5), which depends more on the functional traits of the microbial communities than on their actual biomass. It is important to note that observations on bacterial biomass in the deep ocean are scarce and have large inherent uncertainties: First, often not bacterial

biomass but bacterial cell counts are collected in the reference database and converted with constant conversion factors to biomass (Buitenhuis et al., 2012). These conversion factors are a major source of uncertainty, ranging by orders of magnitude for the sea surface (Buitenhuis et al., 2012). With increasing energy limitation with depth, we expect bacteria to become smaller with depth, similar to the gradient of coastal to open ocean for which cell carbon content decreases (Buitenhuis et al., 2012). Therefore, the reported biomass in the deep sea may be an overestimation when converted with the same conversion factor from cell numbers to biomass. Second, the measured bacterial abundance includes all bacterial cells, whether viable or in a dormant state. Our model represents only the active bacterial biomass. Third, chemoautotrophic organisms are included in the reference data set but not in our model. In conclusion, our modeled biomass concentrations are well within the range of uncertainties, although this range is currently very large due to the lack of empirical data (Figure S24 in Supporting Information S1).

4. Conclusions

The MICDOC model provides a plausible explanation for observed DOC concentration patterns in the global ocean without prescribing reactivities to DOC fractions a priori. The model is in line with widespread experimental evidence of macronutrient limitation of the heterotrophic microbial community. As such, it reconciles the millennial-scale net degradation rates with short-term microbial turnover times of the order of days, and provides a mechanistic underpinning of the previously established net removal rates of bulk DOC. No previous model with an explicit representation of microbial consumers has managed to reproduce the observed patterns of DOC (Anderson et al., 2015; Bendtsen et al., 2002; Hasumi & Nagata, 2014; Yamanaka & Tajika, 1997). The novelty here lies in the quantitative basin-scale synthesis of previous experimental evidence. The relevance of these results concerns the time scales of changes to the DOC inventory: If the short microbial turn-over underpins millennial net removal rates, the DOC inventory would be much less sluggish than previously thought, and would react faster to climate change.

These results have two major implications: First, the good agreement between observations and our model suggests that the dilution hypotheses together with environmental controls are plausible to explain present-day bulk DOC concentration patterns as models reflecting intrinsic recalcitrance by prescribing reactivity classes. Second, if the mechanism presented here dominates, the underlying processes of DOC removal would act on much shorter time scales, making the DOC pool much more variable than previously thought. The net removal is on the millennial scale, but we show that this is likely a result of production and consumption processes on shorter time scales. While millennial net removal rates accurately reproduce concentrations as observed at present, the DOC concentration in the ocean effectively reflects a steady-state concentration through which carbon is constantly cycled. The fate of the DOC pool in the face of climate change depends on these short-term gross rates. The mechanisms that underpin the concentration patterns that, in turn, suggest millennial scale net removal rates in MICDOC are (a) carbon limitation by dilution in most of the deep ocean and (b) macronutrient colimitation at the surface that results in the intrusion of elevated DOC concentrations upon deep water formation in the Atlantic.

These results have immediate consequences for projected changes in the DOC inventory in future climate scenarios. Using the MICDOC approach, we can isolate the regional relevance of the immediate nutrient limitation (i.e., environmental stability hypothesis, Dittmar, 2015) from the carbon limited part (Figure 5). The intersection of the colimitation trade-off line with 1 (Figure 2b) represents the regime shift from macronutrient-colimitation to pure carbon limitation. By optimizing the slope and intercept of the trade-off line to observed DOC concentrations in the global surface ocean, we found that this shift occurs around a phosphate concentration of 1.5 μmol L^{-1}. Applying this threshold to the modeled phosphate concentration allows to assess the geography of limitations of DOC uptake (Figure 5). Our results allow the separation of two regimes, that is, the macronutrient controlled regime at the surface, extending to greater depths in subtropical gyres, and reaching the surface at the Southern Ocean Front. This pattern holds major implications for future scenarios. With ongoing warming and enhanced stratification of the surface ocean, nutrient concentrations in the surface ocean are projected to decline in the future (Polovina et al., 2008). Our results suggest that with an increase in oligotrophic regions, more DOC is accumulated in the surface ocean, as its uptake by the heterotrophic microbial community decreases. The time scale and magnitude of this effect remain to be quantitatively assessed, but equilibrium between local DOC concentrations and microbial properties in this model is reached on the order of years rather than millennia.

In the remaining part of the ocean (83%), microbial DOC uptake is limited by carbon. At this stage, we cannot differentiate between the mechanisms of intrinsic stability and dilution. Two distinct modeling approaches, the process-oriented MICDOC model and the prescribed reactivity class models both achieve comparably good agreement with observations (Figure 3). In MICDOC, macronutrient co-limitation shapes the surface patterns that then enter the deep ocean in deep-water formation regions. The reason for millennial-scale persistence in the deep ocean cannot be conclusively confirmed via this model, although we can show that implementing the dilution mechanism does lead to plausible concentration patterns, as does the prescribed reactivity implementation. While both mechanisms are not mutually exclusive, they have different implications for the fate of the future DOC inventory (Dittmar et al., 2021). Our results underline the importance of understanding their relative roles.

A major difference in the implications for the two mechanisms is the time scales of potential changes to the DOC inventory size. Net removal rate models suggest a rather sluggish DOC pool, in which DOC fractions have lifetimes of hundreds up to ten thousands of years (Hansell et al., 2012). Explicitly considering microbial consumers with turnover times of days emphasizes the potential for changes of the DOC pool on much shorter time scales, suggesting significant fluctuations of the global DOC pool on short time scales. Equation 5 shows that the equilibrium DOC concentration is controlled mainly by the properties of the heterotrophic microbial community, which reacts quickly to changes in environmental conditions (Fuhrman et al., 2006). The exact time scales of change in the marine DOC inventory under explicit consideration of microbial consumption remain to be tested. Although bacterial abundance in the deep sea is low and is therefore limiting DOC degradation rates, our results indicate that changes in DOC degradation rates may occur on shorter time scales than the net removal rates with 16,000 years lifetime. Significant changes in physicochemical conditions in the deep sea are already underway and are expected to increase in the future (Levin & Bris, 2015). The different expected changes that depend on the stabilization mechanism of DOC call for a continuing development of process-oriented models for DOC and understanding the relative roles of DOM stabilization mechanisms. Further observational constraints on for example, modeling the age and composition of the DOC pool as well as additional knowledge on microbial functional traits in the deep sea, would be needed to achieve progress in this regard. For example, stoichiometric constraints in light of newly available data sets (Liang et al., 2023) could help to further narrow down the extent and nature of the limitation of DOC uptake and the interplay of organic carbon, nitrogen and phosphorus pools. With MICDOC, we provide a platform in which such processes can be included once new information on deep sea microorganisms becomes available.

In summary, we present a new model that explains observed patterns of DOC purely by microbial interactions with DOC, namely accumulation in subtropical gyres, declining concentrations along the overturning circulation as well as a relatively stable deep-sea concentration. The main environmental driver behind present-day spatial distributions of DOC in the surface ocean appears to be the availability of macronutrients to the heterotrophic microbial community, which hampers DOC uptake. MICDOC is based on the state of knowledge on microbial physiology, which is mainly derived from culture experiments and observations from the contemporary ocean. We are only just beginning to understand the impact of warming, acidification and deoxygenation on the capacity of microbial communities to degrade and transform organic carbon. To understand the combined effect of multiple environmental controls that may have counteracting effects on DOC production and consumption (Legendre et al., 2015), further development of the heterotrophic component in global models is crucial. By explicitly implementing microbial traits in our model, we provide the first mechanistic groundwork for assessing global fluctuations of the global DOC reservoir related to changes in microbial physiology and ecology in a future ocean.

Data Availability Statement

Model output and code for the MICDOC model are publicly available under https://doi.org/10.5281/zenodo.10407919 (Lennartz et al., 2024).

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