There and back again, an organic carbon journey: mapping pathways and loops

Maike Iris Esther Scheffold[1] and Inga Hense[1]

[1]Institute of Marine Ecosystem and Fishery Science, Center for Earth System Research and Sustainability, University of Hamburg, Hamburg, Germany

Correspondence: Maike Iris Esther Scheffold (maike.scheffold@uni-hamburg.de)

Abstract. Understanding and determining where organic carbon (OC) ends up in the ocean and how long it remains there is one of the most pressing tasks of our time, as the fate of OC in the ocean links to the climate system. To provide an additional tool to accomplish this and other related tasks, we map and conceptualize OC pathways in a qualitative model. The model is complementary to existing concepts of OC processes and pathways which are based mainly on quantifications

5 and observations of current states and dominant processes. Our model, on the contrary, presents general pathway patterns and embedded processes without focusing on dominant processes or pathways or omitting rare ones. By mapping, comparing, and condensing pathways and involved spatial scales, we define three remineralization and two recalcitrant dissolved organic carbon loops that close within the marine systems. Pathways that exit the marine system comprise inorganic atmospheric, OC atmospheric, and long-term sediment loops. With the defined loops and the embedded process options, the model is flexible and

10 can be adapted to different systems, changing understanding or changing mechanisms. As such, it can help tracking pathway changes and assessing the impact of human interventions on pathways, marine ecosystems, and the oceanic organic carbon cycle.

1 Introduction

15 We present a qualitative conceptual model of marine organic carbon (OC) pathways. The model shows general patterns of potential OC pathways that loop within the marine system or exit the system into the deeper sediment or atmosphere. It is the first concept to explicitly resolve pathways and processes alike, without focusing on single dominant processes and fluxes such as the carbon export flux. The congruent and flexible concept facilitates 1) comparing carbon pathways of different marine systems and 2) identifying pathways of OC that close within or leave the marine system. Furthermore, it allows a congruent

20 integration of new findings or changes in OC pathways and processes. In this way, the model can help science and society identifying options and limits of human actions to address the climate emergency and deterioration of nature.

Each OC particle moves along a pathway through marine ecosystems and the OC cycle. An OC particle in the surface ocean can end up in the surface or the deep oceans, be decomposed, or become refractory, to name just a few options. Each pathway is unique in its sequence of processes like sinking and decomposition. There is thus a myriad of pathway options.

25 An all-encompassing description and study of all the different pathway options are therefore neither possible nor meaningful. However, there is a need to understand and model the current and future marine OC dynamics that result from the multitude of these pathways and the human impact on them. Identifying and conceptualizing pathway patterns - the condensed structure of pathways- and involved processes can facilitate this. However, pathway options have not yet been mapped systematically and congruently, nor have general pathway patterns been identified.

30 Most concepts of marine OC dynamics and pathways focus on the OC export to the deep sea and marine sediments through different pumping concepts that describe inter alia the physical transport of OC derived from biota (like the biological gravitational pump (Boyd et al., 2019)), the transport of carbon into and out of specific water layers (e.g. the mixed layer pump (Gardner et al., 1995)) or carbon export via species-specific behaviour (such as the lipid pump (Jónasdóttir et al., 2015)). Commonly, the main research objective is to understand and quantify the efficiency and capacity of these carbon pumps (De La

35 Rocha and Passow, 2007) and the processes (e.g. sinking (De La Rocha and Passow, 2007)), system conditions (like temperature (Cael et al., 2017)) and particle types (separated by e.g. particle size (Fender et al., 2019)) that influence the C export flux to the sediment.

By focusing on C export/ C pumps, the final destination of carbon pathways of interest is predefined as the sediment or deep-sea, and the loss/ attenuation of the pump, which is a deviation from this destination, is only implicitly considered, e.g. by

40 changing the density of sinking particles with depth in some concepts (Turner, 2015). The fate of carbon whose pathway does not end in the sediment or deep ocean, and the return pathways of this carbon to the surface and the involved processes are often not represented with the same level of detail, resolution, or congruence. For instance, Steinberg and Landry (2017) and Cavan et al. (2019) include physical mixing and movements of migrating species as upward transport mechanisms of possible return pathways, by displaying upwards pointing arrows in their graphic concepts, but it remains unclear what is transported upwards.

45 Other studies include loss processes, such as respiration (Anderson and Ducklow, 2001) or remineralization (Boscolo-Galazzo et al., 2018), but without resolving what happens to the products of these processes. Some concepts of carbon pumps and dynamics, such as Sigman and Haug (2004) and Zhang et al. (2018), acknowledge return pathways forming cycles and show them in their graphical representations. However, even these concepts usually address only a selection of possible processes, like upward mixing of DOC and particles (Siegel et al., 2016), or consider these pathways mainly to differentiate how long OC

50 remains in the ocean when comparing different water depths (Sigman and Haug, 2004; Zhang et al., 2018) for example.

Besides the focus on carbon export and pumping, other studies dealing with marine OC focus on the processes and pathways of specific carbon species (e.g. dissolved OC in the microbial pump (Jiao et al., 2010)) and systems (e.g. the twilight zone (Giering et al., 2014)), a selection of species (such as bacteria in the microbial loop (Azam et al., 1994)), and/ or individual processes (e.g. up-mixing (Shen and Benner, 2018)). The current understanding of the significance or dominance of single

55 processes in the respective system drives these foci.

All the above-described concepts are based on quantifications and interpretations and represent our current understanding
of carbon dynamics bound to the system state today and somewhat static. Static in the sense that the concepts represent one
manifestation of, for example, the loss/ attenuation in the pump that implies that this manifestation is generally valid and will
continue to be so. The current state and our understanding of it shine through by the implicit inclusion of concentrations and
60 quantities in the graphical representation. For instance, in Passow and Carlson (2012)), the export arrow becomes thinner with
increasing depth. The thickness carries secondary information about the path. The decreased thickness of the export arrow
implies that the amount of carbon reaching the sediment is very small. While this is true, it is not a conceptual representation
as it already comprises quantification and is not showing unweighted conceptual mechanisms. In addition, the current state is
manifested by focusing on carbon export (as described above) and the (resulting) exclusion of pathways or trophic interactions
65 that are considered unimportant and/ or rare (see e.g. few interactions of higher trophic levels in the concept of Steinberg and
Landry (2017). Thus, existing description of carbon pathways mimics our present viewpoint. However, a conceptual model that
congruently represents the various possible pathways a particle can take without interpretations or quantifications of present-
day systems is missing.

To fill this gap, we propose an additional conceptual model that does not represent specific carbon processes or a single
70 pathway of the OC cycle but general pathway patterns with pathway and process options. Our conceptual model distinguishes
pathway patterns of closed and 'open' OC loops that are generally applicable. We define these general loops by comparing and
condensing similarities of possible pathways of OC in the marine system.

In the following, we describe the qualitative model framework of our concept and how we develop it by asking: 1) what are
the different pathways for an OC particle in marine systems? 2) what are the general pathway patterns that can be condensed?
75 3) what process options do the general pathway patterns include? Answering the first two questions, we obtain an OC pathway
model in its most general state. The last question allows us to specify process options embedded in the pathways, which enhance
the relatability and adaptability of the model to specific ecosystems. We finish by highlighting how our model complements
existing concepts and could benefit research and society.

2 A general conceptual model of the marine organic carbon cycle

2.1 Qualitative model framework

Given that we conceptualize only the OC pathways, inorganic carbon (IC) is only an intermediate step within our concept.
Therefore, we do not resolve carbonate and alkalinity interactions, and we do not display marine carbonate systems such as
coral reefs within our model.

We subdivide OC if the processes or pathways considered are specific to different OC species. In such cases, we distinguish
85 particulate organic carbon (POC), living and non-living OC with sizes larger than 0.7 mm comprising aggregates and marine
snow; dissolved organic carbon (DOC), defined as non-living carbon larger 0.22 mm; and volatile organic compounds (VOCs),
such as dimethylsulfide and methane. In addition, we separately consider recalcitrant DOC (rDOC), defined here as DOC that
is remineralized on time scales between 1.5 and 40,000 years, as opposed to DOC with a turnover time of minutes to weeks

(Hansell 2013). We consider rDOC separately from DOC because rDOC is associated with a different set of processes than
90   more labile forms of DOC and is considered the only form of OC that accumulates in the water column in quantities relevant to
the climate system (Jiao et al., 2010, 2011). We also include dissolved inorganic carbon (DIC). Whilst this DIC pool consists
of various IC species, we do not distinguish them within our model.

In addition, we focus on OC that remains within the marine system – i.e., the water column plus upper sediment that still in-
teracts with the water column. Therefore, we only consider pathways that start as OC within the surface waters, acknowledging
95   that this initial position (Table 1) is an artificial construct since cycles do not start somewhere and marine carbon may originate
from terrestrial runoff, atmospheric deposition, or photosynthesis. As soon as an OC pathway leaves this marine system, either
into the atmosphere or into deeper sediment layers that do not interact with the water column, we no longer consider them
within this model and assign them to "open" loops. These "open" loops close too, but outside our focal marine system.

As long as the particle does not leave the marine system, it is irrelevant for our model how much time the particle spends on
100   the path. As such we are not interested in resolving the time scales of these pathways and do not resolve the accumulation of
OC, standing stocks, in the system. For example, we consider carbon that remains in the standing stock of a whale throughout
its life and is remineralized at the water surface after its death and carbon that is respired by a whale at the water surface
immediately after being consumed as the same pathway. However, we do implicitly include time scales of pathways, since we
consider different spatial scales closely connected to temporal scales (Dickey, 1990).

105   Since this is a qualitative model, we are also not interested in the amount of carbon that passes through the different pathways
or their probabilities. We consider all pathways to being equally possible by assuming that each particle finds the conditions
for each different pathway at the same time. That is, our system can provide the necessary processes and conditions for each
path, i.e. our system provides suitable consumers that reduce sinking of material and at the same time a delay of consumers
that favours sinking.

2.2   What are the different pathways for an organic carbon particle in marine systems?

Our conceptual model bases on the comparison and condensation of possible OC pathways using state-of-the-art knowledge.
To this end, we establish a base pathway model derived from a non-exclusive literature review (later accessible on Pangaea and
now added as a supplement). In this base model, we collect and map the different pathways an OC particle can "go" within the
marine carbon cycle. Each pathway is defined by the *sequence of its processes* (Table 1) and leads either to the sediment, the
115   atmosphere, or back to the initial position in the surface water. The comprehensive representation in the base model enables
the identification of pathways with the same destination (e.g. the atmosphere), the comparison of their sequences of processes,
and the condensation of the similarities in terms of destination and sequence into definitions of the general patterns of the OC
cycle.

2.3   What are the general pathway patterns that can be condensed?

120   To illustrate how to condense and define these general patterns, we use a city with a sandbank beach separated by a lagoon
as an example. People regularly visit the sandbank to spend their evenings on the beach (under the given hygiene conditions,

Ocean Science
Discussions

of course). A street map of the city, comparable to our base pathway model, shows 100 different pathways that all end at the beach. The pathways differ or resemble each other to some extent, but are all different comparing the whole sequence of processes, the streets used. However, there is one denominator that all the pathways have in common. It is essential to cross

125 the lagoon to reach the beach. If the crossing is not possible, no one will arrive at the beach. All pathways depend on this part, being also the minimum (simplest) path, the bottleneck

Analogous to this example, we use the base pathway model to identify critical parts of the mapped pathways. We start by identifying all pathways that form a loop and end in the initial position in the surface layer. By comparing their sequences of processes, we identify critical parts, critical path segments, of these pathways. We define a path segment as the *condensed*

130 *function of the involved processes, which have the same general functionality*, although they may differ e.g. in their spatiotemporal scales (Table 1). In our lagoon example, "crossing the lagoon", which includes processes like taking a public ferry or a private boat, is the condensed function and critical path segment of pathways leading to the sandbank. Most pathways have not one but several critical path segments. We, therefore, describe pathways by a sequence of critical path segments. To stay with the example of the lagoon: The pathways people take to get to the sandbank and from there back home can be minimally

135 described as the sequence of two critical path segments - crossing the lagoon in one direction and crossing the lagoon in the other direction.

For the OC cycle, we identify six critical path segments necessary to define the minimal sequences of all closed OC pathways in our model (Figure 1): OC position change (A), Formation of rDOC (B), rDOC conversion to more labile DOC (C), OC remineralization (D), DIC upward position change (E), and DIC uptake by primary producers (F).

140 The path segments do not contain temporal or spatial information. However, the spatial extent of some path segments changes the properties of the pathway and the pathway pattern. To stay with the lagoon example: The public ferry has two anchor points on the sandbank. It takes twice as long to get to the second stop. After work, during the week, people will use the closer anchor point, while at the weekend, both anchor points will be used, following personal preferences. Since people do not regularly go to the second anchor point during the week, bars at the second anchor point only open at the weekend. Thus, the way people

145 distribute, the opening hours of local restaurants, and what governs the decision, temporal considerations during the week versus preferences at the weekend, change. The path segment "crossing the lagoon" or the process "taking the public ferry" do not allow this differentiation. The same applies to the carbon path segments. For example, whether the OC ends up in the sediment or the water column changes its ecosystem function (e.g. as a food source for benthic organisms), the conditions that determine its pathway (e.g. bioturbation), and the time it takes for the carbon to return to the surface layer (e.g. years versus

150 decades). However, the OC position change segment (A) does not resolve whether the transport ends in the water column or the sediment.

Table 1. Definitions and examples of all relevant terms. The focus is on closed loops.

Term	Definition	Example
Initial position	Abstract start position of the OC pathways.	OC in the surface
Process	A self-contained change in the properties or position of carbon. A process is embedded in a path segment.	Bacterial remineralization
Path segment	The condensed function of processes that have the same general functionality. They are defined by the outcome of the processes, independent of species involved, etc.	Processes: Bacterial remineralization, Fish respiration Path segment: OC remineralization (transformation from OC to IC)
Pathway	A sequence of processes or path segments returning OC to its initial position or leading outside the marine system. A pathway is embedded in a loop.	Sequence of processes: Phytoplankton DOC exudation, Bacterial remineralization, Mixing by autumn storm, Uptake by phytoplankton Sequence of path segments: OC size change, OC remineralization, DIC position change, DIC uptake by primary producers
Space	Spatially bounded volumes with very different environmental conditions.	Surface layer space (SLS)
Closed loop	A closed loop comprises all pathways returning to the initial position. It can be described by the sequence of critical (and optional) path segments and the involved spaces. Sequences of critical path segments describing a loop must be true for all pathways of that loop. Optional path segments comprise processes that are not required to produce a certain outcome. A closed loop is a pathway pattern and is embedded in the OC cycle.	Pathway 1: Phytoplankton DOC exudation, Bacterial remineralization, Mixing by autumn storm, Uptake by phytoplankton for photosynthesis Pathway 2: Zooplankton grazing on phytoplankton, Fish feeding on zooplankton, Fish respiration providing IC, Uptake by macrophytes for photosynthesis *Sequence of critical path segments plus space*: OC remineralization (SLS), DIC uptake by primary producers (SLS) Closed loop: Surface remineralization loop
Open loop	An open loop comprises all pathways that lead outside the marine system.	Open loop: Atmospheric IC loop
Process options	All globally applicable processes embedded in a path segment.	Path segment: OC remineralization Process options: Respiration by primary producers, Bacterial remineralization, POC consumer remineralization, Photoremineralization

| Pathway pattern | Pathway patterns are open and closed loops that can be defined based on differences and commonalities of involved pathways. | Closed and "open" loops, e.g. remineralization and rDOC loops |
| Marine OC cycle | The marine OC cycle consists of all loops (pathway patterns) that close within the marine system. | The combination of closed remineralization and rDOC loops. |

Therefore, we add spatial information by defining four spaces, spatially bounded volumes with distinctly different environmental conditions and processes (Table 1). Following general considerations of ocean layers, the surface space (SLS) encounters sufficient light to support photosynthesizing organisms and primary production. Seasonal and continuous mixing counteract material loss and keep matter near remineralisers. The water column space (WCS), below the well-mixed layer, encounters less frequent, slower, or very rare mixing, depending beside other things on the water depth (DeVries et al., 2012). Matter needs more time to reach the surface again and can escape remineralisers due to changing positions or its refractory or degraded character (Baker et al., 2017). In the upper sedimentary space (USS), remineralisers remineralize even highly degraded matter as it remains in their vicinity longer than in the water column (Middelburg, 2019). The lower sedimentation space (LSS) is mostly abiotic and undisturbed and allows lithification processes. Users of the model can modify the spaces, e.g. by partitioning the water column space. However, any coastal system must be represented by at least two spaces (SLS and USS), and pelagic marine systems by at least three spaces (SLS, WCS and USS).

We now define five closed OC loops (Figure 1 and Table 2) by their unique combinations of 1) their sequences of critical path segments and 2) the involved spaces.

The first set of loops comprise three remineralization loops: a surface remineralization loop (SRL), a water column remineralization loop (WCRL), and an upper sediment remineralization loop (USRL) (Table 2). All three loops include pathways on which OC is remineralized to DIC (path segment D), which is taken up by primary producers in the SLS (F). The path segments "OC position change" (A) and "DIC upward position change" (E) as well as the space in which the OC is remineralized distinguish the remineralization loops. The WCRL includes pathways that lead to a downward position change of OC into the WCS, remineralization in the WCS, and an upward position change of DIC into the SLS, where it is taken up. An exemplary WCRL pathway involves OC uptake by zooplankton in the SLS, its migration into and respiration in the WCS, and the upward mixing of the resulting DIC into the SLS where it is taken up by primary producers. If zooplankton respiration occurs in the SLS, the pathway belongs to the SRL. We define the USRL analogous to the WCRL, but with remineralization taking place in the USS.

The two path segments "Formation of rDOC" (B) and "rDOC conversion to more labile DOC" (C) in the SLS are part of the second set of closed loops, the rDOC loops (Figure 1 and Table 2). The rDOC loops describe the change of labile OC to more recalcitrant forms, its persistence in the system, and its return to bioavailable forms in the SLS. We differentiate a short rDOC loop (SrDOCL), rDOC that accumulates in the surface waters on time scales of human life, and a long-term rDOC loop (LrDOCL), rDOC that persists in the entire water column for magnitudes longer than human life scales. The short-term rDOC loop is defined by the "Formation of rDOC" (B) and "rDOC conversion to more labile DOC" (C) in the SLS, while the rDOC
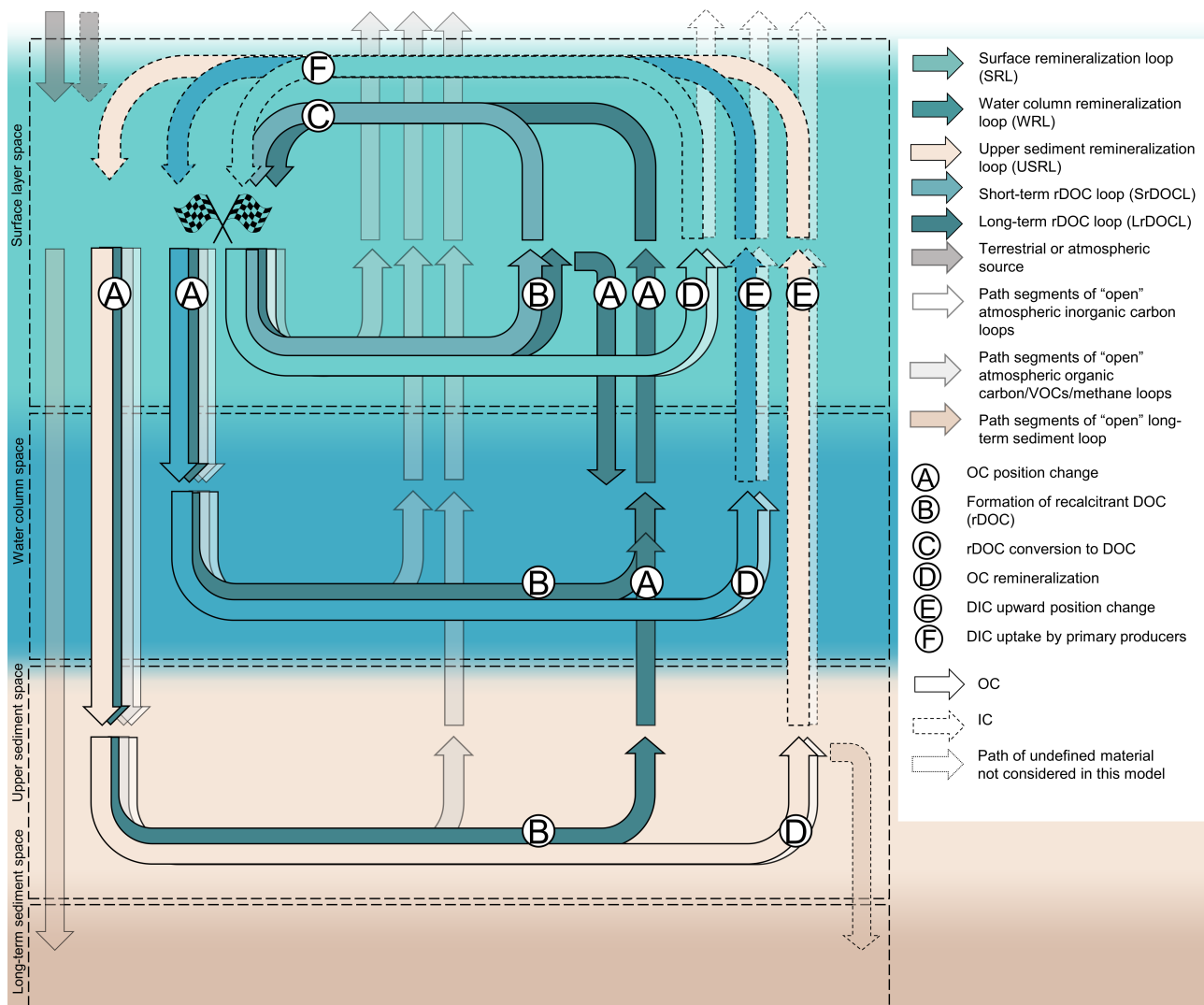
Figure 1. General pathway patterns of OC cycling with three closed remineralization and two closed rDOC loops, the spaces and the involved critical path segments. "Open" loops are only displayed with transparent colours as they are not our focus.

long-term loop additionally comprises the path segment "OC position change" (A), with accumulation mostly or even entirely in the WCS (Figure 1). In contrast to the remineralization pathways, we do not explicitly consider a rDOC loop in the upper

185   sediment, as the temporal scales of rDOC produced there or in the water column overlap to our knowledge. Therefore, the long-term rDOC loop includes rDOC production in the USS alongside its transport to the WCS.

All loops include a continuum of processes that are optional and thus belong to non-critical path segments. Optional path segments do not change the outcome but can still alter the spatiotemporal scales of the pattern. For example, the SRL includes carbon that is remineralized and taken up by primary producers in the SLS. This definition ultimately means that OC, which is

Ocean Science
Discussions

190　transported and processed below the SLS but returned to the SLS as OC to be remineralized and taken up, is also part of the surface remineralization loop. Another example is rDOC, which is part of the WCS remineralization loop if remineralized in the WCS. Only rDOC that reaches the surface and is converted back to more bioavailable forms belongs to the LrDOCL. Because of the climatic importance of rDOC, we distinguish rDOC from DOC as described in the model framework. Technically, however, rDOC represents an intermediate "storage" step of remineralization or open loops.

195　　　Users of the model can freely combine optional path segments along the sequence of critical path segments. However, two separation rules apply to avoid double-counting. The first rule states that the space of the last remineralization before entry and reuse in the SLS defines the remineralization loop. OC that is remineralized several times in different spaces is part of the SRL if remineralized in the SLS the last time before uptake by primary producers in the SLS. Analogous, OC belongs to the WCRL or USRL if it is ultimately remineralized in the WCS or USS. The second rule states that rDOC leaving the surface or

200　produced below the SLS always belongs to the LrDOCL (Table 2).

Table 2. Summary of sequences of critical path segments and spaces defining the closed loops. The separation rule only comes to play, if optional path segments are added, see description of the separation rules. Bold spaces are the major spaces of this loop. Non-bold spaces are intermediate or "walk-through" spaces. Loops: Surface remineralization loop (SRL), Water column remineralization loop (WCRL), Upper sediment remineralization loop (USRL), short and long-term rDOC loop (SrDOCL, LrDOCL). Spaces: Surface layer space (SLS), Water column space (WCS) and Upper sediment space (USS). Path segments: OC position change (A), Formation of rDOC (B), rDOC conversion to more labile DOC (C), OC remineralization (D), DIC upward position change (E) and DIC uptake by primary producers (F).

Closed Loops	Sequence of critical path segments	Involved spaces	Separation rule
SRL	D, F	**SLS**	Ultimate remineralization in SLS before F
WCRL	A, D, E, F	SLS, **WCS**	Ultimate remineralization in WCS before E and F
USRL	A, D, E, F	SLS, WCS, **USS**	Ultimate remineralization in USS before E and F
SrDOCL	B, C	**SLS**	Formation of rDOC in SLS and no A
LrDOCL	B, A, A, C or A, B, A, C	SLS, WCS, **USS**	Formation of rDOC in SLS with A or Formation of rDOC in WCS or USS

　　　Although we focus on the closed loops, it is noteworthy that there are parallel "open" loops of carbon that close outside the marine systems, e.g. in the atmosphere. There are three open-loop patterns. The open IC atmosphere loops describe the outgassing of DIC, produced in different spaces, to the atmosphere. The open OC atmospheric loops comprise the exit of marine OC, marine aerosols, volatile organic compounds (VOCs), and methane through the surface, e.g. via fish predation by

205　birds or outgassing. The open long-term sediment loop describes the burial and lithification of carbon in the LSS, entering geological cycling.

Ocean Science
Discussions

EGU

2.4 What process options do general pathway patterns comprise?

The general pathway patterns, e.g. closed loops, do not resolve processes or involved agents (organisms, OC species, etc.). We add this information in this section and describe global process options embedded in each path segment (Figure 2 and Table 3). This addition allows applying the model to smaller-scale ecosystems, relating existing concepts to our concept, and demonstrates how to add different processes and agents to the model. Global in this context means that the process mechanisms are globally valid but that the frequency, extent, initialization, and agents driving these processes differ. We focus on non-anthropogenic processes and critical path segments.

Two of three remineralization loops include path segments related to the position change of OC or IC. Processes that belong to the path segments A and E are either biotic or abiotic and comprise sinking, diffusion, and advection as well as direct and indirect biota-induced position change (Figure 2 and Table 3).

Particulate matter that sinks from one space in the water column into another is mostly large or dense and/ or escapes consumption or dissolution in the upper space (De La Rocha, 2006). Burial by subsequent matter is the analogous process within the sediment-water interface and the sediment. Matter is buried and compacted by weight deposited above it and "sinks" as it loses volume. Sinking is always downward directed (Boyd et al., 2019) and restricted to POC. Gravitational induced sinking (and burial) is thus part of each downward-pointing path segment A of POC (Figure 2 and Table 3).

DOC and DIC can diffuse in every direction following large or small-scale gradients in the water column, water-sediment boundary layer, and pore-waters in the sediment. We use present-day decreasing DOC concentrations with water depth (Hansell, 2013), higher sedimentary DOC concentrations compared to overlying waters (Burdige et al., 1999), and higher DIC concentrations at the surface compared to the deep sea (Oka, 2020). Hence, DOC diffuses downwards in the water column and upwards within and from the sediment since consumption cannot cope with production (Rowe and Deming, 2011) (path segments A, E in Figure 2). DIC diffuses upwards in A and E (Figure 2).

Other physically induced position changes are related to water or sediment mass movements based on advection. These include large-scale upwelling and downwelling patterns, seasonal mixing, wind-induced turbulence and eddies, and storm-induced resuspension. Advection is globally applicable although its direction, magnitude, and frequency vary. The advection-induced position change occurs in all path segments A and E (Figure 2). Advection does not act downwards into the sediment but upwards in the form of resuspension. Resuspension is limited to the upper part of the sediment, as physical perturbation do not commonly reach below 10 cm (Boudreau, 1998; Bunke et al., 2019).

Biota-induced position changes involve the direct transport of OC in the living tissue of migrating organisms (e.g. a fish feeds in the SLS, migrates down, and dies in the WCS) as well as the internal flux of OC in organisms that span different spaces (e.g. macrophytes (Middelburg, 2019) living in the SLS and the USS). Organisms change their position in the water column (e.g. via diel vertical migration (Steinberg et al., 2002)) or in the sediment (e.g. via burrowing (Middelburg, 2019)) and produce faecal pellets or die after the position change. The result of direct biota-induced position change is POC of all sizes, e.g. living organisms and roots, faeces, and carcasses. Direct biota-induced position change works in all directions and is involved in all critical path segments A of POC (Figure 2).

Indirect biota-induced position change comprises biogenic turbulence (Kunze et al., 2006; Huntley and Zhou, 2004), and induced drift, which describes the transport of substances that adhere to the bodies of swimming organisms (Katija and Dabiri, 2009). Indirect biota-induced position change in the sediment is related to inter alia bioturbation (Berke, 2010), associated with sediment reworking and resuspension, and bioirrigation (Kristensen et al., 2012), which leads to inflows of ocean water into

245 the sediment. Indirect biota-induced position change works in all directions and is involved in all critical path segments A and E for (r)DOC and POC in the water column and the sediment (Figure 2).

The next group of processes belongs to the path segment remineralization of OC (D). We define remineralization as the provision of DIC based on OC and restrict it to the spaces above the LSS, assuming that remineralization in the LSS is negligible.

250 Bacteria and archaea remineralize DOC in path segment D in every space above LSS (all path segments D of DOC, Figure 2), also under different oxygen conditions. The DOC is either of allochthonous origin (e.g. entering via riverine input (Dai et al., 2012)), or of autochthonous origin based on living or non-living POC. For instance, POC dissolves while sinking (Carlson and Hansell, 2015)), is fragmented by turbulence (Ruiz, 1997; Briggs et al., 2020), or photodissolved (Mayer et al., 2006). Consumers directly reduce the size of organic POC by sloppy feeding on living and non-living POC (e.g. zooplankton

255 coprorhexy (Lampitt et al., 1990)), by producing small metabolites, and/ or by excreting DOC (Lampert, 1978). Indirectly, consumers fragment non-living POC by swimming or moving (Dilling and Alldredge, 2000). Further, primary producer exudate DOC in the water column (e.g. under nutrient-limited conditions or through viral lysis (Azam and Malfatti, 2007)) and in the sediment (by macrophytes (Duarte and Cebrián, 1996)). Bacteria, for their part, hydrolyse POC to DOC (Smith et al., 1992) and additionally release DOC by viral lysis (Middelboe et al., 1996). The conversion from POC to DOC (arrows from POC to

260 DOC, Figure 2) that occur before bacterial remineralization are optional path segments since not all OC needs to undergo one of these changes to be remineralized.

In addition, bacteria can oxidize VOCs and methane (e.g. shown in Halsey et al. (2017)) (path segment D of VOCs/methane in Figure 2), produced via abiotic (photochemical degradation of DOC (Kieber et al., 1989)) and biogenic processes (e.g. by phytoplankton (Lenhart et al., 2016) or zooplankton in anaerobic areas of their guts (Weber et al., 2019; Schmale et al., 2018)).

265 Another form of remineralization is respiration by living organisms other than bacteria. Primary producers respire in the photic SLS. Macrophytes additionally respire with their roots in the USS at night (Pedersen et al., 1995). Higher trophic levels, POC-consumers (e.g. zooplankton and fish) and non-bacterial DOC consumers (e.g. suspension-feeding sponges at the sediment-water interface (Wooster et al., 2019)), also remineralize by respiring. We, therefore, include remineralization by primary producers in path segments D in the SLS and USS and respiration by POC(DOC)-consumers in all spaces with aerobic

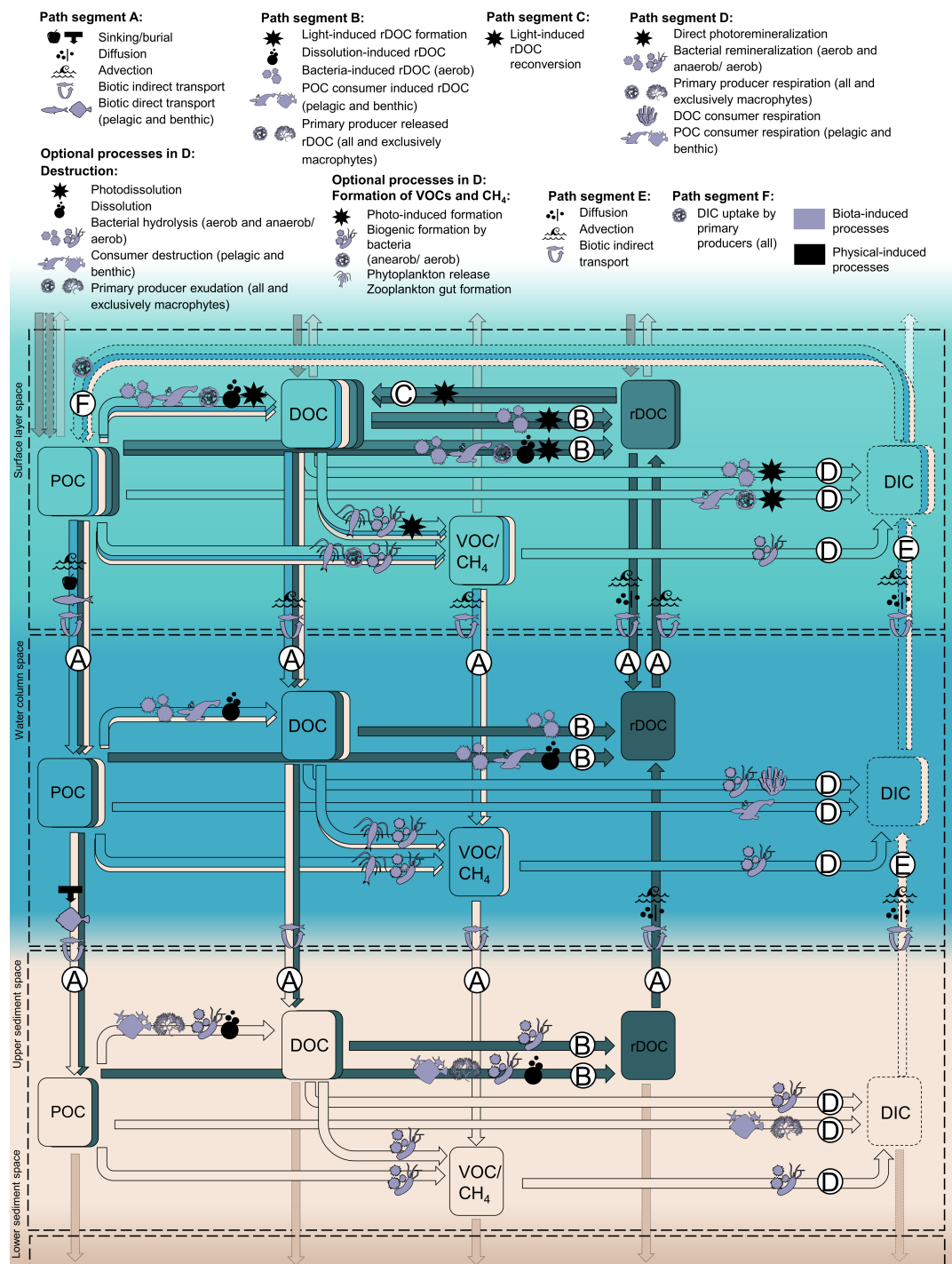270 conditions above the LSS (Figure 2).

Figure 2. OC carbon pathways with critical path segments (A-F), spaces and embedded processes, C species and involved organisms. Open loops are indicated by transparent colours. Organisms can be agents (producing DOC by sloppy feeding) and part of the carbon pool (consumers as part of POC respire DIC) at the same time. Optional fragmentation processes and pathways for DOC and VOCs/methane are included. As such these pathways are not marked with capital letters.

Light-induced photoremineralization, the only physically induced remineralization, directly oxidizes DOC and POC to IC (Mopper and Kieber, 2002; Mayer et al., 2009) and works only in the SLS. We include this process into path segment D in the SLS.

Once OC is remineralized to DIC, this DIC is transported by the above-described processes of position change to the
275 SLS (path segment E). Subsequently, primary producers take up the DIC for photosynthesis (path segment C) and close the remineralization loops.

The rDOC loops include the formation of rDOC (B), the reconversion to DOC in the SLS (C), and, in case of the long-term loop, position change of OC (A). We present some of the involved abiotic and biotic processes, which have been reviewed e.g. in Legendre et al. (2015).

280 Biota supply rDOC via successive microbial processing, successive consumption by higher trophic levels (Jiao et al., 2010, 2011), the release of capsular material by bacteria (Stoderegger and Herndl, 1998), and other reactions of phytoplankton and bacteria described for the DOC production before. Processes of conversion of living and non-living POC to DOC, e.g. via dissolution, can result in highly diluted DOC that is not available for consumption and hence also recalcitrant (Arrieta et al., 2015) (Figure 2, arrow from POC to rDOC). In addition, UV light can change the lability and increase refractory components
285 of the DOC pool (Benner and Biddanda, 1998; Hansell, 2013)(path segment B in the SLS).

rDOC that stays in or returns to the SLS, via the position change processes described above (path segment A), can be converted back to more bioavailable forms by photodegradation/ photooxidation (path segment C in the SLS) (Kieber et al., 1989). We consider other removal processes, such as direct photooxidation from rDOC to DIC (Shen and Benner, 2018), sorption of rDOC into POC (Hansell et al., 2009), and hydrothermal removal mechanisms in hydrothermal vents or the Earth's
290 crust (Lang et al., 2006), as optional path segments of either one of the closed remineralization or open loops. Once the rDOC is converted in the SLS, the rDOC loops are closed.

Ocean Science
Discussions

Table 3. Processes embedded in the critical path segments. Italic C forms are products of the processes. Directions in brackets highlight optional directions that are not part of the minimal sequences of critical path segments.

Organic carbon position change (A)					
Process	**Loops and (spaces)**	**Process description**	**Involved C forms**	**Involved organisms**	**Direction**
Sinking/Burial	WCRL, USRL, LrDOCL (SLS, WCS)	Gravitational sinking	POC		Downwards
	USRL, Lr-DOCL (WCS, USS)	Burial by sinking matter			
Diffusion	LrDOCL (SLS, WCS, USS)	Diffusion in the water column and pore waters	rDOC (DOC)		Downwards, upwards (lateral)
Advection	WCRL, USRL(SLS, WCS)	Large-scale downwelling, seasonal mixing, small-scale turbulence and eddies	POC, DOC, VOCs, methane		Downwards (upwards, lateral)
	LrDOCL (SLS, WCS)		POC, DOC		
	LrDOCL (SLS, WCS, USS)	Large-scale down- and upwelling, seasonal mixing, small-scale turbulence and eddies, physical induced resuspension	rDOC		Downwards upwards, (lateral)
Indirect biota-induced transport	WCRL, USRL (SLS, WCS)	Biota-induced turbulence, induced drift	DOC, VOCs, methane	Swimming and moving species	Downwards (upwards, lateral)
	LrDOCL (SLS, WCS)		DOC		
	USRL (WCS, USS)	Digging, burrowing, bioirrigation, sediment reworking	POC, DOC, VOCs, methane	Moving benthic (-pelagic) and bioturbating species, mammals feeding on benthic species	

Ocean Science
Discussions

EGU

Process	Loops and (spaces)	Process description	Involved C forms	Involved organisms	Direction
	LrDOCL (SLS, WCS)		POC, DOC, rDOC		Downwards, upwards (lateral)

Formation of rDOC (B)

Process	Loops and (spaces)	Process description	Involved C forms	Involved organisms	Direction
Photo-degradation	SRL (SLS)	Degradation of labile to refractory OC by UV light	DOC, POC, *rDOC*		
Dissolution	SRL (SLS) WCRL (WCS) USRL (USS)	Dissolution due to sinking (enhanced by bacteria) or pore-water interactions	POC, *rDOC*		
Bacterial rDOC formation	SRL (SLS) WCRL (WCS) USRL (USS)	Release of capsular material and rDOC under stress conditions	DOC, POC, *rDOC*	Bacteria, viruses	
Primary producer rDOC formation	SRL (SLS)	Release of rDOC (either due to molecule characteristics or dilution)	POC, *rDOC*	Phytoplankton and macrophytes	
	USRL (USS)			Macrophytes' roots	
POC-consumer rDOC formation	SRL (SLS) WCRL (WCS)	Direct (excretion) or indirect release (sloppy feeding) of rDOC (either due to molecule characteristics or dilution)	POC, *rDOC*	POC consumers	
	USRL (USS)			Benthic POC consumers	

Conversion of rDOC to DOC (C)

Process	Loops and (spaces)	Process description	Involved C forms	Involved organisms	Direction
Photooxidation	SRL (SLS)	Photochemical conversion rDOC to DOC	rDOC, *DOC*		

OC remineralization (D)

Process	Loops and (spaces)	Process description	Involved C forms	Involved organisms	Direction
Photo-remineralization	SRL (SLS)	Direct UV remineralization	POC, DOC, *DIC*		
Bacterial remineralization	SRL (SLS) WCRL (WCS) USRL (USS)	Bacterial DOC (VOCs)-based respiration	DOC, VOCs, methane, *DIC*	Bacteria and archaea	

Ocean Science
Discussions

Primary producer remineralization	SRL (SLS)	Respiration of phytoplankton and macrophytes	POC, *DIC*	Phytoplankton and macrophytes	
	USRL (USS)	Respiration of macrophytes		Macrophytes	
POC-consumer remineralization	SRL (SLS) WCRL (WCS)	Respiration of POC consumers	POC, *DIC*	POC consumers	
	USRL (USS)	Respiration of benthic POC consumers		Benthic POC consumers	
DIC upwards position change (E)	WCRL (WCS)	DOC-consumer respiration	DOC, *DIC*	DOC consumers excluding bacteria	
Conversion of rDOC to DOC (C)					
Process	**Loops and (spaces)**	**Process description**	**Involved C forms**	**Involved organisms**	**Direction**
Diffusion	WCRL (SLS, WCS) USRL (SLS, WCS, USS)	Diffusion in the water column and pore waters	DIC		Upwards
Advection	WCRL, USRL (SLS, WCS)	Large-scale down- and up-welling, seasonal mixing, wind-induced turbulence and eddies	DIC		Upwards
	USRL (WCS, USS)	Physical induced resuspension			
Indirect biota-induced transport	WCRL, USRL (SLS, WCS)	Biota-induced turbulence, induced drift	DIC	Swimming and moving species	Upwards
	USRL (WCS, USS)	Digging, burrowing, bioirrigation, sediment reworking and related processes		Moving benthic (-pelagic) species	
DIC uptake by primary producers (F)					
Process	**Loops and (spaces)**	**Process description**	**Involved C forms**	**Involved organisms**	**Direction**
Uptake of DIC	SRL (SLS) WCRL (WCS) USRL (USS)	Photosynthesis	DIC, *POC*	Phytoplankton and macrophytes	

295 3 Discussion and Conclusions

Our qualitative concept of OC cycling is complementary to existing models of OC dynamics and processes in the ocean and resolves general pathway patterns and different process options without assessing the importance or rarity of these.

By not stopping at one process, such as respiration, but showing complete pathways to their end, we illustrate and emphasize the cycling nature of OC dynamics in the ocean. The decoupling of carbon pumping from return pathways in some previous

300   concepts and their graphical representations seems to imply that increased transport of OC into the ocean interior always leads to increased sequestration and storage of atmospheric carbon in the ocean. However, increased export of OC is not necessarily associated with increased carbon storage, which depends, among other things, on the ratio of regenerated and preformed nutrients and on the carbon that escapes the deep ocean (Gnanadesikan and Marinov, 2008). The export of carbon to the sediment and the deep oceans is part of the carbon processing, but not the whole story. Research on and the communication of the

305   potential oceanic carbon sinks necessarily need to consider the return and exit pathways. Our model can help to communicate and acknowledge the cycling nature of OC pathways.

Another add-on of our model is that we refrain from quantification or interpretation and do not indicate dominant pathways or omit rare ones, as our understanding of OC dynamics is constantly changing. Higher trophic levels were previously neglected and are now recognized as relevant to the carbon cycle. For example, large migratory species link to nutrient distribution and

310   overall mixing (Roman and McCarthy, 2010), zooplankton significantly influence the carbon export (Steinberg and Landry, 2017), and fishes and mammals contribute to the carbon cycle through various processes (Martin et al., 2021). In addition, some studies suggest that current models overestimate particle export by underestimating processes that lead to shifts in carbon pools, such as fragmentation (Baker et al., 2017). These ongoing new findings show how short-living and dynamic our understanding of processes and OC pathways is.

315   To account for these changes in understanding, our model provides a conceptual skeleton, an overarching concept that can be brought to life by users. Processes, organisms, pathways, and loops can easily be added, changed, or deleted to accommodate new insights or specific systems. At the same time, existing concepts of OC cycling also fit into our model, e.g. the microbial carbon pump finds its reference in the rDOC loops and the lipid pump in pathways of the WCRL. Overall, this gives our model a high degree of flexibility.

320   This flexibility is necessary since not just our understanding but ocean systems around the globe are changing (Doney et al., 2012). Today's dominant pathway or process may not be dominant tomorrow. For example, the assumption that dense particles predominately sink (e.g. by Le Quere et al. (2005)) is only correct as long as their density-induced sinking is not prevented by default or to a large extent, e.g. by aggregation with microplastics that reduces density and thus sedimentation (Long et al., 2015). Concepts that implicitly or explicitly state that most dense particles sink and only or mainly consider pathways of OC

325   sinking cannot resolve what might happen to the particle instead, for example, when microplastics reduce the sinking of these particles.

In our model, density-induced sinking is only one option among many others. Dense particles can end up in different loops, e.g. in the SRL, staying in the SLS, or the WCRL if transported to deeper water layers by processes other than sinking. Besides these changes in sinking, there are numerous other examples of process changes that have the potential to alter OC cycle

330   pathways, e.g. changes in the phytoplankton community (Vernet et al., 2017), changes in the DOC pool (Lønborg et al., 2020), and depletion of higher trophic levels (Wilmers et al., 2012), to name a few. All of these changes might deconstruct and modify

the pathways of particles. Therefore, the fate of a carbon particle in our model is open. And we present pathway options instead of a selection of dominant ones with a fixed destiny.

How OC moves through the system and where it ends affects the climate system (e.g. via alteration of the biological pump
335 (Barange et al., 2017)), the ecosystem functioning (e.g. via changes in the benthic-pelagic coupling (Griffiths et al., 2017)) but also human well-being and socio-ecological systems (via alterations of the trophic energy flows leading to less productive coastal systems (Ullah et al., 2018)) at all scales. Therefore, there is a societal need to understand today's systems and their possible changes due to anthropogenic interventions under different scenarios.

Our model can serve as a basis for such scenario considerations and assessments of interventions and management strategies
340 in marine ecosystems. Deliberate interventions in OC pathways, like geoengineering, and interventions that incidentally change OC pathways, e.g. fish management strategies, should both be tested for their impact on the different pathways in different systems. For illustration, changes in the food web through fisheries likely alter OC cycling. Our model helps to identify all pathways with involved fishes and invites us to ask: Do changes in fish stocks dry up carbon pathways? Are others taking over? Are there changes in loops? Do these changes differ in different ecosystems? What are the implications for the food web and
345 carbon storage?

Science and society need to find answers to these and many other questions to adapt system-tailored management options, assess the impacts of these options on OC pathways, and identify and evaluate nature-based solutions that are efficient and preserve ocean resources and health for future generations. While our model helps to address these questions and adjust our understanding of the mechanisms of the OC cycle, it needs complementation and extensions.

350 Quantifications of the magnitudes of carbon moving through different pathways in individual ecosystems and qualitative modelling of scenario-based changes in loops and processes need to follow. In particular, to understand whether and how much pathways change due to anthropogenic interventions, our qualitative conceptual model is only a first step. In addition to these methodological next steps, advanced conceptual pathway models need to consider the interactions of alkalinity and solubility with the OC cycle to understand and predict how the OC cycle might change, also in terms of possible consequences for the
355 climate system and the options and barriers that exist for society to alter carbon pathways and adapt to unintended or irreparable changes. Marine ecosystems and the carbon cycle are changing. Just as important, our perception and approaches to address these changes are changing and must adapt even further. We offer a new conceptual model to accommodate these changes, structure them, and make them useful for further research.

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365

Ocean Science
Discussions

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Discussions

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