There and back again, a journey of many pathways: conceptualising the marine organic carbon cycle

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Abstract. Understanding and determining the pathways that organic carbon (OC) takes in the ocean is one of the most pressing tasks of our time, as the fate of OC in the ocean is linked to the climate system and the functionality of marine ecosystems. The multitude and complexity of these pathways are investigated with sophisticated, mainly quantitative methods focusing on individual pathways to resolve their interactions and processes as realistically as possible. In addition to these approaches to

- 5 understand and recreate complexity, there is a need to identify commonalities and differences between individual OC pathways and define their overarching and core structures. Such core structures can provide a framework for the increasing number of sub-concepts, some of which overlap, and promote more structured comparisons and consistent communication, especially between different disciplines. In response, we propose a (visual) concept that defines these structures as higher-level 'pathway patterns'. These pathway patterns are defined by mapping, comparing, and condensing the sequences of processes and spatial
- 10 scales of the marine OC pathways. The result includes the definition of closed-loop patterns, three remineralisation and two recalcitrant dissolved organic carbon loops that close in marine systems, and 'open' loops, condensing pathways leaving the marine system to the atmosphere or deeper sediment layers. In addition, we extend these basic structures (loops) with a synthesis of the underlying processes, pools, and agents. By translating a definition of the biological carbon pump into our pathway patterns, we show how the application and discussion of these patterns facilitate a consistent visualisation, a structured
- 15 comparison of differently resolved concepts and studies, and integration of these in the larger picture of the OC cycle. As a complement to quantitative studies and descriptions of individual pathways, our concept defines new core structures of all OC pathways by decomposing their complexity into basic patterns. These basic patterns provide a skeleton that can be adapted to different systems and filled with life by the users.

1 Introduction

The pathways along which organic carbon (OC) moves through oceanic systems affect not only the climate system (Barange et al., 2017) and ecosystem functioning (Griffiths et al., 2017), but also human well-being and socio-ecological systems (Ullah et al., 2018). Therefore, understanding marine OC pathways and the current and future marine OC dynamics resulting from the multiplicity of these pathways and the human influence on them is an essential and very productive focus of ocean research (Jiao et al., 2018). Studies on marine OC pathways are continuously expanding our understanding of the OC cycle through

25 comprehensive observations and sophisticated numerical models, e.g. by the Joint Global Ocean Flux Study (JGOFS) (Doney and Ducklow, 2006), improved carbon budgets (e.g. by Giering et al. (2014)) and quantitative estimates of the contribution of individual organisms (e.g. in Bianchi et al. (2021)), to name but a few.

Complementing the often-quantitative results, these studies sometimes provide (visual) concepts that abstractly describe and generalise OC pathways as a sequence of processes, higher-level structures or a core mechanism. Due to the multitude of

- 30 disciplines involved, the heterogeneity of marine systems and the complexity of the OC cycle, these concepts have a relatively narrow focus and consider a selection of pathways. For example, some studies conceptualise and generalise pathway structures for specific carbon pools e.g. dissolved OC in the microbial pump (Jiao et al., 2010; Jiao and Zheng, 2011), a selection of species such as bacteria in the microbial loop (Azam et al., 1994) or physical processes of different scales e.g. large-scale or eddy-subduction export (Levy et al., 2013; Omand et al., 2015).
- The different foci and the limited spectrum of the pathways considered lead to concepts that complement each other through different resolutions (focusing on different processes or pools), but also promote partly overlapping sub-concepts. An example is the generalisation of pathways leading to the biota-induced vertical gradient of dissolved inorganic carbon in the oceans, described by the concept of the biological carbon pump (BCP). Several sub-concepts of the BCP have emerged, describing, among other things, the transport of carbon into and out of specific water layers, such as the mixed layer pump (Gardner et al.,
- 40 1995), or carbon export by species-specific behaviour, such as the lipid pump (Jónasdóttir et al., 2015). Recent approaches to further generalise the pump concept by defining its main functions, e.g. particle injection by Boyd et al. (2019), show the need to define structural patterns to make concept such as the BCP more comparable, comprehensive, systematic and adaptable.

It is plausible that studies on individual OC pathways or systems produce specific and small-scale sub-concepts. However, in science, there is an additional need to identify commonalities and to find and define basic unifying structures (Scheiner and Willig, 2011). So far, there has been no attempt to summarise and generalise OC pathways and conceptual ideas into an overarching general concept of the core structures of the marine part of the OC cycle.

Existing concepts, especially those aiming at a more comprehensive representation of the OC cycle, are often not visually congruent within the respective graphics or graphics in other publications. Processes and pathways are not represented with the same level of detail or resolution. For example, Steinberg and Landry (2017), Cavan et al. (2019), Anderson and Ducklow

- 50 (2001) and Boscolo-Galazzo et al. (2018) visually detach some products from the processes that produce them or do not mention the products, such as DIC, in the figures at all. Such illustrations usually work despite these (small) inconsistencies because the aim of such studies is not to create congruent conceptual representations of the OC cycle, and their visualisations are rather tools to highlight their research focus in an overarching picture. However, we would like to emphasise that graphics are a visualisation of the mapper's mental concepts. By deciding what to visualise and at what resolution, and by omitting
- 55 information, parts of this mental concept are obscured, which can make it difficult to understand and use the concepts for studies other than the one for which it was created. Graphics are powerful tools for disseminating information, generalising structures and promoting discussion (Margoluis et al., 2009). Non-congruent graphics do not exploit that full potential.

The lack of an overarching (and congruently visualised) concept of the OC cycle can reduce the transparency of the scientific process and make comparisons and discussions as well as the adaptation of concepts and ideas more difficult (Scheiner 60 and Willig, 2011). Different resolutions and definitions of pathways and pathway structures risk misunderstanding and miscommunication in education (Fortuin et al., 2011), among young but also more experienced researchers or in interdisciplinary communities (Heemskerk et al., 2003) and may foster a growing number of sub-concepts with different resolutions (Scheiner and Willig, 2011), some of which may overlap.

To reduce this risk, we propose to step back from quantitative, specific, and numerically advanced research and to summarise and generalise what is known about the carbon cycle and OC pathways. The result of this step is a general concept that does not represent specific carbon processes or a single pathway but defines the basic and common structures of all pathways as pathway patterns. We define these generalised pathway patterns in linguistic and visual units by comparing and condensing core similarities of possible OC pathways in the marine system. The result is the definition of several pathway patterns of 'closed and open' OC loops that summarise the structure of all pathways that close within the marine system or leave the system into the deeper sediment or atmosphere.

The resulting concept facilitates 1) comparing models and concepts of different resolutions, 2) synthesizing concepts, definitions and scientific languages, 3) adding new scientific knowledge in a congruent and structured way, 4) identifying research gaps and inconsistencies, and 5) placing finite pathways into an overarching framework of the OC cycle. In this way, the concept can help researchers from different disciplines to facilitate research design, discuss individual concepts, and improve

75 interdisciplinary communication, collaboration, and scientific education.

In the following, we describe how we developed our concept based on the questions 1) What are the different pathways for an OC compounds in marine systems? 2) What are the core pathway patterns that can be summarised? 3) Which processes, pools and agents are included in the core pathway patterns? By answering the first two questions, we obtain an OC pathway concept with core structure of marine OC pathways. The last question allows us to identify the processes, pools and agents embedded

80 in these structures, which allow defining smaller-scale pathway patterns that can be adapted to specific research questions and marine systems. In the discussion, we describe as an application example how a definition of BCP can be translated into our concept, and discuss the add-ons of this representation.

2 Concept specifications

Given that we conceptualise only the OC pathways (for a definition of relevant terms of the concept, see Table 1), we do not resolve carbonate and alkalinity interactions, and do not display marine carbonate systems within our concept.

In addition, we focus on OC that remains within the marine system, i.e. the water column plus upper sediment that still interacts with the water column. Therefore, we only consider pathways that start as OC within the surface waters, acknowledging that this initial position (Table 1) is an artificial construct since cycles do not start somewhere and marine carbon may originate from terrestrial run-off, atmospheric deposition, or photosynthesis. As soon as an OC pathway leaves the marine system, either

90 into the atmosphere or into deeper sediment layers that do not interact with the water column, we not detailed describe them within this concept and assign them to 'open' loops. These loops close too, but outside our focal marine system. It is irrelevant for our concept how much time an organic compound spends on the pathway. As such we are not interested in resolving the time scales of pathways and the accumulation of OC, standing stocks, in the system. Thus, it is the same pathway when OC remains in the standing stock of a whale throughout its life and is respired at the surface right before its death and when OC is respired by a whale at the water surface immediately after being consumed. However, we do implicitly include

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We provide a qualitative concept and are not interested in the amount of carbon that passes through the different pathways or the probabilities of OC to do so. We consider all pathways to being equally possible by assuming that each carbon compound finds the conditions for each pathway at the same time. For instance, the system provides suitable consumers that reduce sinking of material and at the same time a spatio-temporal mismatch with consumers that favours sinking.

time scales of pathways, since we consider different spatial scales closely connected to temporal scales (Dickey, 1990).

For identifications of pathway patterns on a higher resolution (Sect. 3.2), we operationally subdivide OC into different pools, if the pathways involve OC of different size, volatility and lability. In such cases, we distinguish particulate organic carbon (POC), embedding living and non-living OC with sizes larger 0.2 μ m (Kharbush et al., 2020), aggregates and marine snow; dissolved organic carbon (DOC), defined as non-living carbon smaller 0.2 μ m (Kharbush et al., 2020); and volatile organic

105 compounds (VOCs), such as dimethyl sulphate and CH₄. In addition, we separately consider recalcitrant (or refractory) DOC (rDOC), defined here as DOC that is remineralised on time scales between 1.5 and 40,000 years for semi-labile to ultra-refractory (Hansell, 2013), as opposed to 0.001 years for labile DOC (Hansell, 2013). We consider rDOC separately from DOC because rDOC 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) as an intermediate pool. Whilst this

110 DIC pool consists of various inorganic (IC) molecules, we do not distinguish them within our concept.

3 A (visual) concept of the marine organic carbon cycle

3.1 Main patterns of the marine organic carbon cycle

Our concept is based on the comparison and condensation of possible OC pathways using state-of-the-art knowledge. To this end, we generate a base pathway concept (see Supplement A) based on a non-systematic literature review. In this base pathway 115 concept, we collect and map the different pathways that an OC compound can "go" within the marine carbon cycle. The different pathways in this concept are defined by *sequences of processes* (Table 1), such as sinking and remineralisation, and head into the sediment, the atmosphere, or back to the initial position in the surface water. We use the base pathway concept to compare the mapped pathways and condense their core structures into generally applicable core patterns of OC pathways.

The core pathway patterns, e.g. closed loops, are stripped of any processes, pools or involved agents (organisms, etc.). We add this information in the next step (Sect. 3.2) allowing a higher resolution of pathway patterns.

Mapped examplePathway 1: Phytoplankton DOC exudation → Bacterial remineralisation → DIC uptake by phytoplanktonpathways in thePathway 2: Zooplankton grazing on phytoplankton → Zooplankton respiration → DIC uptake by macrophytesbase pathway conceptPathway 3: Phytoplankton respiration → DIC outgassing

Term	Definition	Example
Space	Spatially bounded volumes with different environmen-	Surface layer space (SLS), Atmosphere space
	tal conditions.	(AS)
Initial position	Abstract start position of the OC pathways.	OC in the surface space
Process	A self-contained change in the properties or position of	Phytoplankton DOC exudation, Zooplankton
	carbon. A process is embedded in a path segment.	grazing on phytoplankton, Bacterial reminerali-
		sation, Zooplankton respiration, Phytoplankton
		respiration, DIC uptake by phytoplankton, DIC
		uptake by macrophytes, DIC outgassing
Path segment	The condensed function of processes that have the same	OC size change, POC consumption, OC rem-
	general functionality. They are defined by the abstracted	ineralisation, DIC uptake by primary producers,
	result of the processes, independent of species involved,	DIC exit
	etc. Path segment comprise all globally applicable pro-	
	cesses having the same general functionality.	
Pathway	A sequence of processes or path segments. Each path-	Pathway 1: OC size change \rightarrow OC reminerali-
	way is embedded in a pathway pattern.	sation \rightarrow DIC uptake by primary producers
	Although pathways can be described by sequences of	Pathway 2: POC consumption \rightarrow OC reminer-
	general path segments, they always represent individual	alisation \rightarrow DIC uptake by primary producers
	structures and not condensed ones.	Pathway 3: OC remineralisation \rightarrow DIC exit
Pathway patterns	Pathway patterns are superordinate structures of path-	Pathway pattern 1: OC remineralisation [SLS]
	ways. They are defined by the sequence of critical path	\rightarrow DIC uptake by primary producers [SLS]
	segments and the involved spaces.	
	Sequences of critical path segments describing a path-	Pathway pattern 2: OC remineralisation [SLS]
	way pattern must be true for all pathways within the	\rightarrow DIC exit [AS]
	pathway pattern. Syntax: Path segment [Space]	
Closed loops	Closed loops are a subordinate classification of path-	Surface layer remineralisation loop (SLRL):
	way patterns (sub-pattern), comprising all pathways re-	OC remineralisation [SLS] \rightarrow DIC uptake by
	turning to the initial position. Each closed loop can be	primary producers [SLS]
	described by the sequence of critical path segments and	
	the involved spaces. Sequences of critical path segments	
	describing a loop must be true for all pathways of that	
	loop.	

Open loops	'Open' loops are a subordinate classification of pathway	Atmospheric IC loop (AICL): OC remineralisa-
	patterns (sub-patterns), comprising all pathways not re-	tion [SLS] \rightarrow DIC exit [AS]
	turning to the initial position.	
Marine OC cycle	The marine OC cycle consists of all closed loops.	

To explain how to compare and condense pathways and define core patterns of the OC cycle, we use as an analogy a town with a sandbank separated by a lagoon. The inhabitants of the town regularly visit the sandbank to spend their evenings at the beach. A route planner, comparable to our basic pathway concept, shows 100 individual pathways that end at the beach. These pathways are similar, but all differ in the overall sequence of routes and vehicles used.

However, there is a common denominator. To reach the beach, the lagoon must be crossed. This condition is independent of the method of crossing. People get to the sandbank via different processes, such as taking the public ferry or a private boat. The outcome 'people reach the sandbank' and the general functionality 'crossing the lagoon' of these processes coincide. Therefore, we define 'crossing the lagoon' as a path segment (*summarised function of the involved processes with the same general functionality*, Table 1). This path segment is critical to all pathways. If the crossing is not possible, no one will reach the beach. All pathways can thus be generally described by this critical path segment, the bottleneck.

However, this very general description does not capture higher resolution structures. At higher resolution, some pathways to the beach have not one but several critical path segments. We describe these by a sequence of critical path segments. To
135 stay with the lagoon analogy: People who do not live on the harbour front have to use one of three routes to reach the harbour (functionality: 'reach the harbour'). Their pathways can be described minimally by the sequence of 'reaching the harbour' and 'crossing the lagoon', while the pathways of people living at the harbour front can be minimally condensed to and described by the smallest pathway, the critical path segment 'crossing the lagoon'.

- From these two distinct sequences of critical path segments, different pathway patterns can be defined. The most general and superior pattern is the 'entire city-beach route' pattern defined by the path segment 'crossing the lagoon', which is common to all pathways. That sequence is the minimum sequence shared by all pathways and the highest-level pattern. For the subordinate patterns, a distinction is made between a 'harbour front-beach route' pattern (crossing the lagoon) and a 'behind the harbourbeach route' pattern (reaching the harbour and crossing the lagoon). The resolution is a matter of choice. One could even increase the resolution, find commonalities between the routes in the rest of the city and define subordinate route patterns.
- 145 However, if one assumes that the rest of the city has a very diverse and complicated road network, the description of the two subordinate patterns may be sufficient as a resolution to define pressure points and bottlenecks when, for example, construction works block some of the three routes to the harbour.

Similarly, we identify critical path segments of the mapped OC pathways in the basic pathway concept (see Supplement B for a schematic of the methodological steps). One pathway pattern that immediately catches the eye are pathways that loop

150 inside or outside the marine system. We define these patterns as closed and 'open' loops. We focus on the closed patterns and identify all pathways that loop and end at the starting position in the surface layer. We compare their process sequences and the

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general functionality of the processes involved. Based on these comparisons, we define critical path segments and minimum sequences of critical path segments to condense all pathways that belong to closed loops.

- For the OC cycle, we identify six critical path segments necessary to define the minimal sequences of all OC pathways 155 that belong to closed loops (Figure 1): *OC position change (A), Formation of rDOC (B), rDOC conversion to DOC (C), OC remineralisation (D), DIC upward position change (E) and DIC uptake by primary producers (F).* We recognise that not including the rDOC-related path segments would further reduce the number of path segments and loops. However, as described earlier, rDOC is relevant to the climate system and is related to very different phenomena and processes. So although it may not technically be the minimum solution, it is the minimum solution that still captures relevant differences.
- 160 The path segments do not contain any temporal or spatial information. However, the spatial extent of path segments can change the pathway pattern. Staying with the lagoon analogy: 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, depending on personal preferences. Since people do not regularly visit the second anchor point during the week, the bars there only open at the weekend. Thus, the distribution of people, the opening hours of
- 165 the local restaurants and the considerations that determine the decision, time constraints during the week versus preferences at the weekend, change. The 'crossing the lagoon' path segment or the 'use of the public ferry' process do not allow this differentiation. The same applies to the carbon path segments. For example, the function of carbon in the ecosystem (e.g. as a food source for benthic organisms), the environmental conditions that determine its pathway (e.g. bioturbation) and the time it takes for carbon to return to the surface layer (e.g. years or decades) change depending on whether it ends up in the sediment
- 170 or in the water column. However, the OC position change segment (A) does not provide information on whether the transport ends up in the water column or in the sediment.

Hence, pathway patterns cannot be unambiguously defined without spatial information. To systematically add this information, we define five spaces, volumes with distinctly different environmental conditions and processes. After general considerations of the ocean layers, the *surface layer space (SLS)* encounters sufficient light to support photosynthesising organisms

- 175 and primary production. Seasonal and continuous mixing counteract material loss and keep matter close to remineralisers. In the *water column space (WCS)* below the well-mixed layer, mixing occurs less frequently, more slowly or very infrequently, depending among other things on the water depth (DeVries et al., 2012). Matter takes more time to resurface and may escape remineralisers due to changing positions or its recalcitrant or degraded character (Baker et al., 2017). In the *upper sedimentation space (USS)*, remineralisers also remineralise highly degraded material as it remains in their vicinity longer than in the
- 180 water column (Middelburg, 2019). The *lower sedimentary space (LSS)* is largely abiotic and undisturbed and allows lithification processes. In addition, we define the *atmospheric space (AS)* above the marine system. Users of the concept can change the spaces, e.g. by partitioning the water column space, resulting in a different number of closed loops. However, if the minimum number of closed loops is to be conceptually described, each 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). In the following we represent path
- 185 segments with the corresponding letters and in square brackets behind them the spaces in which the associated processes end or take place (syntax example: A [WCS], OC position change ending in the WCS).

We 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 pathway patterns 'closed loops' can be divided into two sub-pattern: *closed reminer*alisation and rDOC loops.

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We define three remineralisation loops: a surface layer remineralisation loop (SLRL), a water column remineralisation loop (WCRL), and an upper sediment remineralisation loop (USRL) (Table 2). All three loops include pathways on which OC is remineralised to DIC (D), which is taken up by primary producers in the SLS (F [SLS]). The path segments 'OC position change' (A) and 'DIC upward position change' (E) as well as the space in which the OC is remineralised distinguish the remineralisation loops. The WCRL includes pathways that lead to a downward position change of OC into the WCS. 195 remineralisation in the WCS, and an upward position change of DIC into the SLS, where it is taken up (WCRL: A [WCS] \rightarrow D $[WCS] \rightarrow E [SLS] \rightarrow F [SLS])$. 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 (WCRL: A [WCS] \rightarrow D [WCS] \rightarrow E [SLS] \rightarrow F [SLS]). If zooplankton respiration occurs in the SLS, the pathway belongs to the SLRL (SLRL: D [SLS] \rightarrow F [SLS]). We define the USRL analogous to the WCRL, but with remineralisation 200 taking place in the USS (USRL: A [USS] \rightarrow D [USS] \rightarrow E [SLS] \rightarrow F [SLS]).

The two path segments 'Formation of rDOC' (B) and 'rDOC conversion to DOC' (C) in the SLS are part of the second sub-patterns 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

- 205 (LrDOCL), rDOC that persists in the entire water column on geological time scales. The short-term rDOC loop is defined by the 'Formation of rDOC' (B) and 'rDOC conversion to DOC' (C) in the SLS (SrDOCL: B [SLS] \rightarrow C [SLS]), while the rDOC long-term loop additionally comprises the path segment 'OC position change' (A), with accumulation mostly or even entirely in the WCS (LrDOCL: B [SLS] \rightarrow A [WCS/USS] \rightarrow A [SLS] \rightarrow C [SLS] or A [WCS/USS] \rightarrow B [WCS/USS] \rightarrow A [SLS] \rightarrow C [SLS]). In contrast to the remineralisation loops, we do not explicitly consider a rDOC loop in the upper sediment, as
- the temporal scales of rDOC produced there or in the water column overlap to our knowledge. Therefore, the long-term rDOC 210 loop includes rDOC production in the USS alongside its transport to the WCS.

All loops comprise a continuum of processes belonging to non-critical (optional) path segments. For example, the SLRL includes OC that is transported and processed below the SLS but returns to the SLS as OC to be remineralised and used by primary producers (SLRL: A [WCS] \rightarrow A [SLS] \rightarrow D [SLS] \rightarrow F [SLS]). Another example is rDOC, which is part of the WCRL

- when remineralised in WCS (WCRL: B [SLS] \rightarrow A [WCS] \rightarrow D [WCS] \rightarrow E [SLS] \rightarrow F [SLS]). Only rDOC that reaches 215 the surface and is converted back into more bioavailable forms in the SLS belongs to the LrDOCL (LrDOCL: ... A [SLS] \rightarrow C [SLS]). Because of the climatic importance of rDOC, we distinguish rDOC from DOC as described before. Technically, however, rDOC represents a "storage" intermediate step of remineralisation or open loops. For the minimal description of the loops, the sequence of critical path segments is sufficient and unambiguous. However, users of the concept can
- 220 combine additional (optional) path segments along the sequence of critical path segments to define individual pathways or sub-pathway patterns.

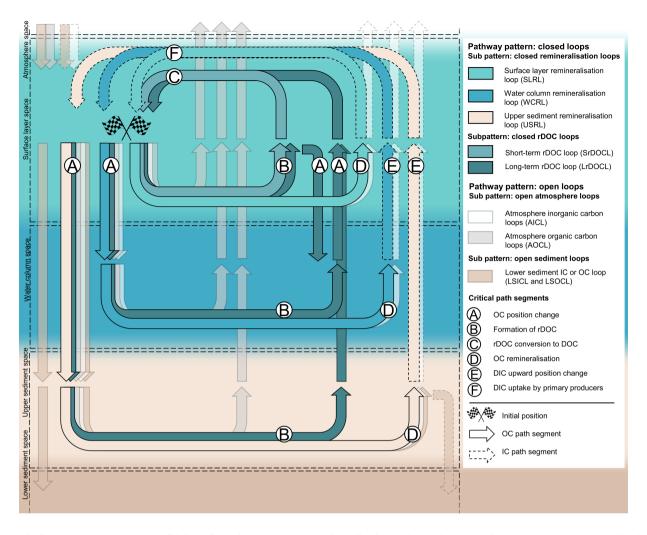


Figure 1. General pathway patterns of OC cycling with three closed remineralisation and two closed rDOC loops, the spaces and the involved critical path segments. 'Open' loops are only displayed with transparent colours as they are not our focus.

In this case, two separation rules apply to avoid double counting when assigning pathways with optional path segments to one of the parent loops. The first rule states that the space of the ultimate remineralisation before entry and reuse in the SLS defines the remineralisation loop. OC that is remineralised several times in different spaces is part of the SLRL if it is last remineralised in the SLS before uptake by primary producers in the SLS. Similarly, OC belongs to the WCRL or USRL if it is ultimately remineralised in the WCS or USS. The second rule states that rDOC leaving the surface or produced below the SLS always belongs to the LrDOCL (Table 2).

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. We define four sub-patterns of 'open' loops. The *atmosphere IC loops (AICLs)*230 describe the outgassing of DIC, produced in different spaces, to the atmosphere. The *atmospheric OC loops (AOCLs)* comprise

Table 2. Summary of sequences of critical path segments and spaces defining the closed loops. The separation rule only comes to play, if additional (at this resolution level optional) path segments are added to describe a sub-pattern or individual pathways. Spaces in square brackets indicate the spaces where the processes happen or end. Bold spaces are the naming spaces of this loop. Non-bold spaces are intermediate or "walk-through" spaces. Loops: Surface layer remineralisation loop (SLRL), Water column remineralisation loop (WCRL), Upper sediment remineralisation 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 DOC (C), OC remineralisation (D), DIC upward position change (E) and DIC uptake by primary producers (F).

Closed Loops	Sequence of critical path segments plus spaces	Separation rule
SLRL	$D \ [\mathbf{SLS}] \to F \ [\mathbf{SLS}]$	Ultimate remineralisation in SLS before F
WCRL	$A [\textbf{WCS}] \rightarrow D [\textbf{WCS}] \rightarrow E [SLS] \rightarrow F [SLS]$	Ultimate remineralisation in WCS before E and F
USRL	$A [\textbf{USS}] \rightarrow D [\textbf{USS}] \rightarrow E [SLS] \rightarrow F [SLS]$	Ultimate remineralisation in USS before E and F
SrDOCL	$\mathbf{B} \; [\mathbf{SLS}] \rightarrow \mathbf{C} \; [\mathbf{SLS}]$	Formation of rDOC in SLS and no A
LrDOCL	B [SLS] \rightarrow A [WCS/USS] \rightarrow A [SLS] \rightarrow C [SLS] or	Formation of rDOC in SLS with A or Formation of
	$A [\textbf{WCS/USS}] \rightarrow B [\textbf{WCS/USS}] \rightarrow A [SLS] \rightarrow C [SLS]$	rDOC in WCS or USS

the exit of marine OC, marine aerosols, volatile organic compounds (VOCs), and CH_4 through the surface to AS, e.g. via fish predation by birds or outgassing. The lower sediment IC and OC loops (LSOCL and LSICL) describe the burial and lithification of carbon in the LSS, entering geological cycling.

3.2 Embedded processes, pools and agents

- 235 Having defined the superordinate pathway patterns, we now add and describe global processes, pools and agents embedded in each path segment (Figure 2 and Table 3). This addition allows to define pathway patterns with higher resolution and to link and complement our concept with existing ones. Global in this context means that the process mechanisms are globally valid, but that the frequency, extent, initialisation and triggers of these processes differ. We focus on non-anthropogenic processes and the previously defined critical path segments. This means that, for example, upward position changes of POC or DOC are 240 not resolved.
 - Two of the three remineralisation loops include the path segments OC position change (A) and DIC upward position change (E). Processes belonging to path segments A and E include sinking, diffusion and advection, and direct and indirect biotainduced transport.

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Organic compounds that sink from one space in the water column to another are usually either large or dense, or escape consumption or dissolution in the upper space (De La Rocha, 2006). Sedimentation and compaction by subsequent matter is the analogous process within the sediment-water interface and sediment. Matter is compacted by the weight deposited over it and "sinks" as it loses volume. Sinking and sedimentation always act downwards and are confined to POC. Gravity-induced sinking (and sedimentation) is thus part of any path segment A of POC (Figure 2).

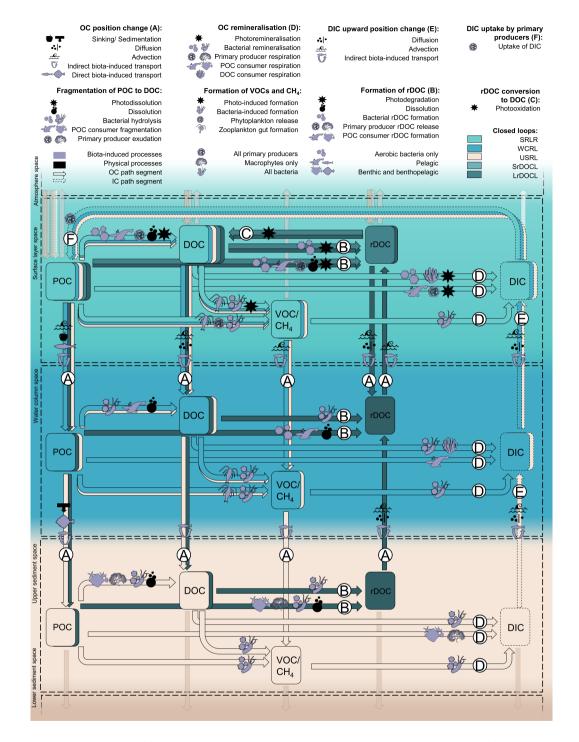


Figure 2. OC pathway patterns with critical path segments (A-F), spaces and embedded processes, C pools and involved organisms. 'Open' loops are indicated by transparent colours. Organisms can be agents (producing DOC by sloppy feeding) and part of the carbon pool (consumers as part of POC respire DIC) at the same time. Optional fragmentation processes and pathways for DOC and VOCs/ CH_4 are included. As such these pathways are not marked with capital letters.

(R)DOC and DIC potentially diffuse in all directions, following large- or small-scale gradients in the water column, at the water-sediment interface and in the pore water of the sediment. We assume that (r)DOC concentrations decrease with depth (Hansell, 2013) but are higher in the sediment than in the overlying water (Burdige et al., 1999; Rowe and Deming, 2011) and that DIC concentrations increase with depth (Oka, 2020). Following these gradients, (r)DOC diffuses downwards in the water column and upwards in and out of the sediment (A of (r)DOC in 2) and DIC always diffuses upwards (E). The upward diffusion of non-refractory DOC from the sediment is not considered as it is part of a non-critical path segment.

Other physically induced position changes are related to water or sediment mass movements based on advection. These include large-scale upwelling and downwelling water movements, 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. Advection does not act downwards into the sediment but upwards in the form of resuspension. Resuspension is only included for rDOC and 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 transport involves 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 living in the SLS and the USS (Middelburg, 2019)). 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 path segments A of POC. Indirect biota-induced transport 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 among others bioturbation (Berke, 2010), associated with sediment reworking and resuspension, and bioirrigation (Kristensen et al., 2012), which leads to inflows of ocean water into the sediment. Indirect biota-induced position change works in all directions and is involved in all path segments of A for (r)DOC

and POC and E in the water column and the sediment.

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

Light-induced photoremineralisation, the only physically induced remineralisation, directly oxidises DOC and POC to IC (Mopper and Kieber, 2002; Mayer et al., 2009) and works only in the SLS. We include this process in D in the SLS.

Table 3. Processes embedded in the critical path segments. Italic C forms are products of the processes. Processes end or take place in the spaces in square brackets in the loop syntax.

OC position change	(A)				
Process	Loop syntax	Process description	Pools	Organisms	Directions
Sinking	WCRL: A [WCS]	Gravitational sinking	POC		Downwards
	LrDOCL: A [WCS]				
Sedimentation	USRL: A [USS]	Sedimentation of	POC		Downwards
	LrDOCL: A [USS]	sinking matter			
Diffusion	WCRL: A [WCS]	Diffusion in the water col-	DOC		Downwards
		umn and pore waters			
	LrDOCL: A [WCS]	-	rDOC		Downwards,
					upwards
Advection	WCRL: A [WCS]	Up- and downwelling, mix-	POC, DO	OC,	Downwards
		ing, turbulence, eddies	VOCs, CH ₄		
	LrDOCL: A [WCS]		POC, DO	OC,	Downwards,
			rDOC		upwards
Indirect biota-	WCRL: A [WCS]	Biota-induced turbulence,	POC, DO	OC, Swimming and movin	g Downwards
induced transport	USRL: A [USS]	induced drift, digging,	VOCs, CH ₄	species (pelagic, bentho-	
		burrowing, bioirrigation,		pelagic and benthic)	
	LrDOCL: A [WCS]	sediment reworking	POC, DO	OC,	Downwards,
	LrDOCL: A [USS]		rDOC		upwards
Direct biota-	WCRL: A [WCS]	Transport in living tissue or	POC	Swimming and movin	g Downwards
induced transport	USRL: A [USS]	OC distribution in organ-		species (pelagic, bentho-	
		isms spanning several		pelagic and benthic), organ	
	LrDOCL: A [WCS]	spaces		isms spanning severa	d Downwards,
	LrDOCL: A [USS]			spaces (e.g. kelp)	upwards

Formation of rDOC (B)						
Process	Loop syntax	Process description	Pools		Organisms	Directions
Photo-	SrDOCL: B [SLS]	Degradation of labile to re-	DOC,	POC,		
degradation	LrDOCL: B [SLS]	calcitrant OC by UV light	rDOC			
Dissolution	SrDOCL: B [SLS]	Dissolution due to sinking	POC, rDO	DC		
	LrDOCL: B [SLS]	(enhanced by bacteria) or				
	LrDOCL: B [WCS]	pore-water interactions				
	LrDOCL: B [USS]					

Bacterial rDOC	SrDOCL: B [SLS]	Release of capsular mate-	DOC, POC,	Bacteria, viruses
formation	LrDOCL: B [SLS]	rial and rDOC under e.g.	rDOC	
	LrDOCL: B [WCS]	stress conditions		
	LrDOCL: B [USS]			
Primary producer	SrDOCL: B [SLS]	Release of rDOC	POC, rDOC	Phytoplankton and e.g.
rDOC release	LrDOCL: B [SLS]			macrophytes
	LrDOCL: B [WCS]			
	LrDOCL: B [USS]			
POC consumer	SrDOCL: B [SLS]	Direct (excretion) or indi-	POC, rDOC	POC consumers (pelagic,
rDOC formation	LrDOCL: B [SLS]	rect release (e.g. via sloppy		bentho-pelagic and benthic)
	LrDOCL: B [WCS]	feeding) of rDOC		
	LrDOCL: B [USS]			

Conversion of rDOC to DOC (C)						
Process	Loop syntax	Process description	Pools	Organisms	Directions	
Photooxidation	SrDOCL: C [SLS]	Photochemical conversion	rDOC, DOC			
	LrDOCL: C [SLS]	rDOC to DOC				

OC remineralisation	n (D)				
Process	Loop syntax	Process description	Pools	Organisms	Directions
Photo-	SLRL: D [SLS]	Direct UV remineralisation	POC, DOC,		
remineralisation			DIC		
Bacterial reminer-	SLRL: D [SLS]	Bacterial DOC (VOCs)-	DOC, VOCs,	Bacteria and archaea	
alisation	WCRL: D [WCS]	based respiration	CH_4, DIC		
	USRL: D [USS]				
Primary producer	SLRL: D [SLS]	Respiration of primary pro-	POC, DIC	Phytoplankton and e.g.	
respiration	USRL: D [USS]	ducers		macrophytes	
POC consumer	SLRL: D [SLS]	Respiration of POC con-	POC, DIC	POC consumers (pelagic,	
respiration	WCRL: D [WCS]	sumers		bentho-pelagic and benthic)	
	USRL: D [USS]				
DOC consumer	SLRL: D [SLS]	Respiration of DOC con-	DOC, DIC	DOC consumers (filter	
respiration	WCRL: D [WCS]	sumers		feeders) excluding bacteria	

DIC upward position change (E)					
Process	Loop syntax	Process description	Pools	Organisms	Directions
Diffusion	WCRL: E [SLS]	Diffusion in the water col-	DIC		Upwards
	USRL: E [SLS]	umn and pore waters			

Advection	WCRL: E [SLS]	Down- and upwelling, mix-	DIC		Upwards
	USRL: E [SLS]	ing, turbulence and eddies,			
		physical induced resuspen-			
		sion			
Indirect biota-	WCRL: E [SLS]	Biota-induced turbulence,	DIC	Swimming and moving	Upwards
induced transport	USRL: E [SLS]	induced drift, digging,		species (pelagic, bentho-	
		burrowing, bioirrigation,		pelagic and benthic)	
		sediment reworking and			
		related processes			
DIC antala ha min	(E)				
DIC uptake by prim	ary producers (F)				
Process	Loop syntax	Process description	Pools	Organisms	Directions
Uptake of DIC	SLRL: F [SLS]	Photosynthesis	DIC, POC	Phytoplankton and e.g.	
	WCRL: F [SLS]			macrophytes	

Bacteria and archaea remineralise DOC in path segment D in every space above LSS, 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 coprorhexy (Lampitt et al., 1990)), by producing small metabolites either or by excreting DOC (Lampert, 1978). Indirectly, consumers fragment non-living POC by swimming or moving (Dilling and Alldredge, 2000). Further, primary producers exudate DOC in the water column (e.g. under nutrient-limited conditions or 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 290 lysis (Middelboe et al., 1996).

USRL: F [SLS]

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The transformation from POC to DOC (arrows from POC to DOC, Figure 2) that takes place before bacterial remineralisation are not part of the previously defined critical path segments, as not every OC compound needs to undergo one of these changes to be remineralised. However, considering only DOC-based pathways, the change in OC size from POC to DOC can be defined as a critical path segment for sub-patterns such as POC-DOC remineralisation loops.

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In addition, bacteria can oxidise VOCs and CH_4 (e.g. shown in Halsey et al. (2017)) (D of VOCs/ CH_4 in Figure 1), produced via abiotic processes (photochemical degradation of DOC (Kieber et al., 1989)) and biogenic processes (production by phytoplankton (Lenhart et al., 2016) and zooplankton in anaerobic areas of their guts (Weber et al., 2019; Schmale et al., 2018)).

Another form of remineralisation is respiration by living organisms other than bacteria. Primary producers respire in the

- 300 photic SLS. The roots of macrophytes additionally produce DIC 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 remineralise by respiration. Therefore, we include remineralisation by primary producers in path segments D in the SLS and USS, respiration by DOC consumers in the SLS and WCS, and respiration by POC consumers in all spaces with aerobic conditions above the LSS.
- 305

in Legendre et al. (2015).

Once OC is remineralised to DIC, this DIC is transported by the above-described processes of position change to the SLS (E [SLS]). Subsequently, primary producers take up the DIC for photosynthesis (F [SLS]) and close the remineralisation 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.

- 310 UV light can change the lability and increase recalcitrant components of the DOC pool via photodegradation (Benner and Biddanda, 1998; Hansell, 2013)(B [SLS]). Biota supply rDOC via successive microbial processing of DOC (Jiao et al., 2010, 2011), the release of capsular material by bacteria (Stoderegger and Herndl, 1998), bacterial hydrolysis of POC (Jiao et al., 2011), bacterial stress responses to low-labile DOC and unfortunate nutrient conditions (Stoderegger and Herndl, 1998), and successive consumption by higher trophic levels (Jiao et al., 2011). In addition, some phytoplankton directly exudates
- rDOC (Jiao et al., 2011). Both microbes and phytoplankton also release rDOC due to viral lysis of host cells (Jiao et al., 2011). 315 In addition, processes from living and non-living POC to DOC, e.g. dissolution, can lead to very diluted DOC that is not available for consumption and therefore recalcitrant (Arrieta et al., 2015) (Figure 2, arrow from POC to rDOC).

rDOC that stays in or returns to the SLS, via the position change processes described above (A [SLS]), can be converted back to more bioavailable forms by photooxidation (C [SLS]) (Kieber et al., 1989). We consider pathways with other rDOC removal processes, such as direct light-induced oxidation from rDOC to DIC (Shen and Benner, 2018), sorption of rDOC into 320

POC (Hansell et al., 2009) and hydrothermal removal mechanisms in hydrothermal vents or the Earth's crust (Lang et al., 2006), as parts of the closed remineralisation or 'open' loops. Once the rDOC is converted to DOC in the SLS, the rDOC loops are closed.

Based on these embedded processes, pools, and agents, we can now define pathway patterns of higher resolution. For example, for SLRL, six sub-patterns can be defined based on the carbon pools involved: a POC-SLRL, a POC-DOC-SLRL, a 325 POC-DOC-VOC/CH₄-SLRL and a POC-VOC/CH₄-SLRL, as well as a DOC-SLRL and a DOC-VOC/CH₄-SLRL. Depending on the research question or desired level of detail, multiple sub-patterns can be defined based on the processes and agents involved. The higher the resolution of the pathway pattern, the more the patterns resemble descriptions of individual pathways. In the following discussion, we use the example of the biological carbon pump to show how such sub-patterns can look like and which insights e.g. a comparison of such different patterns can provide.

4 Discussion

Our concept of the OC cycle condenses pathways to superordinate pathway patterns and provides an overview of embedded processes, pools, and agents, which allows resolving patterns of smaller scale and higher resolution. Our overarching structure complements existing concepts of OC pathways and processes in the ocean, providing a basis for using a consistent terminology. As such, the concept facilitates comparing different definitions of pathway structures, integrating new findings and

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To discuss some of these aspects in an application example, we translate pathways of the biological carbon pump (BCP) into our concept (Figure 3). Based on the definition of Giering and Humphreys (2020), who define the BCP as "the collection of marine biogeochemical processes that convert dissolved inorganic matter in the surface ocean into biomass and transport this

to the ocean interior, where the biomass is returned to its original dissolved inorganic forms", we illustrate different pathway

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patterns with different resolutions and choices of pathways.

placing, for example, pathways of finite length scale in a broader framework.

As defined by Giering and Humphreys (2020), all pathways of the BCP involve the uptake of inorganic carbon into biomass in the surface waters (F [SLS]). This biomass is transported to the interior of the ocean (A [Ocean Interior]), where it is remineralised to DIC (D [Ocean interior]). In Figure 3 panel (a), we fit this information into our concept. For simplicity, we

- 345 disregard the rDOC loops and VOCs/ CH_4 production and start again with the previously introduced initial position. Missing further information, we assume that the ocean interior does not contain the USS and define it as WCS. Based on the definition of Giering and Humphreys (2020) and the restriction of "ocean interior" we classify the BCP as part of the WCRL or the corresponding atmospheric inorganic carbon cycle (AICL). To close the loop, we need to add path segment E not included in the defined BCP.
- 350 If we now resolve involved OC pools (here POC and DOC) in the BCP of Giering and Humphreys (2020), we can define three sub-patterns (sub-loops, when adding path segment E) that still describe all pathways of the defined BCP, but at a higher resolution (panel b). Restricting the sub-patterns to pathways with a specific set of processes changes the inclusivity of the sub-pattern. For example, if the focus lies on the general structure of pathways involving direct biota-induced transport (A), the result is a subset of seven loops (with path segment E). These loops serve only two of the superordinate loops of panels (a)
- and (b) (Figure 3) and thus represent a subset of the defined BCP. This subset resembles patterns condensed in other concepts of BCP such as the mesopelagic-migrant pump and the seasonal lipid pump (Boyd et al., 2019). A focus on the purely physical induced pathways of the BCP leads to six different sub-patterns, which do not resolve remineralisation and DIC uptake, as these are non-physical processes (Figure 3, panel (d)). These six sub-patterns could potentially serve all the higher-level loops in panels (a) and (b) but do not resolve some parts of the definition of the BCP by Giering and Humphreys (2020). Thereby
- 360 these sub-patterns resemble some other, often more traditional, concepts of the BCP, e.g. by Hansell and Carlson (2001) and De La Rocha (2006), that do not consider DIC uptake and remineralisation explicitly. Interestingly, in this subset of the BCP (panel (d)), the input of POC and DOC from outside the marine system may also be part of the BCP, as the biota-induced uptake of DIC is not critical for this set of pathways.

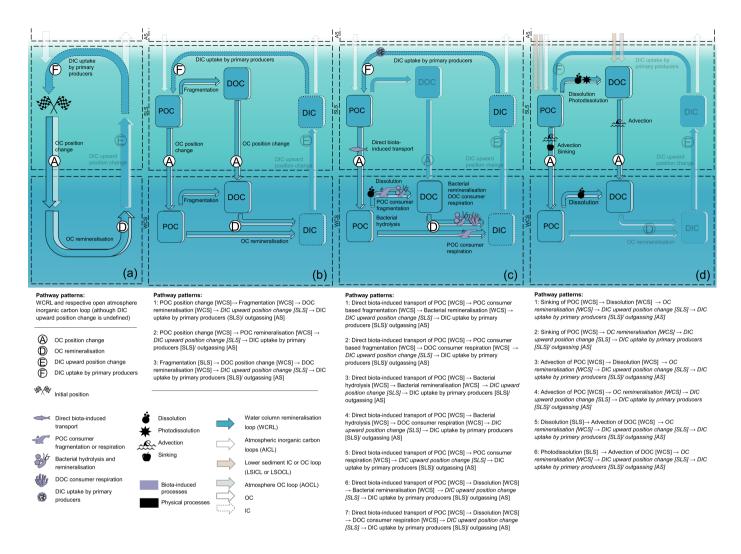


Figure 3. Different pathway patterns of the BCP defined by Giering and Humphreys (2020). Panel (a) shows the superordinate BCP pathway patterns. Panel (b) resolves involved pools. Panel (c) and (d) resolve choices of processes: (c) pathways with direct biota-induced transport and (d) pathways with only physical processes. Transparent or italic path segments are not explicitly included in the definition of the BCP or the selected pathways.

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Integrating the BCP definition of Giering and Humphreys (2020) into our concept illustrates where the BCP concept shows ambiguity and may need to be refined to concretise which pathways belong to the BCP and which do not. Giering and Humphreys (2020) give "ocean interior" as the spatial constraints of the pathways of the BCP. We translate "ocean interior" as WCS, as no further depth constraints are given. Other BCP definitions constrain depth more concretely, for example describing the BCP as export (Buchan et al., 2014; Hansell and Carlson, 2001) and sequestration fluxes (Sigman and Haug, 2004) acting at depths below 100 m and 1000 m (Passow and Carlson, 2012). Because of the ambiguity of the space, we might include

- 370 pathways in our concept, which are not part of the BCP. On the other hand, we exclude the sediment and pathways leading to POC sedimentation from the BCP by using the WCS only, although it is still debated whether or not POC sedimentation belongs to the BCP. Steinberg and Landry (2017) for instance considers POC sedimentation as part of the BCP, while Sigman and Haug (2004) claim that it is not sensu stricto. Anyhow, these examples show that the spaces in which the BCP operates need to be more clearly defined. Based on the BCP definition of Giering and Humphreys (2020), we may include pathways
- 375 that do not belong to the BCP, while excluding some that do. Subdividing the WCS into several spaces, e.g. a space below a sequestration depth, may thus be more appropriate for the representation of the BCP, as the definition of spaces allows a refinement of the pathways that belong to a pathway pattern.

A similar vagueness as with the spaces applies to the OC pools involved. Does the BCP include pathways based on DOC in the SLS, e.g. as defined by Honjo et al. (2014), or not as defined by De La Rocha (2006)? DOC is one of the relevant carbon fluxes to the deep sea, especially in oligotrophic areas (Roshan and DeVries, 2017). Therefore, and because the definition of Giering and Humphreys (2020) does not explicitly exclude the DOC pool, we add DOC to our illustration of BCP in panel (b). However, the presentation would also work without DOC. In such a case, our concept shows which pathways are missing by dispensing DOC.

- Illustrating what is missing also allows placing individual pathways and concepts such as the BCP in a broader framework.
 For example, mentioning pathway section E is a must to place the BCP in the carbon cycle, as there is no dead end in nature.
 Furthermore, our approach helps to identify how different sub-concepts fit into more general definitions (panel (b)-(c) compared to panel (a)), but also where some inconsistencies might occur, e.g. external sources of OC are not part of the biological carbon pump contrary to what is suggested in panel (d). In addition, it facilitates identifying which pathways are not resolved and the potential informative value of studies based on a limited number of pathways. In panel (c), for example, the DOC in the WCS
 comes only from fragmentation of POC. If fragmentation processes decrease significantly, this does not necessarily mean a
- decrease in remineralisation of DOC (D [WCS]), as DOC can also come from the SLS. A study based on the pathways as in panel (d) does not consider DOC from the SLS and therefore has limited informative value about changes in remineralisation of DOC. All mentioned considerations are already part of most studies and publications. But we provide a new tool to structure these considerations and make them more comparable.
- 395 The example also shows how new concepts and processes can be integrated into our concept. Panel (d) resembles more traditional definitions of the BCP, which focus mainly on physically driven processes. The role of organisms, particularly higher trophic levels, has been neglected. Now, however, the contribution of this biota is recognised as relevant to the carbon cycle. For example, large migratory species link to nutrient distribution and overall mixing (Roman and McCarthy, 2010), zooplankton have a significant influence on carbon export (Steinberg and Landry, 2017), reptile falls provides an alternative
- 400 carbon pathway to the sediment (McClain et al., 2019), and fish and mammals contribute to the carbon cycle through various processes (Martin et al., 2021). With these processes, many new pathway patterns emerge, some of which we resolve in panel (c). Our concept provides overarching structures that users can bring to life to integrate new insights. Processes, organisms, pathways, and loops can easily be added, changed, or deleted to incorporate new findings or specific systems into the general structures.

- 405 By generalizing must-pass structures and providing a congruent visual representation, our concept may reduce the potential for misunderstandings of the OC cycle potentially and unintentionally caused by visual concepts of finite length scale. An example of such a potential misunderstanding is the decoupling pathways transporting DIC to depths and return pathways in some earlier visual OC concepts (as e.g. discussed for Boscolo-Galazzo et al. (2018) in the introduction). While these representations are justified for finite length scale studies, this visual decoupling can lead to the false impression that increased transport of OC
- 410 to the deep ocean always leads to increased sequestration and storage of atmospheric carbon. However, increased OC export is not necessarily accompanied by increased carbon storage, which depends, among other things, on the ratio of regenerated to pre-formed nutrients and on the carbon that escapes from the deep ocean (Gnanadesikan and Marinov, 2008). The export of carbon to the deep sea is part of carbon processing, but not the whole story, as we can also see from the example of the definition of the BCP. We propose to use a concept like ours as a reference concept to account for the increasingly interdisciplinary
- scientific community, to increase consistency of (visual) concepts and to bring structure into the larger framework of the OC 415 cycle.

Our concept brings structure to the marine OC cycle but does not capture its complexity. Each OC compound travels its pathway through the OC cycle. An OC compound in the surface ocean may end up on the surface or in the deep sea, be decomposed, or become recalcitrant, to name just a few possibilities. Each pathway is unique in its sequence of processes. So,

there is a multitude of possible pathways. An all-encompassing description of these possibilities is, therefore, neither possible 420 nor meaningful. Accordingly, our concept does not want to and cannot resolve individual pathways. On the contrary, it focuses on critical path segments and overarching structures. Hence, our concept reduces many pathways to a sequence that does not capture their full extent, biological relevance, complexity, and temporal dimension.

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Moreover, our concept is purely abstract and not capable of quantification or forecasting expected changes. It is a skeleton that needs to be filled with life. Further, it proved difficult to find an unambiguous language and visualisation for the concept. For example, we depict organisms that are a pool and organisms that are agents with the same symbol. Adjustments of terms and symbols appear reasonable as soon as users identify problems. We hope that the concept will grow, improve and become more complete with use.

5 Conclusion

- 430 We propose a general (visual) concept for the marine part of the organic carbon cycle. It complements and integrates existing concepts and defines overarching structure of OC pathway patterns (loops) and the processes, pools and agents involved. Building on concepts that focus on the structure of individual or a subset of marine OC pathways, our concept identifies the general structure of all pathways. Details and complexity are disregarded in favour of a systematic structure that can facilitate the identification and comparison of concepts, pathways, pools and studies. The concept can be adapted to a wide range of 435 questions, pathway choices, resolutions and thus serve as a basis for discussion and reference to understand the current and
- future marine OC dynamics arising from the multiplicity of OC pathways and the human influence on them.

Data availability. The base pathway concept is attached as supplement A.

Author contributions. M.I.E.S. designed the study, conducted the research and prepared the manuscript. I.H. designed the study and contributed to the manuscript.

440 Competing interests. The authors declare that they have no conflict of interest.

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References

- Anderson, T. R. and Ducklow, H. W.: Microbial loop carbon cycling in ocean environments studied using a simple steady-state model, Aquatic Microbial Ecology, 26, 37–49, https://doi.org/10.3354/ame026037, 2001.
- 450 Arrieta, J. M., Mayol, E., Hansman, R. L., Herndl, G. J., Dittmar, T., and Duarte, C. M.: Ocean chemistry. Dilution limits dissolved organic carbon utilization in the deep ocean, Science (New York, N.Y.), 348, 331–333, https://doi.org/10.1126/science.1258955, 2015.
 - Azam, F. and Malfatti, F.: Microbial structuring of marine ecosystems, Nature reviews. Microbiology, 5, 782–791, https://doi.org/10.1038/nrmicro1747, 2007.

Azam, F., Smith, D. C., Steward, G. F., and Hagström, A.: Bacteria-organic matter coupling and its significance for oceanic carbon cycling,

- 455 Microbial Ecology, 28, 167–179, https://doi.org/10.1007/BF00166806, 1994.
 - Baker, C. A., Henson, S. A., Cavan, E. L., Giering, S. L. C., Yool, A., Gehlen, M., Belcher, A., Riley, J. S., Smith, H. E. K., and Sanders, R.: Slow-sinking particulate organic carbon in the Atlantic Ocean: Magnitude, flux, and potential controls, Global Biogeochemical Cycles, 31, 1051–1065, https://doi.org/10.1002/2017GB005638, 2017.
- Barange, M., Butenschön, M., Yool, A., Beaumont, N., Fernandes, J. A., Martin, A. P., and Allen, J. I.: The Cost of Reducing the North
 Atlantic Ocean Biological Carbon Pump, Frontiers in Marine Science, 3, 845, https://doi.org/10.3389/fmars.2016.00290, 2017.
- Benner, R. and Biddanda, B.: Photochemical transformations of surface and deep marine dissolved organic matter: Effects on bacterial growth, Limnology and Oceanography, 43, 1373–1378, 1998.
 - Berke, S. K.: Functional groups of ecosystem engineers: a proposed classification with comments on current issues, Integrative and comparative biology, 50, 147–157, https://doi.org/10.1093/icb/icq077, 2010.
- 465 Bianchi, D., Carozza, D. A., Galbraith, E. D., Guiet, J., and DeVries, T.: Estimating global biomass and biogeochemical cycling of marine fish with and without fishing, Science advances, 7, eabd7554, https://doi.org/10.1126/sciadv.abd7554, 2021.
 - Boscolo-Galazzo, F., Crichton, K. A., Barker, S., and Pearson, P. N.: Temperature dependency of metabolic rates in the upper ocean: A positive feedback to global climate change?, Global and Planetary Change, 170, 201–212, https://doi.org/10.1016/j.gloplacha.2018.08.017, 2018.
- 470 Boudreau, B. P.: Mean mixed depth of sediments: The wherefore and the why, Limnology and Oceanography, 43, 524–526, https://doi.org/10.4319/lo.1998.43.3.0524, 1998.
 - Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., and Weber, T.: Multi-faceted particle pumps drive carbon sequestration in the ocean, Nature, 568, 327–335, https://doi.org/10.1038/s41586-019-1098-2, 2019.
 - Briggs, N., Dall'Olmo, G., and Claustre, H.: Major role of particle fragmentation in regulating biological sequestration of CO2 by the oceans,
- 475 Science, 367, 791–793, https://doi.org/10.1126/science.aay1790, 2020.
 - Buchan, A., LeCleir, G. R., Gulvik, C. A., and González, J. M.: Master recyclers: features and functions of bacteria associated with phytoplankton blooms, Nature reviews. Microbiology, 12, 686–698, https://doi.org/10.1038/nrmicro3326, 2014.
 - Bunke, D., Leipe, T., Moros, M., Morys, C., Tauber, F., Virtasalo, J. J., Forster, S., and Arz, H. W.: Natural and Anthropogenic Sediment Mixing Processes in the South-Western Baltic Sea, Frontiers in Marine Science, 6, https://doi.org/10.3389/fmars.2019.00677, 2019.
- 480 Burdige, D. J., Berelson, W. M., Coale, K. H., McManus, J., and Johnson, K. S.: Fluxes of dissolved organic carbon from California continental margin sediments, Geochimica et Cosmochimica Acta, 63, 1507–1515, https://doi.org/10.1016/S0016-7037(99)00066-6, 1999.

- Carlson, C. A. and Hansell, D. A.: Chapter 3 DOM Sources, Sinks, Reactivity, and Budgets, in: Biogeochemistry of marine dissolved organic matter, edited by Carlson, C. A., Hansell, D. A., and Amon, R. M. W., pp. 65–126, Academic Press, London, https://doi.org/10.1016/B978-0-12-405940-5.00003-0, 2015.
- 485 Cavan, E. L., Belcher, A., Atkinson, A., Hill, S. L., Kawaguchi, S., McCormack, S., Meyer, B., Nicol, S., Ratnarajah, L., Schmidt, K., Steinberg, D. K., Tarling, G. A., and Boyd, P. W.: The importance of Antarctic krill in biogeochemical cycles, Nature communications, 10, 4742, https://doi.org/10.1038/s41467-019-12668-7, 2019.
 - Dai, M., Yin, Z., Meng, F., Liu, Q., and Cai, W.-J.: Spatial distribution of riverine DOC inputs to the ocean: an updated global synthesis, Current Opinion in Environmental Sustainability, 4, 170–178, https://doi.org/10.1016/j.cosust.2012.03.003, 2012.
- 490 De La Rocha, C. L.: The Biological Pump, in: The oceans and marine geochemistry, edited by Elderfield, H. and Holland, H. D., Treatise on geochemistry, Elsevier, Amsterdam, 2006.
 - DeVries, T., Primeau, F., and Deutsch, C.: The sequestration efficiency of the biological pump, Geophysical Research Letters, 39, n/a–n/a, https://doi.org/10.1029/2012GL051963, 2012.
 - Dickey, T. D.: Physical-optical-biological scales relevant to recruitment in large marine ecosystems, Large marine ecosystems: Patterns,
- 495 processes, and yields, edited by: Sherman, K., Alexander, LM, and Gold, BD, Am. Assoc. Adv. Sci. Publ, 90, 82–98, 1990.
- Dilling, L. and Alldredge, A. L.: Fragmentation of marine snow by swimming macrozooplankton: A new process impacting carbon cycling in the sea, Deep Sea Research Part I: Oceanographic Research Papers, 47, 1227–1245, https://doi.org/10.1016/S0967-0637(99)00105-3, 2000.

- Duarte, C. M. and Cebrián, J.: The fate of marine autotrophic production, Limnology and Oceanography, 41, 1758–1766, https://doi.org/10.4319/lo.1996.41.8.1758, 1996.
 - Fortuin, K. P. J., van Koppen, C. S. A., and Leemans, R.: The Value of Conceptual Models in Coping with Complexity and Interdisciplinarity in Environmental Sciences Education, BioScience, 61, 802–814, https://doi.org/10.1525/bio.2011.61.10.10, 2011.
- 505 Gardner, W. D., Chung, S. P., Richardson, M. J., and Walsh, I. D.: The oceanic mixed-layer pump, Deep Sea Research Part II: Topical Studies in Oceanography, 42, 757–775, https://doi.org/10.1016/0967-0645(95)00037-Q, 1995.
 - Giering, S. L. C. and Humphreys, M. P.: Biological Pump, in: Encyclopedia of Engineering Geology, edited by Bobrowsky, P. T. and Marker,
 B., Encyclopedia of Earth Sciences Series, pp. 1–6, Springer International Publishing, Cham, https://doi.org/10.1007/978-3-319-39193-9_154-1, 2020.
- 510 Giering, S. L. C., Sanders, R., Lampitt, R. S., Anderson, T. R., Tamburini, C., Boutrif, M., Zubkov, M. V., Marsay, C. M., Henson, S. A., Saw, K., Cook, K., and Mayor, D. J.: Reconciliation of the carbon budget in the ocean's twilight zone, Nature, 507, 480–483, https://doi.org/10.1038/nature13123, 2014.

Gnanadesikan, A. and Marinov, I.: Export is not enough: nutrient cycling and carbon sequestration, Marine Ecology Progress Series, 364, 289–294, https://doi.org/10.3354/meps07550, 2008.

515 Griffiths, J. R., Kadin, M., Nascimento, F. J. A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M. C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S., and Winder, M.: The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world, Global change biology, 23, 2179–2196, https://doi.org/10.1111/gcb.13642, 2017.

<sup>Doney, S. C. and Ducklow, H. W.: A decade of synthesis and modeling in the US Joint Global Ocean Flux Study, Deep Sea Research Part II:
Topical Studies in Oceanography, 53, 451–458, https://doi.org/10.1016/j.dsr2.2006.01.019, 2006.</sup>

Halsey, K. H., Giovannoni, S. J., Graus, M., Zhao, Y., Landry, Z., Thrash, J. C., Vergin, K. L., and de Gouw, J.: Biological cycling of volatile

- organic carbon by phytoplankton and bacterioplankton, Limnology and Oceanography, 62, 2650–2661, https://doi.org/10.1002/lno.10596, 2017.
 - Hansell, D., Carlson, C., Repeta, D., and Schlitzer, R.: Dissolved Organic Matter in the Ocean: A Controversy Stimulates New Insights, Oceanography, 22, 202–211, https://doi.org/10.5670/oceanog.2009.109, 2009.
- Hansell, D. A.: Recalcitrant dissolved organic carbon fractions, Annual review of marine science, 5, 421–445,
 https://doi.org/10.1146/annurev-marine-120710-100757, 2013.
 - Hansell, D. A. and Carlson, C. A.: Marine dissolved organic matter and the carbon cycle, Oceanography, 14, 41–49, 2001.
 - Heemskerk, M., Wilson, K., and Pavao-Zuckerman, M.: Conceptual models as tools for communication across disciplines, Conservation Ecology, 7, 2003.
 - Honjo, S., Eglinton, T., Taylor, C., Ulmer, K., Sievert, S., Bracher, A., German, C., Edgcomb, V., Francois, R., Iglesias-Rodriguez, M. D.,
- 530 van Mooy, B., and Rapeta, D.: Understanding the Role of the Biological Pump in the Global Carbon Cycle: An Imperative for Ocean Science, Oceanography, 27, 10–16, https://doi.org/10.5670/oceanog.2014.78, 2014.
 - Huntley, M. E. and Zhou, M.: Influence of animals on turbulence in the sea, Marine Ecology Progress Series, 273, 65–79, https://doi.org/10.3354/meps273065, 2004.

Jiao, N. and Zheng, Q.: The Microbial Carbon Pump: from Genes to Ecosystems, Applied and Environmental Microbiology, 77, 7439-7444,

- 535 https://doi.org/10.1128/AEM.05640-11, 2011.
 - Jiao, N., Herndl, G. J., Hansell, D. A., Benner, R., Kattner, G., Wilhelm, S. W., Kirchman, D. L., Weinbauer, M. G., Luo, T., Chen, F., and Azam, F.: Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean, Nature reviews. Microbiology, 8, 593–599, https://doi.org/10.1038/nrmicro2386, 2010.
 - Jiao, N., Azam, F., and Sanders, S.: Microbial Carbon Pump in the Ocean, Science/AAAS, https://doi.org/10.1126/science.opms.sb0001,
- 540 2011.

545

- Jiao, N., Guo, Z., Legendre, L., Suttle, C., Rivkin, R., and Azam, F.: Editorial for the special issue on marine carbon sequestration and climate change, National Science Review, 5, 456–457, https://doi.org/10.1093/nsr/nwy068, 2018.
- Jónasdóttir, S. H., Visser, A. W., Richardson, K., and Heath, M. R.: Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic, Proceedings of the National Academy of Sciences of the United States of America, 112, 12122–12126, https://doi.org/10.1073/pnas.1512110112, 2015.
- Katija, K. and Dabiri, J. O.: A viscosity-enhanced mechanism for biogenic ocean mixing, Nature, 460, 624–626, https://doi.org/10.1038/nature08207, 2009.
 - Kharbush, J. J., Close, H. G., van Mooy, B. A. S., Arnosti, C., Smittenberg, R. H., Le Moigne, F. A. C., Mollenhauer, G., Scholz-Böttcher, B., Obreht, I., Koch, B. P., Becker, K. W., Iversen, M. H., and Mohr, W.: Particulate Organic Carbon Deconstructed: Molecular and Chemical
- 550 Composition of Particulate Organic Carbon in the Ocean, Frontiers in Marine Science, 7, 518, https://doi.org/10.3389/fmars.2020.00518, 2020.
 - Kieber, D. J., McDaniel, J., and Mopper, K.: Photochemical source of biological substrates in sea water: implications for carbon cycling, Nature, 341, 637–639, https://doi.org/10.1038/341637a0, 1989.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., and Banta, G. T.: What is bioturbation? The need for a

precise definition for fauna in aquatic sciences, Marine Ecology Progress Series, 446, 285–302, https://doi.org/10.3354/meps09506, 2012.

- Kunze, E., Dower, J. F., Beveridge, I., Dewey, R., and Bartlett, K. P.: Observations of biologically generated turbulence in a coastal inlet, Science (New York, N.Y.), 313, 1768–1770, https://doi.org/10.1126/science.1129378, 2006.
- Lampert, W.: Release of dissolved organic carbon by grazing zooplankton, Limnology and Oceanography, 23, 831–834, https://doi.org/10.4319/lo.1978.23.4.0831, 1978.
- 560 Lampitt, R. S., Noji, T., and von Bodungen, B.: What happens to zooplankton faecal pellets? Implications for material flux, Marine Biology, 104, 15–23, https://doi.org/10.1007/BF01313152, 1990.
 - Lang, S. Q., Butterfield, D. A., Lilley, M. D., Paul Johnson, H., and Hedges, J. I.: Dissolved organic carbon in ridge-axis and ridge-flank hydrothermal systems, Geochimica et Cosmochimica Acta, 70, 3830–3842, https://doi.org/10.1016/j.gca.2006.04.031, 2006.
- Legendre, L., Rivkin, R. B., Weinbauer, M. G., Guidi, L., and Uitz, J.: The microbial carbon pump concept: Potential biogeochemical significance in the globally changing ocean. Progress in Oceanography, 134, 432–450. https://doi.org/10.1016/i.pocean.2015.01.008, 2015.
 - Lenhart, K., Klintzsch, T., Langer, G., Nehrke, G., Bunge, M., Schnell, S., and Keppler, F.: Evidence for methane production by the marine algae Emiliania huxleyi, Biogeosciences, 13, 3163–3174, https://doi.org/10.5194/bg-13-3163-2016, 2016.
 - Levy, M., Bopp, L., Karleskind, P., Resplandy, L., Ethe, C., and Pinsard, F.: Physical pathways for carbon transfers between the surface mixed layer and the ocean interior, Global Biogeochemical Cycles, 27, 1001–1012, https://doi.org/10.1002/gbc.20092, 2013.
- 570 Margoluis, R., Stem, C., Salafsky, N., and Brown, M.: Using conceptual models as a planning and evaluation tool in conservation, Evaluation and program planning, 32, 138–147, https://doi.org/10.1016/j.evalprogplan.2008.09.007, 2009.

Martin, A. H., Pearson, H. C., Saba, G. K., and Olsen, E. M.: Integral functions of marine vertebrates in the ocean carbon cycle and climate change mitigation, One Earth, 4, 680–693, https://doi.org/10.1016/j.oneear.2021.04.019, 2021.

- Mayer, L. M., Schick, L. L., Skorko, K., and Boss, E.: Photodissolution of particulate organic matter from sediments, Limnology and Oceanography, 51, 1064–1071, https://doi.org/10.4319/lo.2006.51.2.1064, 2006.
 - Mayer, L. M., Schick, L. L., Hardy, K. R., and Estapa, M. L.: Photodissolution and other photochemical changes upon irradiation of algal detritus, Limnology and Oceanography, 54, 1688–1698, https://doi.org/10.4319/lo.2009.54.5.1688, 2009.

McClain, C. R., Nunnally, C., Dixon, R., Rouse, G. W., and Benfield, M.: Alligators in the abyss: The first experimental reptilian food fall in the deep ocean, PloS one, 14, e0225 345, https://doi.org/10.1371/journal.pone.0225345, 2019.

- 580 Middelboe, M., Jorgensen, N., and Kroer, N.: Effects of viruses on nutrient turnover and growth efficiency of noninfected marine bacterioplankton, Applied and environmental microbiology, 62, 1991–1997, https://doi.org/10.1128/aem.62.6.1991-1997.1996, 1996.
 - Middelburg, J. J.: Carbon Processing at the Seafloor, in: Marine Carbon Biogeochemistry, edited by Middelburg, J. J., SpringerBriefs in Earth System Sciences, pp. 57–75, Springer International Publishing, Cham, https://doi.org/10.1007/978-3-030-10822-9_4, 2019.

Mopper, K. and Kieber, D. J.: Photochemistry and the cycling of carbon, sulfer, nitrogen and phosphorus, in: Biogeochemistry of marine dissolved organic matter, edited by Hansell, D. A. and Carlson, C. A., pp. 455–508, Academic Press, Amsterdam and Boston, 2002.

- Oka, A.: Ocean carbon pump decomposition and its application to CMIP5 earth system model simulations, Progress in Earth and Planetary Science, 7, 1–17, https://doi.org/10.1186/s40645-020-00338-y, 2020.
- Omand, M. M., D'Asaro, E. A., Lee, C. M., Perry, M. J., Briggs, N., Cetinić, I., and Mahadevan, A.: Eddy-driven subduction exports particulate organic carbon from the spring bloom, Science (New York, N.Y.), 348, 222–225, https://doi.org/10.1126/science.1260062, 2015.
 - Passow, U. and Carlson, C. A.: The biological pump in a high CO2 world, Marine Ecology Progress Series, 470, 249–271, https://doi.org/10.3354/meps09985, 2012.

- Pedersen, O., Sand-Jensen, K., and Revsbech, N. P.: Diel Pulses of O2 and CO2 in Sandy Lake Sediments Inhabited by Lobelia Dortmanna, Ecology, 76, 1536–1545, https://doi.org/10.2307/1938155, 1995.
- 595 Roman, J. and McCarthy, J. J.: The whale pump: marine mammals enhance primary productivity in a coastal basin, PloS one, 5, e13 255, https://doi.org/10.1371/journal.pone.0013255, 2010.
 - Roshan, S. and DeVries, T.: Efficient dissolved organic carbon production and export in the oligotrophic ocean, Nature Communications, 8, 2036, https://doi.org/10.1038/s41467-017-02227-3, 2017.

Rowe, G. T. and Deming, J. W.: An alternative view of the role of heterotrophic microbes in the cycling of organic matter in deep-sea sediments. Marine Biology Research, 7, 629–636, https://doi.org/10.1080/17451000.2011.560269, 2011.

- Ruiz, J.: What generates daily cycles of marine snow?, Deep Sea Research Part I: Oceanographic Research Papers, 44, 1105–1126, https://doi.org/10.1016/S0967-0637(97)00012-5, 1997.
 - Scheiner, S. M. and Willig, M. R.: The theory of ecology, University of Chicago Press, 2011.
- Schmale, O., Wäge, J., Mohrholz, V., Wasmund, N., Gräwe, U., Rehder, G., Labrenz, M., and Loick-Wilde, N.: The contribution of zoo-
- plankton to methane supersaturation in the oxygenated upper waters of the central Baltic Sea, Limnology and Oceanography, 63, 412–430,
 2018.
 - Shen, Y. and Benner, R.: Mixing it up in the ocean carbon cycle and the removal of refractory dissolved organic carbon, Scientific reports, 8, 2542, https://doi.org/10.1038/s41598-018-20857-5, 2018.

Sigman, D. M. and Haug, G. H.: 6.18 - The Biological Pump in the Past, in: 6: Theoceans and marine geochemistry, edited by Elderfield, H., pp. 491–528, Elsevier, Amsterdam, https://doi.org/10.1016/B0-08-043751-6/06118-1, 2004.

- Smith, D. C., Simon, M., Alldredge, A. L., and Azam, F.: Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution, Nature, 359, 139–142, https://doi.org/10.1038/359139a0, 1992.
 - Steinberg, D. K. and Landry, M. R.: Zooplankton and the Ocean Carbon Cycle, Annual review of marine science, 9, 413–444, https://doi.org/10.1146/annurev-marine-010814-015924, 2017.
- 615 Steinberg, D. K., Goldthwait, S. A., and Hansell, D. A.: Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea, Deep Sea Research Part I: Oceanographic Research Papers, 49, 1445–1461, https://doi.org/10.1016/S0967-0637(02)00037-7, 2002.
 - Stoderegger, K. and Herndl, G. J.: Production and release of bacterial capsular material and its subsequent utilization by marine bacterioplankton, Limnology and Oceanography, 43, 877–884, https://doi.org/10.4319/lo.1998.43.5.0877, 1998.
- 620 Ullah, H., Nagelkerken, I., Goldenberg, S. U., and Fordham, D. A.: Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation, PLoS biology, 16, e2003 446, https://doi.org/10.1371/journal.pbio.2003446, 2018.
 - Weber, T., Wiseman, N. A., and Kock, A.: Global ocean methane emissions dominated by shallow coastal waters, Nature Communications, 10, 4584, https://doi.org/10.1038/s41467-019-12541-7, 2019.

Wooster, M. K., McMurray, S. E., Pawlik, J. R., Morán, X. A. G., and Berumen, M. L.: Feeding and respiration by giant barrel sponges across
 a gradient of food abundance in the Red Sea, Limnology and Oceanography, 64, 1790–1801, https://doi.org/10.1002/lno.11151, 2019.