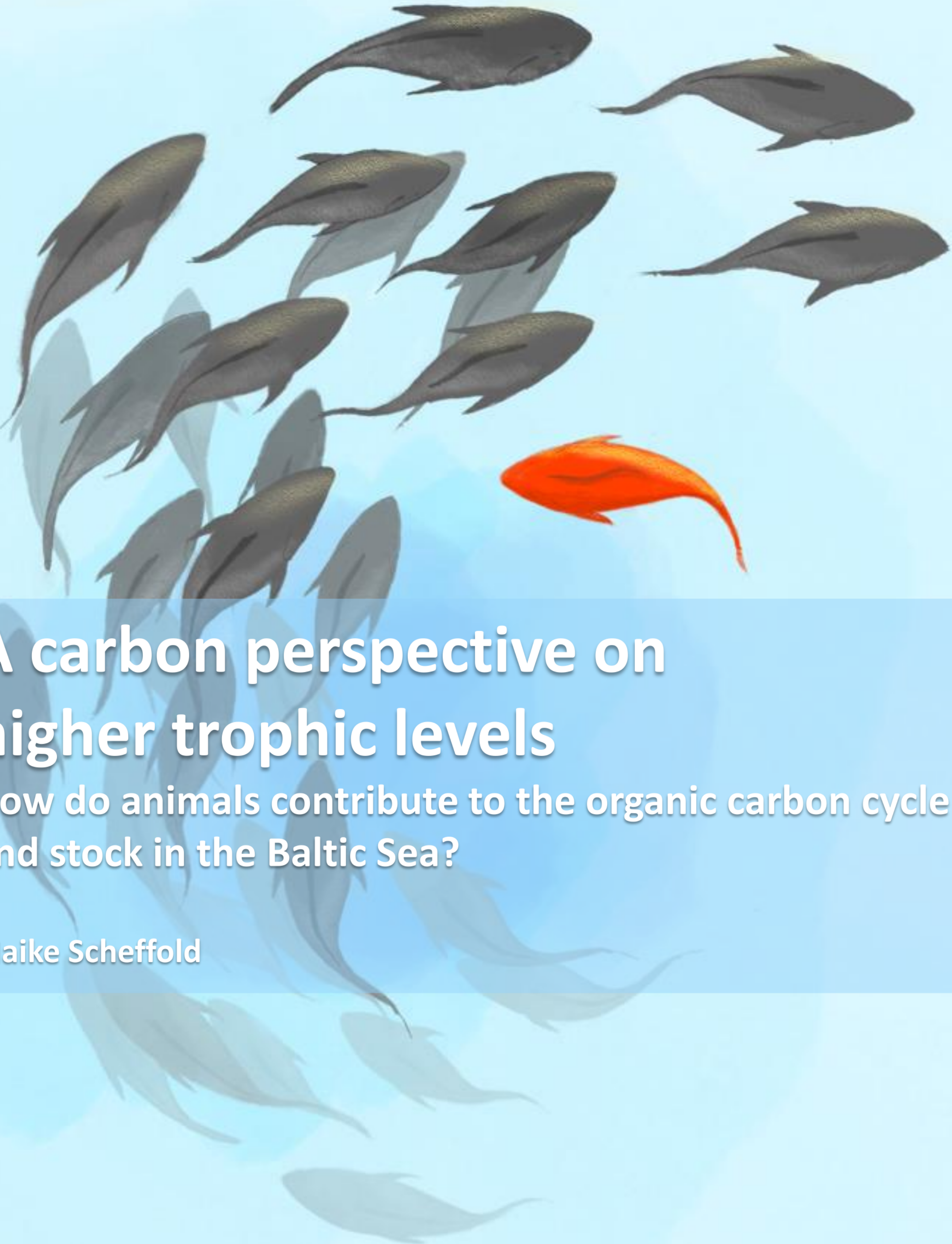
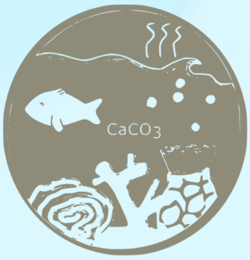


A carbon perspective on higher trophic levels

How do animals contribute to the organic carbon cycle and stock in the Baltic Sea?

Maike Scheffold



A carbon perspective on higher trophic levels

How do animals contribute to the organic carbon cycle and stock in the Baltic Sea?

DISSERTATION

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After being so emotional, I want to finish with some wise and meme-worthy words I found on the internet and kept in my "I open at the close" notes for some time:

Writing a PhD was easy.
It was like riding a bike.
Only that it was very hot
as the street was on fire,
and the bike,
and everything else,
because it was hell.

Abstract

The world's oceans are an integral part of the Earth's climate system, contributing significantly to the mitigation of human-induced climate change through carbon cycling and storage. Marine organisms of all kinds, from the smallest virus to the largest whale, play various roles in both cycling and storage. Traditionally however, organisms higher up in the food web such as fish and marine mammals, have been given little to no consideration in this context, as their contribution was considered quantitatively negligible. Recent studies, conversely, show that these organisms can indeed make a significant contribution. However, despite increasing research, our understanding of how fish and marine mammals affect the ocean carbon cycle is still incomplete due to a lack of data, concepts and descriptions that encompass these organisms.

This incomplete understanding is particularly critical as populations of higher trophic levels are in steep decline worldwide. The contribution of these organisms may be changing as a result, while at the same time it has not even been fully understood, let alone quantified, especially in regional ecosystems. The Baltic Sea is one of the regional ecosystems where fish and marine mammals have not yet been accounted for in the carbon cycle and are simultaneously subject to significant population changes.

The Baltic Sea is a unique brackish ecosystem in Northeastern Europe. Exposed to high anthropogenic exploitation pressures and changing environmental conditions, the Baltic Sea has undergone several major transitions in the last decade. One consequence of these transitions includes the drastic reduction of the cod stock, one of the key higher trophic level species within the Baltic Sea. The sharp decline in the piscivorous cod population has implications for the food web, ecology of the Baltic Sea, and the livelihoods of many people who depend on this system. However, how the decline of cod affects carbon cycling and storage is unknown.

In this thesis, I want to advance the understanding of the contribution of higher trophic levels to organic carbon (OC) cycling and storage both globally and specifically within the Baltic Sea ecosystem.

To do this, we first establish a general concept of the OC cycle that encompasses all organisms and is globally valid but can be applied and adapted to local systems. The concept thus provides the framework for the Baltic Sea-specific investigations that follow.

Since higher trophic level stocks contribute to the total OC stock of marine systems, we examine how much OC currently exists in the individual pools, such as the sediment and the cod population, in the Baltic Sea. This initial quantification not only provides the baseline against which future stock quantifications can be compared but also allows comparing stocks of individual pools with each other. This comparison shows that the higher trophic levels with their contemporary stocks do not contribute significantly to the carbon stock of the Baltic Sea.

However, this does not mean that these organisms are irrelevant altogether, as they participate in carbon cycle processes, e.g. via the food web. Consequently, an ecosystem with and without a species of the higher trophic levels may recycle OC differently and be characterised by a different distribution of carbon in the pools. We investigate this relationship using the example of cod in the Baltic Sea. To do this, we use the concept developed previously to

describe and compare theoretical pathways and OC cycles in the Baltic Sea in a state with either an intact or a collapsed cod stock. We further divide the system state with collapsed cod into two variants. In one, cod control the stock of everything subordinate to it in the food web. In the other variant, the cod only control the population size of their main food source, sprat. The comparison shows the conditions under which the collapse of the cod population can lead to relevant changes in the OC cycle. For example, the Baltic Sea can be a carbon sink or source, depending on the extent of trophic control. Higher trophic levels, such as cod, may thus be more relevant in the Baltic Sea than their contribution to the overall stock would suggest.

Although our investigations are mainly theoretical and conceptual, they fit into a picture that is increasingly emerging: Fish and other higher trophic levels can most likely make a non-negligible contribution to the marine carbon cycle and thus potentially to climate change mitigation. To account for the roles and contribution of these organisms in the future, scientific gaps need to be filled and a perspective shift in policy and management needs to be advanced.

Zusammenfassung

Die Weltmeere sind ein wichtiger Bestandteil des Klimasystems der Erde und leisten mit ihrem Kohlenstoffkreislauf und ihren Kohlenstoffspeichern einen wesentlichen Beitrag zur Minderung des menschgemachten Klimawandels. Meereslebewesen aller Art vom kleinesten Virus bis zum größten Wal spielen in beidem, dem Kreislauf und der Speicherung, verschiedene Rollen. Traditionell wurden Organismen in höheren Positionen im Nahrungsnetz wie Fisch und Meeressäuger, in diesem Zusammenhang kaum bis gar nicht betrachtet, da ihr Beitrag als quantitativ vernachlässigbar galt. Neueste Studien zeigen hingegen, dass diese Organismen durchaus einen signifikanten Beitrag leisten können. Trotz zunehmender Forschung ist unser Verständnis davon, wie Fische und Meeressäuger den Kohlenstoffkreislauf der Meere beeinflussen jedoch noch immer lückenhaft, da es unter anderem zu wenige Daten, Konzepte und Beschreibungen gibt, die diese Organismen umfassen.

Dieses unvollständige Verständnis ist besonders kritisch, da die Populationen der höheren trophischen Ebenen weltweit stark rückläufig sind. Der Beitrag dieser Organismen könnte sich infolgedessen verändern, während er gleichzeitig noch nicht einmal vollständig verstanden, geschweige denn quantifiziert wurde, insbesondere in regionalen Ökosystemen. Eines der regionalen Ökosysteme, in denen Fische und Meeressäuger im Kohlenstoffkreislauf noch nicht berücksichtigt wurden und gleichzeitig erheblichen Populationsveränderungen ausgesetzt sind, ist die Ostsee.

Die Ostsee ist ein einzigartiges brackisches Ökosystem im Nordosten Europas. Hohen anthropogenen Nutzungsdruck und sich ändernden Umweltbedingungen ausgesetzt, hat die Ostsee im letzten Jahrzehnt mehrere grundlegende Wandel erlebt, die unter anderem zu einer drastischen Reduzierung des Dorschbestandes geführt haben. Der fischfressende Dorsch ist eine Schlüsselspezies der höheren trophischen Ebenen in der Ostsee. Die starke Abnahme seiner Population hat Auswirkungen auf das Nahrungsnetz und die Ökologie der Ostsee sowie auf die Lebensgrundlage vieler Menschen, die von diesem System abhängen. Wie der Rückgang des Dorsches den Kohlenstoffkreislauf und -speicher beeinflusst, ist jedoch unbekannt.

In dieser Arbeit, möchte ich das Verständnis des Beitrages von Organismen der höheren trophischen Ebenen zum organischen Kohlenstoffkreislauf und -speicher global, und insbesondere im Ökosystem der Ostsee voranbringen.

Dafür erstellen wir zuerst ein generelles Konzept des organischen Kohlenstoffkreislaufes, welches alle Organismen umfasst und global gültig ist, sich aber auf kleinskaligere Systeme anwenden und anpassen lässt. Das Konzept bietet damit den Rahmen für die Ostsee-spezifischen Untersuchungen, die wir anschließen.

Da die Bestände höherer trophischer Ebenen zum Gesamtbestand an organischem Kohlenstoff mariner Systeme beitragen, untersuchen wir zuerst wieviel organischer Kohlenstoff derzeit in einzelnen Reservoirs (Pools) der Ostsee, wie z.B. dem Sediment und der Dorschpopulation, existiert. Diese erste Quantifizierung stellt nicht nur die Basis dar, an welcher sich zukünftige Bestandsquantifizierungen abgleichen können, sondern ermöglicht auch den Vergleich der Bestände einzelner Pools untereinander. Dieser Vergleich zeigt, dass die höheren trophischen Ebenen mit ihren derzeitigen Beständen nicht signifikant zum Kohlenstoffbestand der Ostsee beitragen.

Das heißt jedoch nicht, dass diese Organismen insgesamt unrelevant sind, da sie, z.B. über das Nahrungsnetz, in Prozessen des Kohlenstoffkreislaufes mitwirken. Ein Ökosystem mit und ohne eine Spezies der höheren trophischen Ebenen, recycelt organischen Kohlenstoff möglicherweise anders und zeichnet sich durch eine unterschiedliche Verteilung des Kohlenstoffs in den einzelnen Pools aus. Diesen Zusammenhang untersuchen wir am Beispiel des Dorsches in der Ostsee. Dafür nutzen wir das zuvor entwickelte Konzept und beschreiben und vergleichen den theoretisch vorhandenen organischen Kohlenstoffkreislauf in der Ostsee in einem Zustand mit einem intakten und einem Zustand mit kollabierten Dorschbestand. Den Systemzustand mit kollabiertem Dorsch unterteilen wir weiter in zwei Varianten. In der einen kontrolliert Dorsch den Bestand aller ihm im Nahrungsnetz untergeordneten Organismen. In der anderen Variante kontrolliert der Dorsch nur die Populationsgröße seiner Hauptnahrungsquelle Sprotte. Der Vergleich zeigt die Bedingungen unter denen der Kollaps der Dorschpopulation zu relevanten Änderungen im organischen Kohlenstoffkreislauf führen kann. Unter anderem kann die Ostsee, je nach Ausmaß der trophischen Kontrolle, eine Kohlenstoffsenke oder -quelle sein. Höhere trophische Ebenen, wie der Dorsch, könnten in der Ostsee also relevanter sein, als ihr Beitrag zum Gesamtbestand vermuten lässt.

Obgleich unserer Untersuchungen hauptsächlich theoretischer und konzeptioneller Natur sind, passen sie in das Bild, das sich immer mehr abzeichnet: Fische und andere Organismen der höheren trophischen Ebenen können wahrscheinlich nicht unerheblich zum Kohlenstoffkreislauf der Meere und damit möglicherweise zur Minderung des Klimawandels beitragen. Um den Rollen und dem Beitrag dieser Organismen zukünftig Rechnung zu tragen, müssen wissenschaftliche Lücken geschlossen und ein Perspektivwandel in Politik und Management vorangetrieben werden.

Contents

List of Figures

List of Tables

1 | INTRODUCTION

“Fish[1] are friends, not (just) food” - Bruce, the great white shark from the fish-friendly shark support group in the Pixar[2] film "Finding Nemo", is quite sure of that. Even though I have slightly modified the quote to "just" food, there is truth in these words. They suggest that all organisms in the ocean have multiple roles and should not be reduced to one. Of course, natural predators like sharks see fish mainly as food (and perhaps as cleaning aids), and Bruce will probably abandon his attitude and ruin his run of fish-free days as soon as he gets hungry or smells blood (as the film proves), but we as humans might follow Bruce’s lead and see the multitude of roles that organisms have in the ocean.

In this thesis, I want to advance the understanding of the roles and the contribution of higher trophic levels to the organic carbon (OC) cycle and stocks, and take first steps towards assessing this contribution in the Baltic Sea ecosystem. To this end, I combine conceptualisation, quantification and a theoretical comparison study. As a result, I conclude that fish, as an example of higher trophic levels, are more than just food and that incorporating the different roles of higher trophic level organisms into policy and marine governance might promote co-benefits for climate, biodiversity, and society.

In this introduction, I give a brief overview of the role of the oceans in the global OC cycle and storage. Subsequently, I review what is already known about the roles of higher trophic levels in both and explain how humans change these roles and the functionality of the oceanic carbon cycle through the degradation of marine fauna. I also highlight the problems and issues that arise in this context that render this topic both relevant and challenging. Finally, I give a brief overview of the aim and outline of this thesis and the Baltic Sea ecosystem.

The oceans’ role in carbon cycling and storage

The oceans are part of the Earth’s natural climate system and the global carbon cycle and represent the second-largest global carbon reservoir storing about 39,500 Gt C (Friedlingstein et al., 2020).

The ocean absorbs atmospheric carbon through chemical, physical, and biological mechanisms. Chemo-physically, carbon dioxide enters the oceans following the partial pressure difference of carbon dioxide in the atmosphere and the ocean surface layer (Bopp et al., 2015) and can form different dissolved inorganic carbon species when reacting with water. Depending on, among other things, large-scale circulations and vertical mixing (Broecker and Peng,

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[1] For this thesis, I use the colloquial term fish, rather than fishes, to refer to multiple fish species.
[2] A film produced by Pixar Animation Studios and released by Walt Disney Pictures.

1992; Roshan and DeVries, 2017), these dissolved carbon species can be transported in the oceans to greater depths, to resurface only within centuries to millennia (Riebesell et al., 2009). The solubility of carbon and the subsequent convection of it with water masses (referred to as the solubility pump) are responsible for up to one-third of the dissolved inorganic carbon (DIC) gradient (Passow and Carlson, 2012), i.e. the DIC concentrations that increase with depth, constituting the major oceanic carbon stock with 38,000 Gt C (Friedlingstein et al., 2020).

The biologically induced carbon cycle is driven by the so-called biological pump that is responsible for the other two-thirds of the DIC gradient (Passow and Carlson, 2012). The biological uptake of carbon in the ocean occurs primarily through phytoplankton, tiny unicellular algae that photosynthesise. As primary producers, they form OC from inorganic carbon (IC) in the light-flooded upper layer and thus form the basis of the food web and the carbon cycle. Sinking organisms or particles, e.g. dead organisms or faeces, transport OC to greater depths and contribute significantly to the so-called export production or flux, i.e. the proportion of OC produced in the surface layer that sinks beyond 100 m (Passow and Carlson, 2012). In deeper layers, the OC can be fragmented, remineralised to DIC by microbes or buried, to name but a few. In addition to sinking, the processing of OC in the food web and the active transport of this carbon by moving organisms to deeper layers also contribute to the increased DIC concentrations in the deeper sea (Giering et al., 2014; Steinberg and Landry, 2017) and sedimentation of particulate organic carbon (POC) (Le Moigne, 2019). Alongside this, swimming and feeding activities, excretions, and migration of organisms contribute to the formation and transport of dissolved organic carbon (DOC) and refractory DOC (rDOC), which is highly resistant to microbial remineralisation. Besides DIC and sedimented POC, DOC and rDOC represent significant carbon stocks in the oceans (Jiao et al., 2010; Jiao and Zheng, 2011).

Carbon in deeper parts of the oceans, whether OC or IC, can remain for centuries to millennia, depending primarily on the depth of the oceans and on overturning circulations (DeVries et al., 2012; Riebesell et al., 2009). The rDOC pool is depth-independent and accumulates in the entire water column (Jiao et al., 2010; Jiao and Zheng, 2011) for up to 40,000 years (Hansell, 2013) due to its resistance to microbial remineralisation. Carbon buried and lithified in oceanic sediments can even enter the geological cycle and be withdrawn from the atmospheric reservoir for a period much longer than the time humans have been living on Earth. In addition to non-living carbon stocks, there are also stocks of living biomass in the oceans. These stocks are part of the oceans' carbon reservoir, provided that the stocks of living organisms remain stable and self-renewing over time (Saba et al., 2021; Martin et al., 2021).

Although the uptake, cycling, and storage of carbon in the oceans vary locally and regionally (Fassbender et al., 2017) and are sensitive to climate variability (DeVries et al., 2019), the global oceans impose a significant influence over the climate system. In addition to the natural carbon cycles, the oceans are responsible for absorbing about 25% of anthropogenic carbon dioxide emissions (Watson et al., 2020) and storing this carbon in its interior; mitigating rising carbon dioxide concentrations in the atmosphere and the associated climatic change.

The additional buffering comes at a high price for the oceans, which become more acidic the more carbon they absorb (Raven et al., 2005). The effects of changes such as acidification and climate change on organisms have been a focus of marine biology research, but in recent years the antithetical approach has gained popularity. With a growing number of publications examining the impacts of various organisms such as phytoplankton (Asselot et al., 2021, 2022) on ocean physics and temperatures, discussing zoogeochemical impacts e.g. on nutrient cycling (Schmitz et al., 2014, 2018), and recognising the climate change mitigation potential of e.g. well-managed marine reserves (Roberts et al., 2017), the impacts of biota on the oceans and climate system are an emerging area of research.

Roles of higher trophic levels

For a long time, the focus of the research on the biota-induced carbon cycle has been on the roles of lower trophic levels- the planktonic food web and microbes. Primary producers, decomposers such as microbes, and primary consumers such as zooplankton are recognised as being significant for the carbon cycle. For instance, zooplankton change the size of OC through fragmentation in different water layers, which promotes microbial remineralisation (Giering et al., 2014), transport OC to deeper layers through migration (Steinberg et al., 2000), and contribute to the DIC gradient in the ocean by respiration in these layers (Cavan et al., 2017).

On the other hand, higher trophic levels, such as fish and marine mammals, were mainly considered passive actors affected by changes in the marine system. Therefore, the focus was more on the effects of (human-induced) changes on these marine organisms, such as the effects of higher temperatures on spawning areas (Drinkwater, 2005; Sandø et al., 2020) or reduced sea ice cover on mammal populations (Kovacs et al., 2011). The roles of higher trophic levels in the carbon cycle have been largely underestimated or neglected.

However, there is growing evidence that all organisms, including the larger ones further up the food web, can influence their local environment, e.g. fish as habitat providers (O'Leary and Roberts, 2017) and whales through the transfer of nutrients (Roman et al., 2014); as well as larger scale processes, including the marine organic carbon cycle (see Figure 1.1).

Fish and marine mammals contribute directly and indirectly to the OC cycle. They provide OC of various sizes via for instance defecation, excretion, and sinking carcasses, promoting microbial degradation and phagotrophic consumption (Saba et al., 2021). At the same time, higher trophic levels transport OC vertically and horizontally (Roman et al., 2014) and can increase the DIC gradient in the ocean by respiring in different water depths (Martin et al., 2021; Bianchi et al., 2021). The amount of OC actively transported varies greatly but can be up to 40% compared to the total export flux (Saba et al., 2021). These organisms mix water layers, carbon, and nutrients by swimming and moving (Kunze et al., 2006; Huntley and Zhou, 2004). In addition, bony fish produce and excrete inorganic carbonates that sink to the sediment layer or buffer acidification by enhancing alkalinity (Wilson et al., 2011). Globally, these fish-based carbonates make up 3-15% of the total marine carbonate production (Wilson et al., 2009).

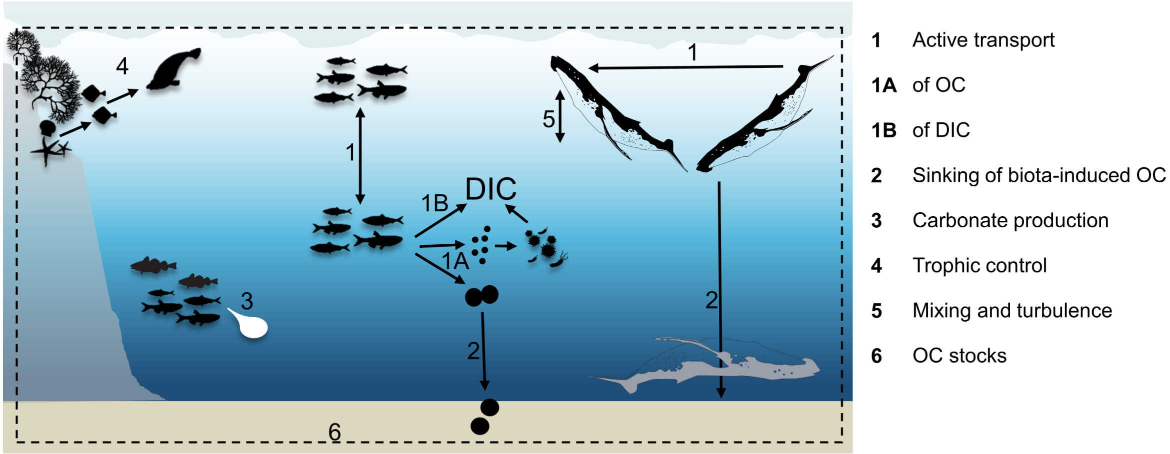

Figure 1.1: Roles and contribution of fish and marine mammals to the OC cycle and stocks.

Indirectly, the higher trophic levels contribute to the carbon cycle by influencing the populations of lower trophic levels through fertilisation and top-down control. Fish and marine mammals excrete nutrients enhancing primary production (Lapointe et al., 2014) and shaping community structures (Shantz et al., 2015). Top-down control can lead to trophic cascades, meaning that a change within the abundance of a higher trophic level influences not only its prey but also the prey of its prey, for instance, primary producers such as kelp (Wilmers et al., 2012). The final role of higher trophic levels within the carbon cycle pertains to the carbon stock contained within their own biomass (Martin et al., 2021). If their populations remain stable over the years, they represent carbon stocks.

Most of these processes have been described and reviewed in recent years, for example, in Martin et al. (2021). However, the importance of these processes for global and regional patterns of carbon cycling and carbon budgets is still in its infancy, as quantifying these mechanisms is challenging and is only now coming into scientific focus. Furthermore, most studies quantifying the carbon services of marine mammals and fish face a problem: the living conditions of these organisms, as well as their numbers, size, and health, are transient. Insights gained may thus not keep pace with changes in the oceans.

Changing oceans - changing cycle?

Not only climate change, acidification, and increasing pollution pose a threat to the oceans, but also a severe defaunation. Higher trophic levels, fish, and marine mammals have been decimated for centuries to meet human needs, e.g. for protein. Whale populations are, at best, 25% of what they were before industrial whaling with the blue whale population having been reduced to only 1% of its original population (Pershing et al., 2010). Like the whales, large and slow-growing fish species are also becoming increasingly rare (Myers and Worm, 2003; Juan-Jordá et al., 2011). As some of these species, such as sharks, are apex predators in their ecosystems, these positions in the ecosystems are increasingly vacant or occupied by other species with partly cascading effects for the entire ecosystems (Baum and Worm, 2009). Ocean defaunation is well known, has been reflected in concepts such as "shifting baselines" (Pauly, 1995; Jackson, 2011), "fishing the food web" (Pauly et al., 1998), and "trophic downgrading" (Estes et al., 2011), and resulted in a loss of about 2.7 Gt of marine biomass (Hatton et al., 2021). The oceans are significantly emptier than they once were.

The consequences of this increasing emptiness are only gradually recognised. Evidence suggests that the collapse of populations of apex predators such as sharks (Wirsing et al., 2008; Leroux and Schmitz, 2015; Limberger et al., 2019) and otters (Wilmers et al., 2012) is changing the functioning of entire ecosystems and affecting significant carbon stocks such as blue carbon ecosystems (Heithaus et al., 2014; Atwood et al., 2015) (Box 1.1). The decline in global populations of whales and fish has altered the global marine carbon cycle and energy flows (Hatton et al., 2021). For example, Bianchi et al. (2021) show that the decline in fish stocks has led to a 30% decrease in carbon exports. Consequently, the oceans likely circulate and store carbon differently, maybe even less efficiently, than before.

Box 1.1

Blue carbon: The carbon sequestered by oceans and coastal ecosystems.

Blue carbon ecosystems: Traditionally limited to coastal ecosystems such as mangroves, kelp forests, seagrass beds and tidal marshes with relevant stocks of mostly sedimentary blue carbon. There is an ongoing discussion to include oceanic ecosystems as well.

Aim and outline of this thesis

The potential dependence of human societies on the services of higher trophic levels in the carbon cycle and in carbon storage and the simultaneous reduction of their biomass for food supply lead to conflicts of use. Accelerating climate change exacerbates these conflicts and may result in carbon considerations becoming a precondition for human actions. Part of such considerations is to understand whether the use of marine resources leads to a loss of carbon stocks or changes in the carbon cycle. For a long time, such a carbon perspective was neglected in marine management, arguing that only phytoplankton were relevant for increasing or decreasing carbon stocks and export, and that phytoplankton management was considered ineffective or impossible (Howard et al., 2017). As evidence mounts that not only phytoplankton but also already managed organisms play important roles, assessing the impacts of human actions in marine ecosystems from a carbon perspective is likely to become increasingly important and gives rise to a challenging and dynamic area of research and marine management.

To assess the carbon impacts resulting from the use of higher trophic levels, we need to define and, if possible, quantify the contribution of higher trophic levels to the OC cycle and storage globally, but also in local and regional systems. Based on this knowledge, we can then understand the unintended consequences of e.g. fisheries on this contribution and decide whether the carbon services of higher trophic levels, and their possible changes, need to feed into marine management decisions and planning.

In this thesis, I aim to advance such an assessment. To this end, we develop a new (visual) concept of the OC cycle in **Study I**. Conventional concepts are mostly sub-concepts, as they often do not go beyond addressing and conceptualising a selection of OC pathways based on, for example, single groups of organisms, as in the microbial loop defined by Azam et al. (1994); or individual processes, as in the eddy-subduction export described by Omand et al. (2015). The (visual) concept adds an overarching framework to such (sub-)concepts, describes general structures of the OC cycle, encompasses all types of organisms and processes involved in the cycle, is globally valid, and can be adapted to different ecosystems and resolutions. It can therefore serve as a basis for the next step: describing the OC cycle and stocks, as well as the involved organisms and their contributions to regional ecosystems, such as the Baltic Sea.

The Baltic Sea ecosystem (Box 1.2) is very well monitored, under high environmental and anthropogenic pressure, has experienced significant reductions in fish stocks and marine mammals, and is subject to several conservation and sustainable management agreements (e.g. the Helsinki Convention and the EU Marine Strategy Framework Directive (MSFD)). This combination of reduced formerly significant stocks of higher trophic levels, functioning management structures, and relatively good data makes the Baltic Sea a very suitable case study to investigate the influence of higher trophic levels on the regional-scales OC cycles and stocks.

Since higher trophic levels contribute to the OC cycle as standing stocks and through their involvement in and execution of processes, we study these two aspects in the Baltic Sea. Therefore, we first evaluate how higher trophic levels contribute to the overall OC stock of the Baltic Sea. To this end, within **Study II** we identify relevant OC pools in the Baltic Sea and quantify the contemporary stocks of these pools for the whole ecosystem. As the first consistent and comparable quantification of this kind in the Baltic Sea, the calculated estimates thus represent the baseline of the entire OC stock of this ecosystem. With the help of this baseline, it is possible to monitor and calculate future changes in these stocks. Both are a prerequisite for incorporating a carbon perspective into future impact assessments of planned management measures.

Subsequently, in **Study III**, we use the concept from Study I to theoretically discuss whether and how the abundance of a key higher trophic level species - cod - could change OC cycle structures and stocks in the Central Baltic Sea (CBS), which has the highest potential for longer-term burial of OC in the Baltic Sea (Carman and Cederwall, 2001). For this purpose, we compare theoretically derived stocks and OC cycles in two states of the CBS - a reference state with high cod abundance and a modified state with very low cod abundance. Further, we describe how the extent of trophic control might alter the influence of cod by distinguishing between a version of the CBS with collapsed cod stocks with extensive top-down control and a version with mixed top-down and bottom-up control. By systematically discussing OC pathways and the contribution of higher trophic levels, it is possible to identify the conditions under which a decline in cod abundance influences the status of the CBS as a carbon source or sink. At the same time, the description of possible changes in living stocks and carbon distributions in the water column shows what consequences a collapse in the cod population could have beyond the OC cycle, e.g. for food webs below the surface waters.

Based on the results of Study I, Study II, and Study III, I return to the global level and, together with my co-authors, summarise the roles of fish in marine ecosystems (**Study IV**).

Through this perspective study, we aim to highlight the benefits associated with healthy fish stocks and the need to provide a scientific and policy basis to enable even more integrative marine management that could harness these benefits.

Although the results of this thesis are partly unquantified and theoretical, they are intended to provide a basis for assessing the consequences of changes at higher trophic levels in the Baltic Sea and for defining the services and values at risk or already lost that will guide future marine management and fisheries.

Box 1.2: The Baltic Sea

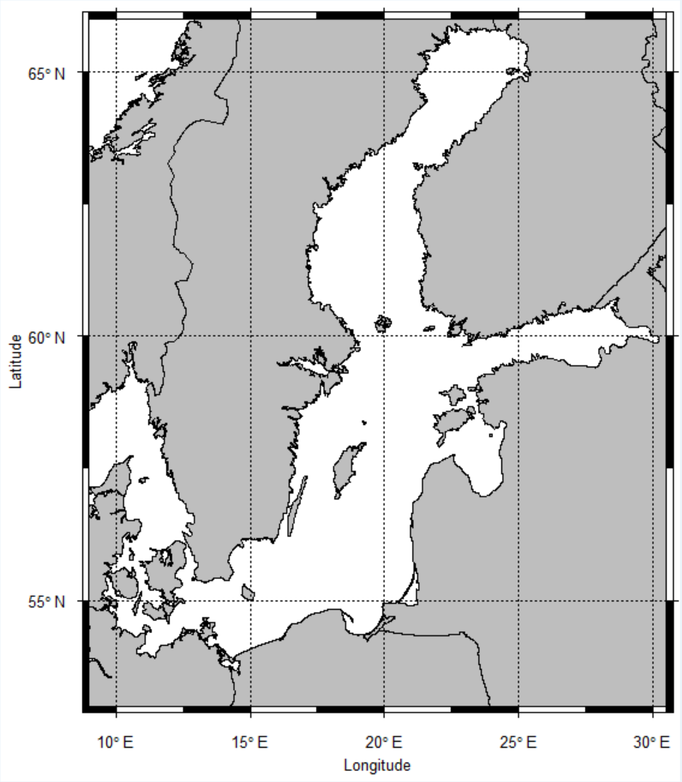

Figure 1.2: The Baltic Sea.

The Baltic Sea is located between 9.5-30° E and 54.5-65.5° N (Figure 1.2) in the Northeast of Europe. It is an almost entirely enclosed brackish ecosystem characterised by a unique Southwest-Northeast gradient of salinity and biodiversity. The Baltic Sea is comparably shallow with a mean depth of 53 m (Jakobsson et al., 2019), with the deepest parts in the Central Baltic Sea (CBS). Its relatively simple food web is characterised by a few key species, among which the piscivorous cod is to mention.

Surrounded by countries with high agricultural activity, the Baltic Sea faces eutrophication from riverine inputs, high fishing pressure and is subject to climate change-induced alterations in temperature and salinity. The ecosystem has already experienced several regime shifts in recent decades (Österblom et al., 2007), including a shift from cod to sprat dominance in the 1980s (Casini et al., 2008).

Despite combating eutrophication by regulating nutrient inputs from rivers and restricting fisheries in the Baltic Sea, severe bottom hypoxia and anoxia (Carstensen et al., 2014a) and declining fish stocks with decreasing size structure (Möllmann et al., 2021; Svedäng and Hornborg, 2017) are recorded.

2 | STUDIES OF THIS THESIS

Contribution to the studies of this thesis

Study I

Scheffold, M. I. E. and Hense, I. (2022): There and back again, a journey of many pathways: conceptualising the marine organic carbon cycle. (In Ocean Science, 18 (2), pp. 437–454. DOI: 10.5194/os-18-437-2022)

My contribution: I co-designed the study, collected the pathway information, performed the comparison and conceptualisation, was mainly responsible for writing the manuscript and handling the submission and review.

Study II

Scheffold, M. I. E. and Hense, I. (2020): Quantifying Contemporary Organic Carbon Stocks of the Baltic Sea Ecosystem. (In Frontiers in Marine Science, 7, p. 1052. DOI: 10.3389/fmars.2020.571956)

My contribution: I co-designed the study and decided on the pools of interest. I collected the data, decided on the method, performed the calculations, was mainly responsible for writing the manuscript and handling the submission and review.

Additional data publishing

Scheffold, M. I. E. and Hense, I. (2020): Estimates of biomass carbon stocks of the Baltic Sea ecosystem, version 2. (PANGAEA repository, DOI: 10.1594/PANGAEA.925062)

My contribution: I compiled the data, wrote the R codes and documented the methodology.

Study III

Scheffold, M. I. E. and Hense, I. (2022): Same same, but different- how a cod collapse might change organic carbon pathway structures in the Central Baltic Sea. (manuscript)

My contribution: I designed the study, decided on the versions for comparison, performed the theoretical analysis and was mainly responsible for writing the manuscript.

Study IV

Martin, A. H., **Scheffold, M. I. E.** and O'Leary, B. C. (2022): Leverage management of fish for climate, biodiversity, and society. (manuscript)

My contribution: I co-designed the study and participated in the discussion and in the writing process.

2.1 Study I: A concept of the organic carbon cycle

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

Maike Iris Esther Scheffold & Inga Hense

Understanding and determining the pathways that organic carbon (OC) takes in the ocean is one of the 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 typically 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 understand and recreate complexity, there is a need to identify commonalities and differences between individual OC pathways and define their overarching structures. Such structures can provide a framework for the growing number of partly overlapping concepts, which conceptualise selected OC pathways, and promote more systematic comparisons and consistent communication, especially between different disciplines. In response, we propose a (visual) concept in which we define such higher-level 'structures' by comparing and condensing marine OC pathways based on their sequences of processes and the layers of the marine system in which they operate. The resulting structures comprise 'closed loops', three remineralisation and two recalcitrant dissolved organic carbon (rDOC) loops that close within marine systems, and 'open loops', condensing pathways leaving the marine system to the atmosphere or deeper sediment layers. In addition, we provide a synthesis of embedded processes, OC pools, and process-performing organisms (agents) embedded in these loops. By translating a definition of the biological carbon pump into our concept, we show how the application and discussion of our defined structures facilitate a consistent visualisation, a systematic comparison of differently resolved concepts and studies, and integration of these in the larger picture of the marine OC cycle. As a complement to quantitative studies and descriptions of individual pathways, our concept decomposes the complexity of OC pathways by defining new universal structures. These structures provide a skeleton that can be adapted to different systems and filled with life by the users.

Keywords: OC cycle concept, OC pathways, overarching structures, remineralisation loops, visualisation, schemata

Published in Ocean Science

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 is an essential and very productive focus of ocean research (Jiao et al., 2018). 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, are continuously expanding our understanding of OC pathways and the marine OC cycle.

Complementing the often-quantitative results, these studies sometimes provide (visual) concepts that abstractly describe and generalise OC pathways as a sequence of processes or a core mechanism. Due to the multitude of disciplines involved, the heterogeneity of ocean systems and the complexity of the marine OC cycle, these concepts often only consider a selection of pathways related to the respective research focus. For example, some studies conceptualise and generalise pathways for specific carbon pools e.g. dissolved OC in the microbial pump (Jiao et al., 2010; Jiao and Zheng, 2011), for a selection of species such as bacteria in the microbial loop (Azam et al., 1994) or for 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 (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., 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 elements to make concept such as the BCP more comparable, comprehensive, systematic and adaptable.

It is plausible and useful 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, no attempt has been made to summarise and generalise the OC pathways and conceptual ideas into an overarching general concept that represents structures of the marine OC cycle.

Existing concepts, especially those aiming at a more comprehensive representation of the marine OC cycle, are often not visually congruent within the respective graphics or compared to schemata in other publications. Processes and pathways are for instance not represented with the same level of detail. For example, Steinberg and Landry (2017), Cavan et al. (2019), Anderson and Ducklow (2001) and Boscolo-Galazzo et al. (2018) visually detach processes from their products, such as DIC, or do not mention some products in the figures at all. As the aim of such studies is not to create congruent conceptual representations of the marine OC cycle, their visualizations are still useful 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 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, displaying concepts 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 marine OC cycle can reduce the transparency of the scientific process and can make comparisons and discussions as well as the adaptation of already existing concepts and ideas more difficult (Scheiner and Willig, 2011). Different resolutions and definitions of pathways and overarching 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 (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 marine OC cycle and pathways. The result of this step is a general concept that does not represent specific carbon processes or a single pathway but defines common structures of all pathways. We define these structures in linguistic and visual units by comparing and condensing similarities of possible OC pathways in the marine system. The result is the definition of several structures of 'closed' and 'open OC loops' that include 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 conceptual frameworks, 2) synthesising definitions and scientific language, 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 marine OC cycle. In this way, the concept can help researchers from different disciplines to facilitate research design, discuss individual concepts, and improve interdisciplinary communication, collaboration, and scientific education.

In the following, we describe how we develop our concept based on the questions 1) What are the different pathways for an OC compound in marine systems? 2) Which structures can be condensed? 3) Which processes, pools and agents are embedded in these structures? By answering the first two questions, we obtain a concept of universal structures of marine OC pathways. By answering question (3) we identify processes, pools, and agents embedded in these structures, which allow defining smaller-scale structures 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.

Concept specifications

Given that we conceptualise only the OC pathways (for a definition of relevant terms of the concept, see Table 2.1), 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 2.1) is an artificial construct since cycles do not start (or end) anywhere and marine carbon may originate from terrestrial run-off, atmospheric deposition, or photosynthesis. In this concept, we do not describe in detail those OC pathways that have left the marine system, either for the atmosphere or for deeper sediment layers that do not interact with the water column, and we 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 time scales of pathways, since we consider different spatial scales closely connected to temporal scales (Dickey, 1990).

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.

To identify structures at higher resolution, 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 μm (Kharbush et al., 2020), aggregates and marine snow; dissolved organic carbon (DOC), defined as non-living carbon smaller 0.2 μm (Kharbush et al., 2020); and volatile organic compounds (VOCs), such as dimethyl sulphate and CH_4.

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; Jiao and Zheng, 2011). We also include dissolved inorganic carbon (DIC) as an intermediate pool. Whilst this DIC pool consists of various inorganic carbon (IC) molecules, we do not distinguish them within our concept.

A (visual) concept of the marine organic carbon cycle

Main structures 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 literature-based pathway concept (see Appendix I, Figure 4.1.1) by collecting and mapping the different pathways that an OC compound can "take" within the marine OC cycle based on a non-systematic literature review. The individual pathways in this concept are defined by *sequences of processes* (Table 2.1), such as sinking and remineralisation, and either return to the initial position in the surface waters or leave the marine system to the sediment or the atmosphere. We compare the OC pathways in the literature-based pathway concept and condense their similarities into generally applicable structures.

The structures, e.g. closed loops, are stripped of any processes, pools or involved agents (definitions see Table 2.1). We add this information in the next step allowing the definition of additional structures of higher resolution.

To explain how the pathways of the literature-based pathway concept can be compared and condensed to define structures of the marine 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 literature-based pathway concept, shows 100 individual pathways that end at the beach. These pathways are similar, but all differ in the overall sequence of streets and vehicles used.

There is, however, a common denominator for all pathways. To reach the beach, the lagoon must be crossed. This condition is independent of the way of crossing. People reach the sandbank in different ways, e.g. by public ferry or private boat. The result ‘people reach the sandbank’ and the general functionality ‘crossing the lagoon’ of these processes coincide. Therefore, we define ‘crossing the lagoon’ as a functional segment (*summarised function of the involved processes with the same general functionality*, Table 2.1) common to all pathways to the beach. It should be noted that this does not mean that all pathways ONLY need this functional segment. The functional segment ‘crossing the lagoon’ is at least required to reach the beach and the bottleneck of ALL beach pathways.

At a higher resolution, which allows more complexity, differences of the beach pathways can be identified and grouped by defining the functional segments shared by these groups. For instance, people who do not live at the harbour front (functionality: ‘living behind the harbour front’) use one of three roads to reach the harbour (functionality: ‘reaching the harbour’). These pathways share the sequence of the functional segments ‘living behind the harbour front’, ‘reaching the harbour’ and ‘crossing the lagoon’. People living at the harbour front (functionality: ‘living at the harbour front’) only have to cross the lagoon and share the sequence of ‘living at the harbour front’ and ‘crossing the lagoon’.

Table 2.1: Definitions and examples of relevant terms based on three individual pathways.

Example pathways in the literature-based pathway concept	**Pathway 1:** Phytoplankton DOC exudation → Bacterial remineralisation → DIC uptake by phytoplankton **Pathway 2:** Zooplankton grazing on phytoplankton → Zooplankton respiration → DIC uptake by macrophytes **Pathway 3:** Phytoplankton respiration → DIC outgassing

Term	Definition	Examples based on pathways 1-3
Pool	A reservoir of a certain substance, in this case organic carbon. Pools can be living and non-living.	Phytoplankton, DOC, Bacteria, DIC, Zooplankton, Macrophytes
Agent	An organism that initiates or executes a process.	Phytoplankton, Bacteria, Zooplankton, Macrophytes
Space	A spatially bounded volume with different environmental conditions.	Surface layer space (SLS), Atmosphere space (AS)
Initial position	Abstract start position of the OC pathways (OC in the SLS).	OC in the surface layer space (SLS)
Process	A self-contained change in the properties or position of carbon. A process is embedded in a functional segment.	Phytoplankton DOC exudation, Zooplankton grazing on phytoplankton, Bacterial remineralisation, Zooplankton respiration, Phytoplankton respiration, DIC uptake by phytoplankton, DIC uptake by macrophytes, DIC outgassing
Functional segment	The condensed function of processes that have the same general functionality. They are defined by the abstracted result of the processes, independent of species involved, etc. Functional segments comprise all globally applicable processes having the same general functionality.	OC size change, POC consumption, OC remineralisation, DIC uptake by primary producers, DIC exit
Pathway	An individual sequence of processes. The sequence can be translated to a sequence of functional segments. Each pathway is embedded in a structure. Although pathways can be described by sequences of functional segments, they always represent individual features and not condensed ones.	Pathway 1: OC size change → OC remineralisation → DIC uptake by primary producers Pathway 2: POC consumption → OC remineralisation → DIC uptake by primary producers Pathway 3: OC remineralisation → DIC exit
Structure	A structure is a superordinate generalisation/ condensation of multiple pathways. A structure is defined by a unique combination of a sequence of functional segments and the involved spaces. Syntax: Functional segment [Space]	Structure 1: OC remineralisation [SLS] → DIC uptake by primary producers [SLS] Structure 2: OC remineralisation [SLS] → DIC exit [AS]

Continued on next page

Table 2.1 – continued from previous page

Term	Definition	Examples based on pathways 1-3
	Sequences of functional segments must be true for all pathways within the structure. Depending on the resolution, different structures can be defined. Structures can always be related to each other, e.g. the surface layer remineralisation loop is part of the superordinate structure closed loop (see below).	
Closed loop	A structure that comprises all pathways returning to the initial position is named closed loops. Closed loops are the most overarching structure in the marine OC cycle.	Surface layer remineralisation loop (SLRL): OC remineralisation [SLS] → DIC uptake by primary producers [SLS]
Open loops	A structure that comprises all pathways not returning to the initial position is named 'open' loops.	Atmosphere IC loop (AICL): OC remineralisation [SLS] → DIC exit [AS]
Marine OC cycle	The marine OC cycle consists of all closed loops.	

Based on these distinct sequences of functional segments, different structures can be defined. The most general and superordinate structure is the 'entire town-beach' structure defined by the functional segment 'crossing the lagoon', which is common to all pathways. That sequence is the minimum sequence shared by all pathways and defines the highest-level structure. At the higher resolution, a distinction can be made between a 'harbour front-beach' structure (living at the harbour-front and crossing the lagoon) and a 'behind the harbour-beach' structure (living behind the harbour-front, reaching the harbour and crossing the lagoon). The sequences of functional segments minimally describe all pathways within these structures.

The resolution and thus the definition of structures is a matter of choice. One could for example also distinguish other structures based on the method of crossing the lagoon or find further differences and commonalities between the pathways in the rest of the town and define additional structures. However, assuming that the rest of the town has a very diverse and complicated road network, the 'harbour front-beach' and the 'behind the harbour-beach' structure may be sufficient to define, for instance, pressure points and bottlenecks when construction works block the three streets to the harbour.

Similarly to the description above, we define structures of the marine OC pathways based on the literature-based pathway concept (see Appendix I, Figure 4.1.2 for a schematic of the methodological steps). One structure that immediately catches the eye are pathways that loop inside or outside the marine system. We define these structures as closed and 'open' loops. The closed loops are the highest structure in the marine OC cycle and the focus of this study. In the following, we define general structures hierarchically below the closed loops by comparing the pathways of these loops as described above. The structures we want to define should be as general as possible while still covering relevant differences.

We identify six functional segments that are necessary to describe the desired structures (Figure 2.1.1): *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 excluding the rDOC-related functional segments would further reduce the number of functional segments and structures. 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.

The depths OC reaches on its pathways is another of these relevant difference that we want to resolve, as these depths affect the function of OC in the ecosystem (e.g. as a food source for benthic organisms), the environmental conditions it encounters (e.g. bioturbation) and the time it takes to return to the surface layer (e.g. years or decades). However, the functional segment OC position change (A) does not provide information on whether the position change ends in the water column or in the sediment.

Hence, to unambiguously define structures that account for the differences described above we need to add 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 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 sediment space (USS)*, remineralisers also remineralise highly degraded material as it remains in their vicinity longer than in the water column (Middelburg, 2019). The *lower sediment space (LSS)* is largely abiotic and undisturbed and allows lithification processes. In addition, we define the *atmosphere space (AS)* above the marine system. The use and choice of spaces depend on the intended resolution of the structures. Users of the concept can change the spaces, e.g. by subdividing the water column space, resulting in a different number of closed loops, or omit the spatial extent completely if they aim for an even more general description than ours. However, if the minimum number of closed loops is to be conceptually described at the same level of resolution as ours, 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 functional 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).

Based on the unique combinations of 1) the sequence of functional segments and 2) the involved spaces, we now define three *closed remineralisation* and two *rDOC loops* (Figure 2.1.1 and Table 2.2).

The remineralisation loops comprise: a *surface layer remineralisation loop (SLRL)*, a *water column remineralisation loop (WCRL)*, and an *upper sediment remineralisation loop (USRL)*

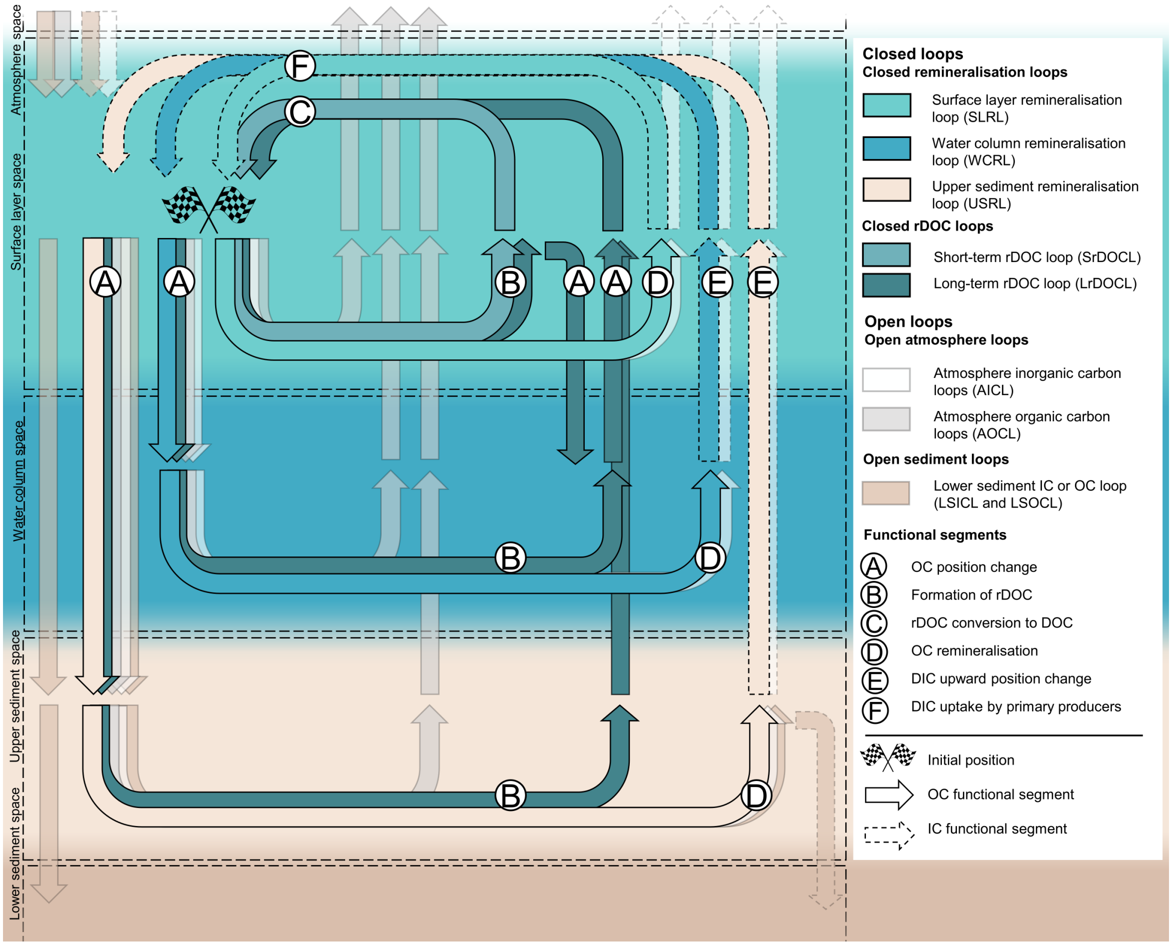

Figure 2.1.1: General structures of the marine OC cycling with three closed remineralisation and two closed rDOC loops, the spaces and the involved functional segments. 'Open' loops are only displayed with transparent colours as they are not our focus.

(Table 2.2). 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 functional 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, remineralisation in the WCS, and an upward position change of DIC into the SLS, where it is taken up (WCRL: A [WCS] → D [WCS] → E [SLS] → 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] → D [WCS] → E [SLS] → F [SLS]). If zooplankton respiration occurs in the SLS, the pathway belongs to the SLRL (SLRL: D [SLS] → F [SLS]). We define the USRL analogous to the WCRL, but with remineralisation taking place in the USS (USRL: A [USS] → D [USS] → E [SLS] → F [SLS]).

The two functional segments 'Formation of rDOC' (B) and 'rDOC conversion to DOC' (C) in the SLS are part of another set of closed loops, the rDOC loops (Figure 2.1.1 and Table 2.2). 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

Table 2.2: Summary of sequences of functional segments and spaces defining the remineralisation and rDOC loops. The separation rule comes to play, when assigning a pathway to one of the defined loops. 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). functional 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 functional segments plus spaces	Separation rule
SLRL	D [**SLS**] → F [**SLS**]	Ultimate remineralisation in SLS before F
WCRL	A [**WCS**] → D [**WCS**] → E [SLS] → F [SLS]	Ultimate remineralisation in WCS before E and F
USRL	A [**USS**] → D [**USS**] → E [SLS] → F [SLS]	Ultimate remineralisation in USS before E and F
SrDOCL	B [**SLS**]→ C [**SLS**]	Formation of rDOC in SLS and no A
LrDOCL	B [SLS] → A [**WCS/USS**]→ A [SLS] → C [SLS]	Formation of rDOC in SLS with A
	or	
	A [**WCS/USS**]→ B [**WCS/USS**]→ A [SLS] → C [SLS]	Formation of rDOC in WCS or USS

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 can persist 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] → C [SLS]), while the rDOC long-term loop additionally comprises the functional segment 'OC position change' (A), with accumulation mostly or even entirely in the WCS (LrDOCL: B [SLS] → A [WCS/USS] → A [SLS] → C [SLS] or A [WCS/USS] → B [WCS/USS] → A [SLS] → 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 loop includes rDOC production in the USS alongside its transport to the WCS. It has to be noted, that only rDOC that reaches the surface and is converted back into more bioavailable forms in the SLS belongs to the LrDOCL (LrDOCL: ... A [SLS] → C [SLS]). rDOC can for instance be part of the WCRL when remineralised in WCS (WCRL: B [SLS] → A [WCS] → D [WCS] → E [SLS] → F [SLS]). Because of the climatic importance of rDOC, we distinguish rDOC from DOC as described before. Technically, however, rDOC represents an intermediate "storage" step of remineralisation or open loops.

All loops comprise a continuum of processes that are not addressed in the defined sequences of functional segments. For example, the SLRL also includes pathways on which OC 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] → A [SLS] → D [SLS] → F [SLS]). To avoid double counting when assigning pathways like this to one of our defined loops, two separation rules apply. 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 eventually remineralised in the SLS before taken up 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 2.2).

For the minimal description of the remineralisation and rDOC loops, the sequences of the above-defined functional segments are sufficient and unambiguous. However, users of the concept can identify and combine other functional segments to define different higher-resolution structures.

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 structures of 'open' loops. The *atmosphere IC loops (AICLs)* describe the outgassing of DIC, produced in different spaces, to the atmosphere. The *atmospheric OC loops (AOCLs)* comprise 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 (LSOCL)* and *lower sediment OC loops (LSICL)* describe the burial and lithification of carbon in the LSS, entering geological cycling.

Embedded processes, pools and agents

Having defined the structures of remineralisation and rDOC loops, we now add and describe global processes, pools and agents embedded in each functional segment (Figure 2.1.2 and Table 2.3). This addition allows to define structures 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 functional segments. This means that, for example, upward position changes of POC or DOC are not resolved.

Two of the three remineralisation loops include the functional segments OC position change (A) and DIC upward position change (E). Processes belonging to functional segments A and E include sinking, diffusion and advection, and direct and indirect biota-induced transport.

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 are the analogous processes 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 functional segment A of POC (Figure 2.1.2).

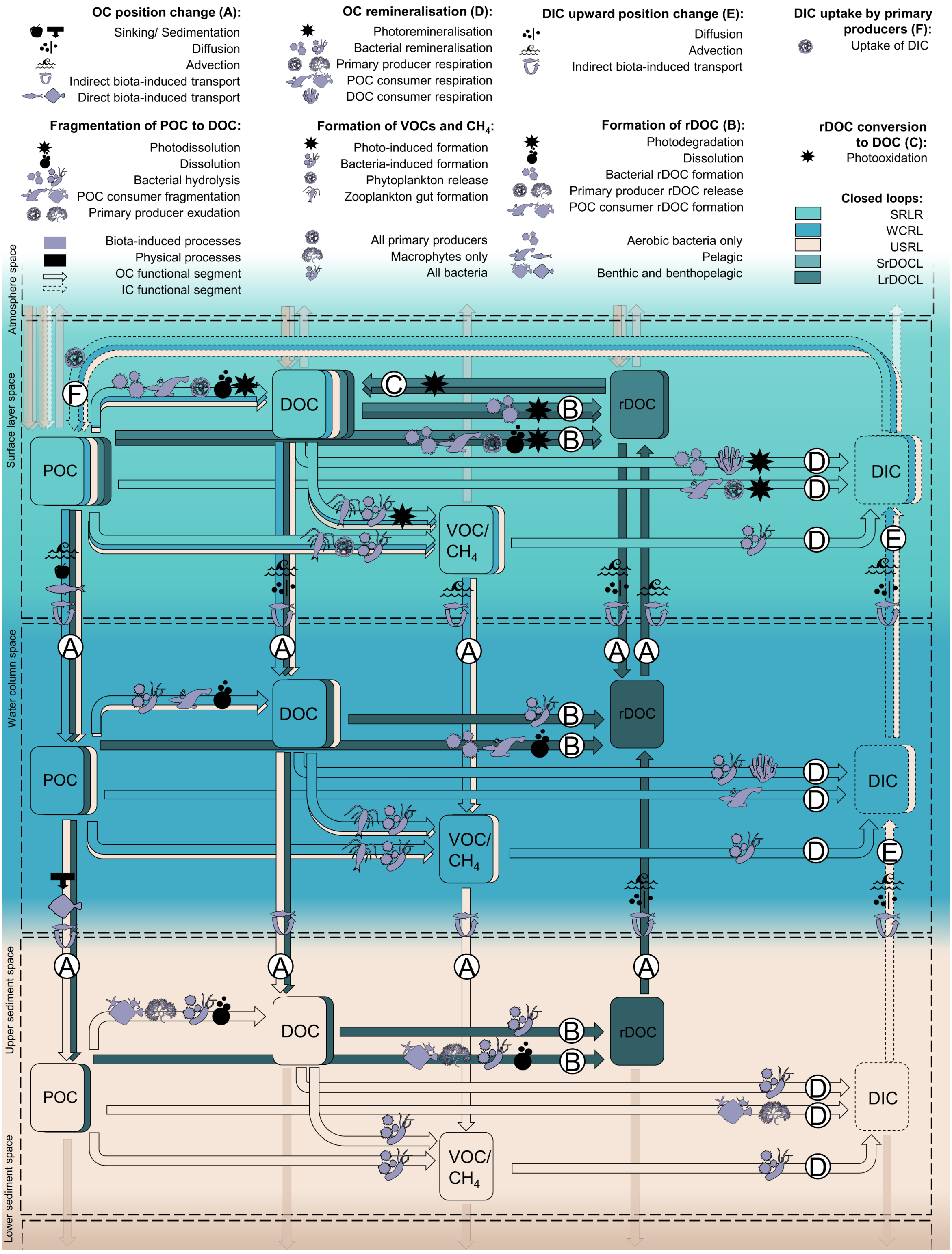

Figure 2.1.2: Defined OC structures with functional segments A-F, spaces and embedded processes, OC pools and involved organisms. 'Open' loops are indicated by transparent colours. Organisms can be agents (producing DOC by sloppy feeding) and part of the carbon pool (consumers as part of POC respire DIC) at the same time. Fragmentation processes and pathways for DOC and VOCs/ CH_4 are included. As they are not resolved in the loops, these pathways are not marked with capital letters.

(r)DOC (DOC and rDOC) 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 Figure 2.1.2) and DIC always diffuses upwards (E). The upward diffusion of non-refractory DOC from the sediment is not considered in the defined functional segments as upward movements are not common to all pathways of the remineralisation loops.

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 any functional 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 any functional 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 any functional segments of A for (r)DOC and POC and E in the water column and the sediment.

The following processes belong to the functional 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 2.3: Processes embedded in the functional segments of the defined loops. Italic pools 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] LrDOCL: A [WCS]	Gravitational sinking	POC		Downwards
Sedimentation	USRL: A [USS] LrDOCL: A [USS]	Sedimentation of sinking matter	POC		Downwards
Diffusion	WCRL: A [WCS]	Diffusion in the water column and pore waters	DOC		Downwards
	LrDOCL: A [WCS]		rDOC		Downwards, upwards
Advection	WCRL: A [WCS]	Up- and downwelling, mixing, turbulence, eddies	POC, DOC, VOCs, CH_4		Downwards
	LrDOCL: A [WCS]		POC, DOC, rDOC		Downwards, upwards
Indirect biota-induced transport	WCRL: A [WCS] USRL: A [USS]	Biota-induced turbulence, induced drift, digging, burrowing, bioirrigation, sediment reworking	POC, DOC, VOCs, CH_4	Swimming and moving species (pelagic, benthopelagic and benthic)	Downwards
	LrDOCL: A [WCS] LrDOCL: A [USS]		POC, DOC, rDOC		Downwards, upwards
Direct biota-induced transport	WCRL: A [WCS] USRL: A [USS]	Transport in living tissue or OC distribution in organisms spanning several spaces	POC	Swimming and moving species (pelagic, benthopelagic and benthic), organisms spanning several spaces (e.g. kelp)	Downwards
	LrDOCL: A [WCS] LrDOCL: A [USS]				Downwards, upwards

Formation of rDOC (B)

Process	**Loop syntax**	**Process description**	**Pools**	**Organisms**	**Directions**
Photodegradation	SrDOCL: B [SLS] LrDOCL: B [SLS]	Degradation of labile to recalcitrant OC by UV light	DOC, POC, *rDOC*		

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Table 2.3 – continued from previous page

Process	**Loop syntax**	**Process description**	**Pools**	**Organisms**	**Directions**
Dissolution	SrDOCL: B [SLS] LrDOCL: B [SLS] LrDOCL: B [WCS] LrDOCL: B [USS]	Dissolution due to sinking (enhanced by bacteria) or pore-water interactions	POC, *rDOC*		
Bacterial rDOC formation	SrDOCL: B [SLS] LrDOCL: B [SLS] LrDOCL: B [WCS] LrDOCL: B [USS]	Release of capsular mate- rial and rDOC under e.g. stress conditions	DOC, POC, *rDOC*	Bacteria, viruses	
Primary producer rDOC release	SrDOCL: B [SLS] LrDOCL: B [SLS] LrDOCL: B [WCS] LrDOCL: B [USS]	Release of rDOC	POC, *rDOC*	Phytoplankton and e.g. macrophytes	
POC consumer rDOC formation	SrDOCL: B [SLS] LrDOCL: B [SLS] LrDOCL: B [WCS] LrDOCL: B [USS]	Direct (excretion) or indirect release (e.g. via sloppy feeding) of rDOC	POC, *rDOC*	POC consumers (pelagic, bentho-pelagic and benthic)	
Conversion of rDOC to DOC (C)					
Process	**Loop syntax**	**Process description**	**Pools**	**Organisms**	**Directions**
Photooxidation	SrDOCL: C [SLS] LrDOCL: C [SLS]	Photochemical conversion of rDOC to DOC	rDOC, *DOC*		
OC remineralisation (D)					
Process	**Loop syntax**	**Process description**	**Pools**	**Organisms**	**Directions**
Photoremineralisation	SLRL: D [SLS]	Direct UV remineralisation	POC, DOC, *DIC*		
Bacterial remineralisation	SLRL: D [SLS] WCRL: D [WCS] USRL: D [USS]	Bacterial DOC (VOCs)-based respiration	DOC, VOCs, CH_4 , *DIC*	Bacteria and archaea	
Primary producer respiration	SLRL: D [SLS] USRL: D [USS]	Respiration of primary producers	POC, *DIC*	Phytoplankton and e.g. macrophytes	

Continued on next page

Table 2.3 – continued from previous page

Process	Loop syntax	Process description	Pools	Organisms	Directions
POC consumer respiration	SLRL: D [SLS] WCRL: D [WCS] USRL: D [USS]	Respiration of POC consumers	POC, *DIC*	POC consumers (pelagic, bentho-pelagic and benthic)	
DOC consumer respiration	SLRL: D [SLS] WCRL: D [WCS]	Respiration of DOC consumers	DOC, *DIC*	DOC consumers (filter feeders) excluding bacteria	
DIC upward position change (E)					
Process	**Loop syntax**	**Process description**	**Pools**	**Organisms**	**Directions**
Diffusion	WCRL: E [SLS] USRL: E [SLS]	Diffusion in the water column and pore waters	DIC		Upwards
Advection	WCRL: E [SLS] USRL: E [SLS]	Down- and upwelling, mixing, turbulence and eddies, physical induced resuspension	DIC		Upwards
Indirect biota-induced transport	WCRL: E [SLS] USRL: E [SLS]	Biota-induced turbulence, induced drift, digging, burrowing, bioirrigation, sediment reworking and related processes	DIC	Swimming and moving species (pelagic, bentho-pelagic and benthic)	Upwards
DIC uptake by primary producers (F)					
Process	**Loop syntax**	**Process description**	**Pools**	**Organisms**	**Directions**
Uptake of DIC	SLRL: F [SLS] WCRL: F [SLS] USRL: F [SLS]	Photosynthesis	DIC, *POC*	Phytoplankton and e.g. macrophytes	

Bacteria and archaea remineralise DOC in functional 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 reduce the size of organic POC by sloppy feeding on living and non-living POC by e.g. zooplankton coprorhexy (Lampitt et al., 1990), by producing small metabolites, by excreting DOC (Lampert, 1978) or by swimming or moving (Dilling and Alldredge, 2000;

Goldthwait et al., 2004). 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 lysis (Middelboe et al., 1996).

The transformation from POC to DOC (arrows from POC to DOC, Figure 2.1.2) that takes place before bacterial remineralisation are not defined as functional segment of the remineralisation loops, as not every OC compound needs to undergo one of these changes to be remineralised. However, when e.g. considering only DOC-based pathways, the change in OC size from POC to DOC can be defined as a common functional segment and used to define structures such as POC-DOC remineralisation loops.

In addition, bacteria can oxidise VOCs and CH_4 (D of VOCs/ CH_4 in Figure 2.1.1) as, for example, shown by Halsey et al. (2017). The VOCs and CH_4 origin from abiotic processes such as photochemical degradation of DOC (Kieber et al., 1989) and biogenic processes, e.g. 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 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 functional 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.

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 LrDOCL, OC position change (A). We present some of the involved abiotic and biotic processes, which have been reviewed e.g. in Legendre et al. (2015).

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; Jiao and Zheng, 2011), the release of capsular material by bacteria (Stoderegger and Herndl, 1998), bacterial hydrolysis of POC (Jiao and Zheng, 2011), bacterial stress responses to low-labile DOC and unfortunate nutrient conditions (Stoderegger and Herndl, 1998), and successive consumption by higher trophic levels (Jiao and Zheng, 2011). In addition, some phytoplankton directly exudates rDOC (Jiao and Zheng, 2011). Both microbes and phytoplankton also release rDOC due to viral lysis of host cells (Jiao and Zheng, 2011). Furthermore, processes that convert living and non-living POC into DOC, e.g. dissolution, can dilute DOC to the point where it can no longer serve as sufficient nutrition for microbes and can be considered technically recalcitrant (Arrieta et al., 2015) (Figure 2.1.2, 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 on 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 structures of higher resolution. For example, for SLRL, six structures can be defined based on the carbon pools involved: a POC-SLRL, a POC-DOC-SLRL, a POC-DOC-VOC/CH_4-SLRL and a POC-VOC/CH_4-SLRL, as well as a DOC-SLRL and a DOC-VOC/CH_4-SLRL. Depending on the research question or desired level of detail, multiple structures can be defined based on the processes and agents involved. The higher the resolution of the structure, the more the structures resemble descriptions of individual pathways. In the following discussion, we use the example of the biological carbon pump to show how different structures can look like and which insights e.g. a comparison of such different structures can provide.

Discussion

Our concept of the marine OC cycle condenses pathways to superordinate structures and provides an overview of embedded processes, pools, and agents, which allows resolving structures of smaller scale and higher resolution. Our overarching structures complement 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 conceptualised pathways, integrating new findings and placing, for example, pathways of finite length scale in a broader framework.

To discuss some of these aspects in an application example, we translate pathways of the biological carbon pump (BCP) into our concept (Figure 2.1.3). Based on the definition of Giering et al. (2020)[1], 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 structures with different resolutions and choices of pathways.

Using the syntax of our concept and functional segments A-F, the defined BCP involves the uptake of inorganic carbon into biomass in the surface waters (F [SLS]) and the OC position change to the interior of the ocean (A [Ocean Interior]), where it is remineralised to DIC (D [Ocean interior]) (Figure 2.1.3 panel (a)). For simplicity, we disregard rDOC, VOCs and CH_4 and start again with the previously introduced initial position. As it is not clarified in the definition, we assume that the ocean interior does not contain the USS and define it as WCS. Based on this restriction of "ocean interior" we classify the BCP as part of the WCRL or the corresponding atmosphere inorganic carbon cycle (AICL). Note that we need to add

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[1] If not mentioned differently, we always refer to the BCP definition by Giering et al. (2020) in the following discussion.

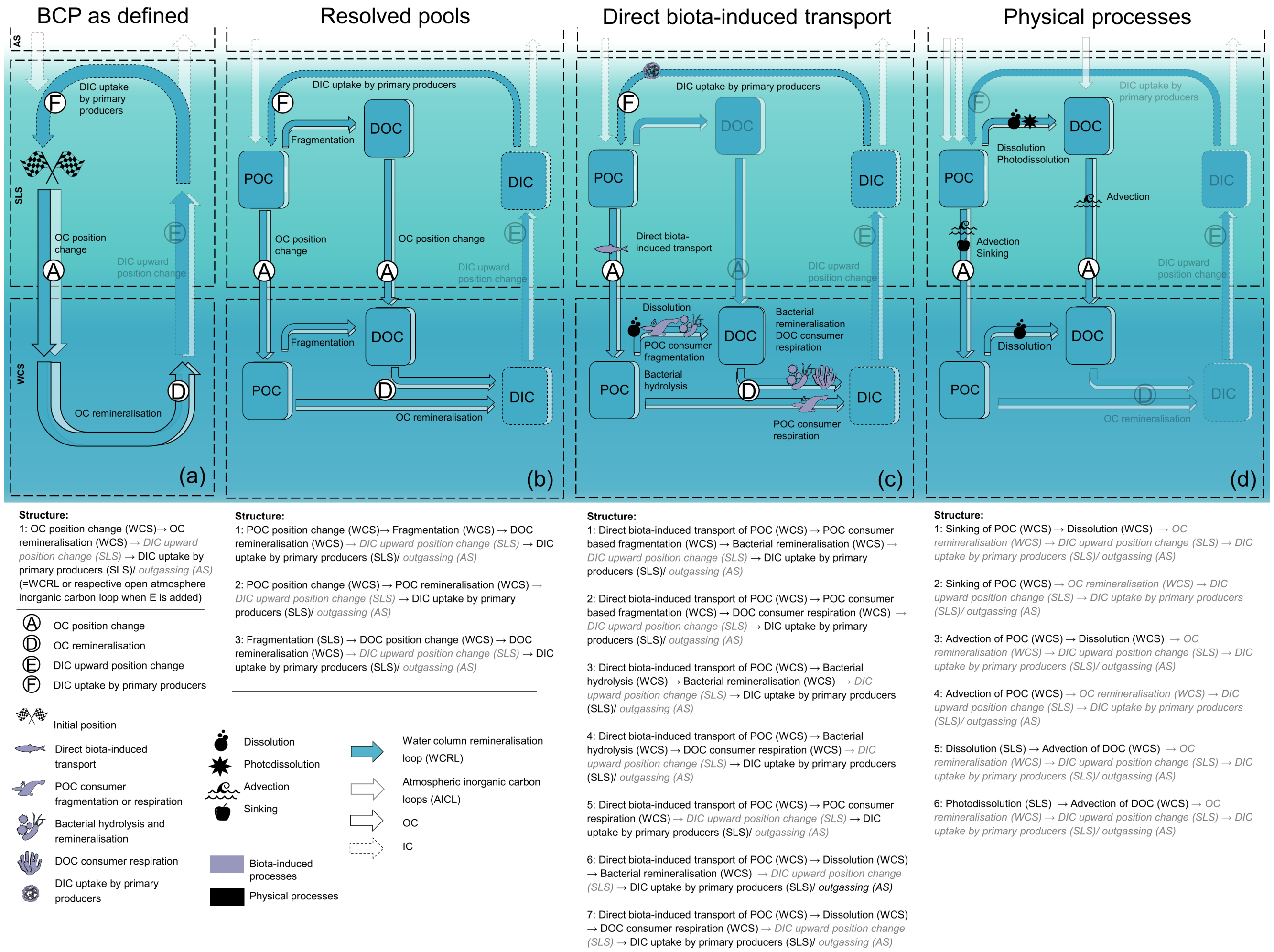
functional segment E to count the BCP to the WCRL as E is not included in the defined BCP.

If we now resolve the OC pools involved in the BCP (here POC and DOC), we can define three BCP structures of higher resolution (panel b). Each of these structures defines a part of the BCP. All together, they capture all pathways of the defined BCP. Taking only pathways with a specific set of processes into account, produces structures that do no longer comprise all pathways of the BCP. For example, focusing on pathways with direct biota-induced transport (A), results in seven structures. These structures only serve structure 2 from panel (b) (Figure 2.1.3) and thus represent only a part of the defined BCP. This part resembles other concepts of BCPs such as the mesopelagic-migrant pump and the seasonal lipid pump (Boyd et al., 2019). Focusing on the purely physically induced pathways of the BCP leads to six different structures that do not resolve remineralisation (D) and DIC uptake (F) as they are non-physical processes (Figure 3, panel (d)). These six structures could potentially serve all of the higher-level structures in panel (b) of the defined BCP if we add D and F, but do also not cover all the pathways of the BCP (see panel (c)). Nevertheless, the structures in d) resemble some, often more traditional, concepts of the BCP, e.g. from Hansell and Carlson (2001) and De La Rocha (2006), which do not explicitly consider DIC uptake and remineralisation.

Integrating the BCP definition of Giering et al. (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 et al. (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). This ambiguity of the space in which the BCP operates means that we may identify pathways as part of the BCP that are not, while excluding others that actually are. It is therefore necessary to define the spaces in which the BCP operates more distinctly. 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 structure.

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 et al. (2020) does not explicitly exclude the DOC pool, we resolve DOC with our illustration of the 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 OC cycle, as there is no dead end in nature. Furthermore, our approach helps to identify how different sub-concepts fit into more general definitions (panels (b)-(c)



Structure:
1: OC position change (WCS)→ OC remineralisation (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)* (=WCRL or respective open atmosphere inorganic carbon loop when E is added)

Ⓐ OC position change
Ⓓ OC remineralisation
Ⓔ DIC upward position change
Ⓕ DIC uptake by primary producers

Structure:
1: POC position change (WCS)→ Fragmentation (WCS) → DOC remineralisation (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

2: POC position change (WCS) → POC remineralisation (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

3: Fragmentation (SLS) → DOC position change (WCS) → DOC remineralisation (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

Structure:
1: Direct biota-induced transport of POC (WCS) → POC consumer based fragmentation (WCS) → Bacterial remineralisation (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

2: Direct biota-induced transport of POC (WCS) → POC consumer based fragmentation (WCS) → DOC consumer respiration (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

3: Direct biota-induced transport of POC (WCS) → Bacterial hydrolysis (WCS) → Bacterial remineralisation (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

4: Direct biota-induced transport of POC (WCS) → Bacterial hydrolysis (WCS) → DOC consumer respiration (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

5: Direct biota-induced transport of POC (WCS) → POC consumer respiration (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

6: Direct biota-induced transport of POC (WCS) → Dissolution (WCS) → Bacterial remineralisation (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

7: Direct biota-induced transport of POC (WCS) → Dissolution (WCS) → DOC consumer respiration (WCS) → *DIC upward position change (SLS)* → DIC uptake by primary producers (SLS)/ *outgassing (AS)*

Structure:
1: Sinking of POC (WCS) → Dissolution (WCS) *→ OC remineralisation (WCS) → DIC upward position change (SLS) → DIC uptake by primary producers (SLS)/ outgassing (AS)*

2: Sinking of POC (WCS) *→ OC remineralisation (WCS) → DIC upward position change (SLS) → DIC uptake by primary producers (SLS)/ outgassing (AS)*

3: Advection of POC (WCS) → Dissolution (WCS) *→ OC remineralisation (WCS) → DIC upward position change (SLS) → DIC uptake by primary producers (SLS)/ outgassing (AS)*

4: Advection of POC (WCS) *→ OC remineralisation (WCS) → DIC upward position change (SLS) → DIC uptake by primary producers (SLS)/ outgassing (AS)*

5: Dissolution (SLS) → Advection of DOC (WCS) *→ OC remineralisation (WCS) → DIC upward position change (SLS) → DIC uptake by primary producers (SLS)/ outgassing (AS)*

6: Photodissolution (SLS) → Advection of DOC (WCS) *→ OC remineralisation (WCS) → DIC upward position change (SLS) → DIC uptake by primary producers (SLS)/ outgassing (AS)*

Figure 2.1.3: The illustration of the BCP defined by Giering et al. (2020) with our concept. Panel (a) shows the superordinate BCP structures based on the definition. Panel (b) additionally 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/grey functional segments are not explicitly included in the definition of the BCP or the selected pathways. Note that all structures are part of the WCRL or AICL when adding functional segment E to a) - c) and D, E and F to d). Note further, that panel d) does only belong to the defined BCP if functional segments D and F are added.

compared to panel (a)), but also where some inconsistencies might occur, e.g. remineralisation included a)- c) or not 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 originate from the SLS. A study based on the pathways as in panel (c) 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 systematise these considerations and make them more comparable.

The BCP example further 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, was considered quantitatively secondary and therefore 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 carbon pathway to the sediment (McClain et al., 2019), and fish and mammals contribute to the marine OC cycle through various processes (Martin et al., 2021). With these processes, many new structures 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 general structures.

By generalizing structures and providing a congruent visual representation, our concept may reduce the potential for misunderstandings of the marine OC cycle potentially and unintentionally caused by visual concepts of finite length scale. An example of such a potential misunderstanding is the representation of pathways transporting DIC to depths without resolving what happens subsequently to DIC, found 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 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 address the increasingly interdisciplinary scientific community, to strengthen the coherence of (visual) concepts and to identify the overarching structures of individual pathways.

The provision of overarching structures comes at the cost of not capturing the complexity of the marine OC cycle. 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 nor meaningful. Accordingly, our concept does not want to and cannot resolve individual pathways. On the contrary, it focuses on overarching structures and the minimal functional segments necessary to describe them. Hence, our concept reduces many pathways to a sequence that does not capture their full extent, biological relevance, complexity, and temporal dimension.

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 proves 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.

Conclusion

We propose a general (visual) concept for the marine part of the organic carbon cycle. It complements and integrates existing concepts and defines overarching OC structures such as remineralisation and rDOC loops and the processes, pools and agents involved. Building on concepts that focus on individual or a subset of marine OC pathways, our concept identifies general structures of all pathways. Details and complexity are disregarded in favour of a systematic structures that can facilitate the identification and comparison of concepts, pathways, pools and studies. The concept can be adapted to a wide range of 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.

2.2 Study II: The Baltic Sea organic carbon stocks

Quantifying contemporary organic carbon stocks of the Baltic Sea ecosystem

Maike Scheffold & Inga Hense

The identification of carbon pools and the quantification of carbon stocks is necessary to (1) track changes in ecosystem dynamics, (2) inform science-based ecosystem and blue-carbon management, and (3) evaluate ecosystem and food web models. However, estimates of organic carbon stocks in marine ecosystems are incomplete or inconsistent. Therefore, we provide a first consistent estimate of relevant organic carbon stocks of a distinct marine ecosystem- the Baltic Sea. We estimate its contemporary standing stocks of 18 non-living and living organic carbon pools using data from literature and open-access databases. In contrast to existing data, our estimates are valid for the entire Baltic Sea, include necessary pools and are verifiable, as we describe data sources, methods and the associated uncertainties in detail to allow reproduction and critical evaluation. The total organic carbon (TOC) in the Baltic Sea ecosystem amounts to 1,050 ± 90 gC/m^2 (440 ± 40 Mt). The non-living stocks account for about 98.8% and the living stocks for 1.2% of the TOC. Our estimates indicate that benthos has the highest living organic carbon stock and that the stock of particulate organic carbon (POC) has been underestimated in some previous studies. In addition, we find a partially inverted biomass distribution with a higher stock of primary consumers than primary producers. Our estimates provide a baseline of the size and distribution of the organic carbon in the Baltic Sea for the current period. Analyses of inorganic carbon stocks and the interplay between inorganic and organic stocks must follow to further define the baseline of total carbon stocks in the Baltic Sea.

Keywords: standing stocks, blue carbon, sediment carbon, macrophytes stock, inverted biomass pyramid, biomass estimates

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Introduction

The identification of carbon pools and the quantification of carbon stocks is necessary to (1) track changes in ecosystem dynamics, (2) inform science-based ecosystem or blue carbon management, and (3) evaluate ecosystem and food web models. To meet these needs in the Baltic Sea, we identify living and non-living organic carbon pools of the Baltic Sea ecosystem and quantify their contemporary stocks.

The semi-enclosed, brackish Baltic Sea lies in the northern part of Europe and covers an area of about 420,000 km^2; including the Danish Strait and the Kattegat. With an average depth of ∼53 m (Jakobsson et al., 2019) and a high surface-to-volume ratio it is relatively shallow compared to other marine systems. Surrounded by nine countries and with a drainage system about four times larger than its sea surface, the Baltic Sea system is influenced by the input of river freshwater and terrestrial organic material, while the water exchange with the neighbouring North Sea is limited. Due to a strong meridional gradient of environmental factors, physical and biological characteristics differ within the Baltic Sea and shape very different habitats (i.e., Snoeijs-Leijonmalm and Andrén (2017)). Anthropogenic pressure, such as climate change, overfishing and eutrophication, is increasingly changing the Baltic Sea ecosystem and thus the size and distribution of its carbon stocks.

Box 2.2.1

Pool: a reservoir containing a substance

Stock: amount of a substance (here carbon) in a reservoir (pool)

Previous studies have not or not sufficiently quantified the organic carbon stocks of the relevant carbon pools (Box 2.2.1) in the entire Baltic Sea. Most studies focus on small ecosystems or basins within the Baltic Sea rather than on the Baltic Sea ecosystem as a whole. Carbon stocks are estimated for small scales (Kumblad et al., 2003; Tomczak et al., 2009), different basins (Elmgren, 1984; Sandberg et al., 2004; Niiranen et al., 2013), and/or for a specific subset of carbon pools (Kuparinen et al., 1996; Carstensen et al., 2003; Boström et al., 2014).

Almost all of today's carbon stock estimates are by-products or input parameters of other studies where carbon stocks are only a secondary object of interest. This has two consequences. First, organic carbon stocks are often based on limited data such as values of single years (Bossier et al., 2018), data with low spatial coverage (Bauer et al., 2018) or adopted values from other, mostly older, publications (Baird et al., 1991; Sandberg et al., 2000).

Second, data and methods used for estimating carbon stocks are not sufficiently described (Sandberg et al., 2000; Harvey et al., 2003; ICES, 2005b). In most cases, it is not possible to reproduce the carbon estimates nor to evaluate the references, assumptions and constraints of methods and data.

The existing estimates of organic carbon stocks are either not valid for the entire Baltic Sea ecosystem and its area, do not contain all relevant carbon pools, are based on limited data or cannot be reproduced. To fill this gap, we provide the first consistent stock estimate of 18 currently existing living and non-living organic carbon pools of the Baltic Sea ecosystem presented in mass/area (gC/m^2). With our estimates, we establish a reproducible baseline for the current period that is needed to evaluate the ecosystem models of the Baltic Sea and to estimate changes in the size of organic carbon stocks and their distribution within the organic carbon pools of the Baltic Sea.

Material and methods

We identify 18 organic carbon pools in living biomass and non-living organic matter important for the carbon cycling in the Baltic Sea. The living pools include organisms responsible to build up organic biomass out of inorganic carbon (primary producers) and organisms that consume living organic carbon pools or decompose extrinsic organic material to build up their biomass (consumers and detrivores). We include pools of high biomass and pools of commercially relevant species as well as pools of lower biomass that potentially influence processes of organic carbon cycling or act as mediators between different pools as suggested by Lutz and Martin (2014) and Atwood et al. (2015).

We differentiate species-specific carbon pools for higher trophic levels directly addressed by anthropogenic activities and management, for example with species-specific catch advice and population monitoring. Although these species of higher trophic levels are possibly of small standing stock, they are included as they potentially provide different marine ecosystem carbon services and could link human activities and larger carbon stocks (Lutz and Martin, 2014; Schmitz et al., 2014). Vice versa, we combine several species as homogeneous pools if they are not addressed by species-specific management and only contribute to the carbon cycle via the food web and by sinking. We do not specify age groups because we estimate the standing stock biomass of the living pools and not age-specific food consumption or distribution patterns.

We select particulate and dissolved organic carbon in the water column (POC, DOC) and particulate organic carbon in the upper sediment as non-living pools. The sediment carbon stock is calculated for the top layer (10 cm) that is above the average mixing depth of 5–10 cm of the Baltic Sea (Bunke et al., 2019) and thus still involved in the carbon cycling via natural and anthropogenic mixing processes. This restriction follows the methods of former studies estimating marine sediment carbon stocks (Burrows et al., 2017; Diesing et al., 2017; Luisetti et al., 2019). However, this limit does not reflect a natural limit of organic carbon and our estimate only represents a fraction of the total organic sediment carbon stock.

We estimate the *contemporary* standing stock. Therefore, we average biomass or carbon concentrations over timespans covered in the individual data sets (on average ∼15 years) to omit seasonal and interannual variability. However, we acknowledge that changes in the organic carbon stocks may have occurred in the past and are likely to occur in future due to anthropogenic drivers in this region (Tamelander et al., 2017; Lønborg et al., 2020).

To estimate the standing stocks of the living and non-living carbon pools per area of the Baltic Sea in gC/m^2, we use existing data from various literature and open-access databases. In the following, we conceptually describe how we aggregate the data over time and space and discuss the validity of our estimates. Data, calculations, carbon conversion factors and codes for data processing can be found and downloaded at PANGAEA (Scheffold and Hense, 2020a).

Data formatting

Data for our chosen individual pools are available in different formats and units, for example in number of individuals per area (mammals), carbon content per dry weight (sediment carbon) or in absolute values of wet weight (fish, benthos, sediment carbon and zooplankton) (Table 2.4). In a first step, we convert these different units into wet weight/carbon per area or volume.

We divide all absolute values by associated areas (benthos and fish) or sampled volumes (zooplankton). For this purpose, we use either information on spatial extents or sampled volumes from the associated literature or we calculate areas using bathymetric data of NOAA with the R-package marmap (Pante and Simon-Bouhet, 2013).

Table 2.4: Data specifications of the original data. Number of data points represent data points after formatting. Abbreviations: BP = Baltic Proper, BS = Bothnian Sea, BB = Bothnian Bay, lbr= literature-based review, GoR= Gulf of Riga, GoF = Gulf of Finland, WW = wet weight, and TSB = Total stock biomass.

Pool	**Original unit**	**Depth information**	**Spatial coverage/ Location of data points**	**Temporal coverage**	**Nr. of data points**	**Source**
DOC water column	mgC/m^3, mgC/l, mgC/dm^3, μmolC/l, molC/l	Down to 459 m	BP, BP including western Baltic and Kattegat, Gdansk Deep, Bornholm Deep, Gotland Deep, BS, BB, Arkona Basin, Bay of Mecklenburg, Lübeck and Kiel	2001, 2009–2011, and 2014–2015 (lbr covering 1977–2011)	60	Schneider et al. (2003); Nausch et al. (2006); Gustafsson et al. (2014); Maciejewska and Pempkowiak (2014); Hoikkala et al. (2015); Szymczycha et al. (2017)
POC water column	mgC/l, mgC/dm^3, μmolC/l	Down to 459 m	BP and Gotland Basin, Bornholm Deep, Arkona Basin, Bay of Mecklenburg, Lübeck and Kiel, GoR, Bothnian Sea	2001, 2009–2011, 2013–2016, and 1993–2005	59	Andersson and Rudehäll (1993); Donali et al. (1999); Schneider et al. (2003); Nausch et al. (2006); Maciejewska and Pempkowiak (2014); Szymczycha et al. (2017); Cisternas-Novoa et al. (2019); Winogradow et al. (2019)

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Table 2.4 – continued from previous page

Pool	Original unit	Depth information	Spatial coverage/ Location of data points	Temporal coverage	Nr. of data points	Source
Sediment organic carbon	tC/ha, kg/m^2, POC (%DW)	Down to 10 cm of sediment	BP, BB, BS, GoR and GoF	Data not older than 1990, 2013–2014	42	Carman and Cederwall (2001); Leipe et al. (2011); Flemming and Delafontaine (2016); Nilsson et al. (2019)
Phytoplankton	mgWW/m^3	Down to 40 m	Entire Baltic Sea (excluding BS and BB)	2002 and 2008– 2017	4,089	Biomass data of ICES (ICES, 2018d)
Bacteria	mgC/m^3	Down to 271 m	Baltic Sea basins except BS	1983–1984 and 1987	31	Virtanen (1985); Gast and Gocke (1988); Heinänen (1991)
Protozooplankton	mgWW/m^3	Down to 40 m	Entire Baltic Sea (excluding BS and BB)	2002 and 2008– 2017	3,677	ICES biomass data (ICES, 2018d)
Zooplankton	mgWW/m^3	Down to 400 m	Entire Baltic Sea	1979, 1981 and 1987 until 2017	5,331	ICES biomass data ICES (2018c)
Macrophytes	tC/ha, gDW/m^2	Down to 10 m	Coastal areas of Finland and Denmark, GoF, Puck Bay and the archipelago of Luleå (BB), Askö	1976, 2010–2011, and 2012–2014 (lbr covering 1990–2010)	49 aboveground	Kautsky (1981); Risén et al. (2013); Boström et al. (2014); Jankowska et al. (2014, 2015, 2016); Dahl et al. (2016); Röhr et al. (2016)
		Down to 4 m	Coastal areas of Finland and Denmark, GoF, Askö, Puck Bay	2010–2011 and 2012–2014 (lbr covering 1990–2010)	39 belowground	Risén et al. (2013); Boström et al. (2014); Jankowska et al. (2014); Dahl et al. (2016); Röhr et al. (2016)

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Table 2.4 – continued from previous page

Pool	**Original unit**	**Depth information**	**Spatial coverage/ Location of data points**	**Temporal coverage**	**Nr. of data points**	**Source**
Benthos	gC/m^2, tWW	Down to 350 m	Major Baltic Sea basins	1980s, 1990s, and 2000–2013	62	Carman and Cederwall (2001); Gogina et al. (2016)
Sprat	tWW (TSB)	NA	ICES management units 22–32	1974–2017	44	Annex Table A in ICES (2018b)
Herring	tWW (TSB)	NA	20–24 28.1 25–29 and 32	1991–2017 1977–2017 1975–2018	111	Annex Table A in ICES (2018b)
Flounder	tWW (TSB)	NA	24–25	1978–2004	27	ICES (2005b)
Plaice	tWW (TSB)	NA	21–23 24–32	1999–2017 2002–2018	37	ICES (2018a)
Cod	tWW (TSB)	NA	22–24 25–32	1994–2017 2000–2012	37	ICES (2013, 2017)
Gray Seal	ind./km^2	NA	Åland Sea, Northern BP, Western Gotland Basin, GoF, Bornholm Basin, Arkona Basin, Bay of Mecklenburg, Gdansk, BB, Basin, Eastern Gotland Basin, BS	2003–2014	70	HELCOM Gray Seal database (HELCOM, 2015)
Ringed Seal	ind./km^2	NA	BB, Quark, GoF, Åland Sea, Northern BP, GoR, BS, Archipelagos Sea	2000–2014	25	HELCOM Ringed Seal database (HELCOM, 2015)
Harbour Seal	ind./km^2	NA	Western Gotland Basin, Bornholm Basin, Arkona Basin, Bay of Mecklenburg, Kiel Bay, Sound, Great Belt, Kattegat	2000–2014	425	HELCOM Harbour Seal database (HELCOM, 2015)

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Table 2.4 – continued from previous page

Pool	Original unit	Depth information	Spatial coverage/ Location of data points	Temporal coverage	Nr. of data points	Source
Harbour Porpoise	ind./km^2	NA	Belt and BP	1991–2012, 1995–2006	25	Sveegaard (2011); Benke et al. (2014)

For mammals, we multiply the number of sighted individuals per area by a mean weight per individual. We calculate this mean weight based on age- and sex-distribution data of the Baltic Sea for gray seals [~94 kg based on Lundstedt-Enkel et al. (2008) and Kauhala et al. (2012)] and harbour seals [~42 kg based on Härkönen and Heide-Jørgensen (1990) and Härkönen et al. (1999)]. To approximate the mean weight of ringed seals (~58 kg), we use data on sex- and age- distribution from the northwestern coast of Hudson Bay and from Svalbard (Holst et al., 2006; Krafft et al., 2006). Although different seal populations have different sex- and age- distributions, we assume that the characteristics are comparable. For harbour porpoises, we use an average weight of 65 kg reported by Miller and Wahlberg (2013).

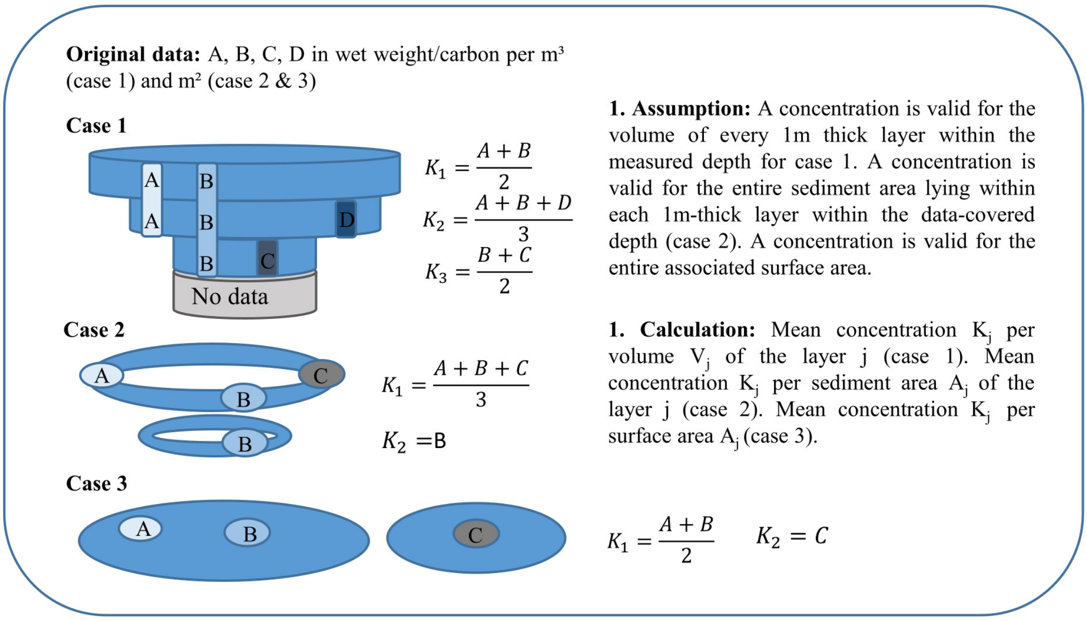
To obtain sediment carbon concentrations, we multiply particulate organic carbon contents per dry weight (POC%) and dry bulk densities (DBD) for accumulation, transport and erosion bottoms for every centimetre down to 10 cm. If only POC% or DBD is provided, we use the DBD-POC% and POC%-POC concentration correlations given by Leipe et al. (2011) for Baltic Sea sediments. Since these correlations do not cover sediments with POC contents below 2.5%, we additionally use the mud content-POC% correlation by Leipe et al. (2011) and mud content-POC concentration correlations given for a variety of sediments with POC% $< 2.5\%$ by Flemming and Delafontaine (2016).

The plankton data require three steps of formatting. First, to separate the data of phytoplankton (purely autotrophic) and protozooplankton (mixo- to heterotrophic), we identify protozooplankton based on non-exclusive literature research on trophic status and occurrence during the year. For example, mixotrophic species in late summer, winter and spring months belong to protozooplankton. Due to a large amount of phytoplankton and protozooplankton data, we do not expect the manual sorting to severely bias our stock estimates.

Second, plankton data often include several entries per site and date. These are either species-specific subsamples of the same measurements (same depth range, date, site) or measurements for different depth ranges (0–1 m, 2–5 m). We sum species-specific subsamples to obtain bulk concentrations.

Third, phytoplankton and protozooplankton data were not measured at all depths between 20 and 40 m. We use a linear regression to approximate missing concentrations. Although the vertical profile of phytoplankton concentrations is far from being linear, we only lack values below 20 m. The probability that sub-surface maxima occur at these depths is low as several studies show a euphotic zone with primary production of maximum 20 m depth (i.e., Feistel et al. (2008); Snoeijs-Leijonmalm et al. (2017); Purina et al. (2018); Vanharanta et al. (2020)). Thus, the use of a linear regression is appropriate in this case.

To distinguish between living and non-living organic particles in POC in the water column,



Original data: A, B, C, D in wet weight/carbon per m³ (case 1) and m² (case 2 & 3)

1. Assumption: A concentration is valid for the volume of every 1m thick layer within the measured depth for case 1. A concentration is valid for the entire sediment area lying within each 1m-thick layer within the data-covered depth (case 2). A concentration is valid for the entire associated surface area.

1. Calculation: Mean concentration K_j per volume V_j of the layer j (case 1). Mean concentration K_j per sediment area A_j of the layer j (case 2). Mean concentration K_j per surface area A_j (case 3).

Figure 2.2.1: Calculation of the mean concentration per layer, sediment or surface area (K_j) for case 1, 2, and 3 pools. A, B, C, D, wet weight or carbon per m^3/m^2; A_j, sediment area within layer j or associated surface area; V_j, volume of the layer j; and K_j, mean concentration.

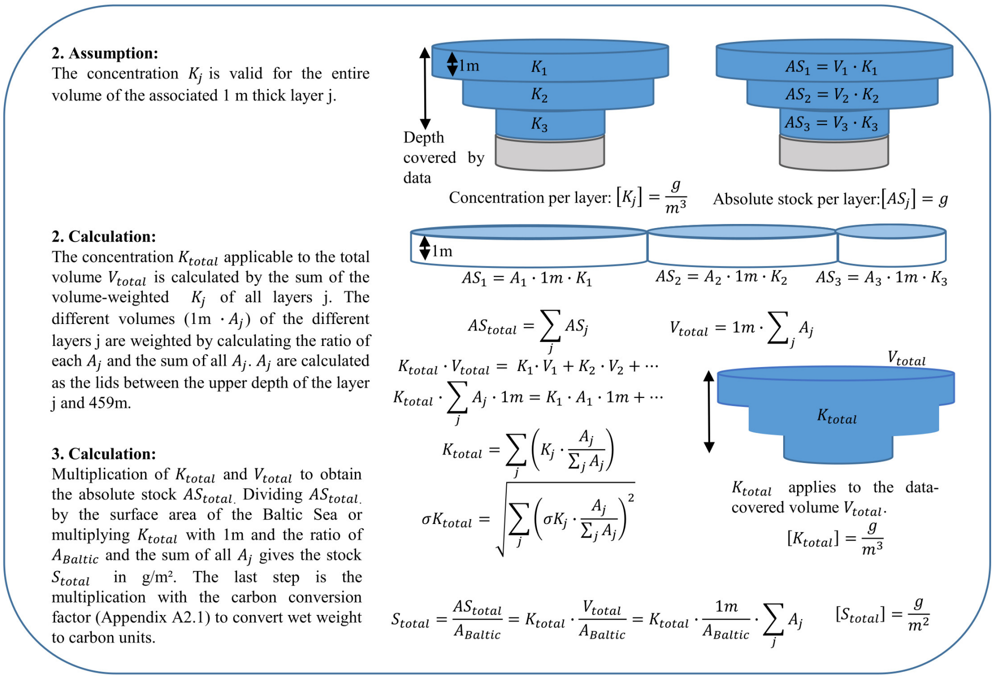
we multiply the POC concentrations in the surface waters by the seasonal detritus content (December–February 0.63, March–May 0.64, June–August 0.80, September–November 0.92) given by Andersson and Rudehäll (1993) or the corresponding mean detritus content (0.75 ± 0.12). We consider the living content for the upper 20 m only since we assume that the POC below the upper 20 m of the water column is detrital and migratory zooplankton species, sub-surface phytoplankton as well as dormant resting stages occasionally caught during POC measurements are non-living or metabolically inactive. Although a simplification, we consider this assumption sufficient for quantifying the stock.

Quantification of stocks

Following the formatting of the data, the data come in three spatial specifications: volume-specific with a certain depth range (Case 1), area-specific with a certain depth range (Case 2) or area-specific without any associated depth (Case 3). Case 1 pools contain phytoplankton, protozooplankton, zooplankton, bacteria, POC, DOC and sediment organic carbon. Case 2 data are associated with the benthic environments including macrophytes and benthos. The last case contains fish and mammals.

For case 1 stocks except the sediment stock, we assume that a wet-weight/carbon concentration per volume specified for a certain depth range applies to each covered 1m-thick water layer j and average all concentrations of the same layer j. We obtain a mean concentration per layer j (K_j) (Figure 2.2.1, 1. Assumption and 1. Calculation) that applies to the volume of the layer j (V_j)(Figure 2.2.2).

Since the total absolute stock (AS_{total}) is the sum of the absolute stocks (AS_j) of all layers, a larger Vj translates into a higher share of absolute stock of that layer (AS_j) of the total



2. Assumption:
The concentration K_j is valid for the entire volume of the associated 1 m thick layer j.

2. Calculation:
The concentration K_{total} applicable to the total volume V_{total} is calculated by the sum of the volume-weighted K_j of all layers j. The different volumes (1m $\cdot A_j$) of the different layers j are weighted by calculating the ratio of each A_j and the sum of all A_j. A_j are calculated as the lids between the upper depth of the layer j and 459m.

3. Calculation:
Multiplication of K_{total} and V_{total} to obtain the absolute stock AS_{total}. Dividing AS_{total} by the surface area of the Baltic Sea or multiplying K_{total} with 1m and the ratio of A_{Baltic} and the sum of all A_j gives the stock S_{total} in g/m². The last step is the multiplication with the carbon conversion factor (Appendix A2.1) to convert wet weight to carbon units.

Concentration per layer: $[K_j] = \frac{g}{m^3}$ Absolute stock per layer: $[AS_j] = g$

$$AS_1 = A_1 \cdot 1m \cdot K_1 \quad AS_2 = A_2 \cdot 1m \cdot K_2 \quad AS_3 = A_3 \cdot 1m \cdot K_3$$

$$AS_{total} = \sum_j AS_j \qquad V_{total} = 1m \cdot \sum_j A_j$$

$$K_{total} \cdot V_{total} = K_1 \cdot V_1 + K_2 \cdot V_2 + \cdots$$

$$K_{total} \cdot \sum_j A_j \cdot 1m = K_1 \cdot A_1 \cdot 1m + \cdots$$

$$K_{total} = \sum_j \left(K_j \cdot \frac{A_j}{\sum_j A_j} \right)$$

$$\sigma K_{total} = \sqrt{\sum_j \left(\sigma K_j \cdot \frac{A_j}{\sum_j A_j} \right)^2}$$

K_{total} applies to the data-covered volume V_{total}. $[K_{total}] = \frac{g}{m^3}$

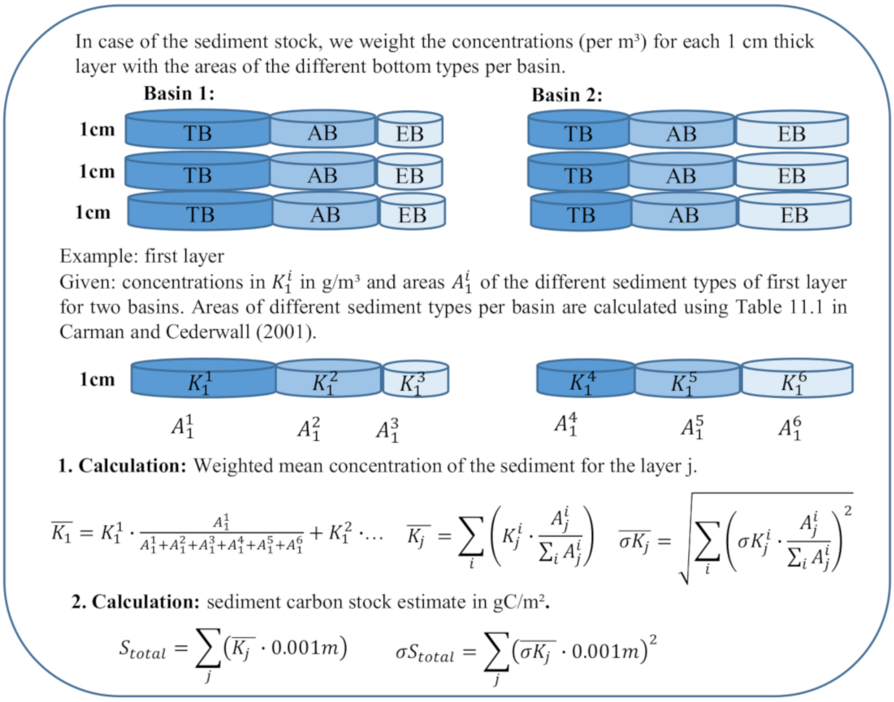
$$S_{total} = \frac{AS_{total}}{A_{Baltic}} = K_{total} \cdot \frac{V_{total}}{A_{Baltic}} = K_{total} \cdot \frac{1m}{A_{Baltic}} \cdot \sum_j A_j \qquad [S_{total}] = \frac{g}{m^2}$$

Figure 2.2.2: Calculations and assumptions for case 1 stocks. AS_j, absolute stock of layer j; AS_{total}, total absolute stock of the entire volume V_{total}; S_{total}, total stock in g/m^2; V_{total}, total volume; V_j, volume of the layer j; A_j, area of the layer j; K_j, mean concentration of layer j in g/m^3; σK_j, standard deviation of the mean concentration per layer j; K_{total}, weighted concentration of all layers covered by the data; σK_{total}, standard deviation of the mean concentration; and A_{Baltic}, area of the Baltic Sea.

stock (Figure 2.2.2). To calculate the mean concentration of the total data-covered volume (K_{total}), we thus weight all K_j according to the ratio of V_j to the total volume (V_{total}). This volume-ratio translates into a ratio of the area of each layer j (A_j) and the sum of all areas covered by the data since all layers are 1 m thick (Figure 2.2.2, 2. Calculation). K_{total} is the sum of the products of each K_j with the associated area ratio [A_j/sum(A_j)] (Figure 2.2.2, 2. Calculation). For case 1 stocks, A_j is the lid of the volume between the upper depth of the layer and 459 m (maximum depth of the Baltic Sea). To obtain the stock per m^2 (S_{total}), we multiply K_{total} with V_{total} and divide it by the area of the Baltic Sea (420,000 km^2).

For the sediment stock, carbon concentrations are given for different sediment depths and bottom types in different basins. We calculate a weighted concentration ($\overline{K_j}$) for each covered 1 cm-thick layer of sediment down to a depth of 10 cm by weighting the carbon concentrations with the corresponding areas of transport, erosion and accumulation bottoms in the different basins (Figure 2.2.3, 1. Calculation), which we calculate with the percentages in Table 11.1 by Carman and Cederwall (2001). The total sediment stock is the sum of each $\overline{K_j}$ multiplied with 1 cm (Figure 2.2.3, 2. Calculation).

The calculations for case 2 and 3 are similar since both stocks are associated with areas. The main difference is that case 2 stocks apply to sediment areas with additional depth ranges (i.e., 2–3 m, 0–10 m). For case 2, we thus assume that concentrations given for a certain depth range apply to the sediment area lying within each 1 m-thick layer covered by the depth range, i.e., 10 g/m^2 for 0–2 m applies to the sediment area lying within 0–1 m and 1–2 m (Figure 2.2.1).



In case of the sediment stock, we weight the concentrations (per m³) for each 1 cm thick layer with the areas of the different bottom types per basin.

Example: first layer

Given: concentrations in K_1^i in g/m³ and areas A_1^i of the different sediment types of first layer for two basins. Areas of different sediment types per basin are calculated using Table 11.1 in Carman and Cederwall (2001).

1. Calculation: Weighted mean concentration of the sediment for the layer j.

$$\overline{K_1} = K_1^1 \cdot \frac{A_1^1}{A_1^1+A_1^2+A_1^3+A_1^4+A_1^5+A_1^6} + K_1^2 \cdot \ldots \qquad \overline{K_j} = \sum_i \left(K_j^i \cdot \frac{A_j^i}{\sum_i A_j^i} \right) \qquad \overline{\sigma K_j} = \sqrt{\sum_i \left(\sigma K_j^i \cdot \frac{A_j^i}{\sum_i A_j^i} \right)^2}$$

2. Calculation: sediment carbon stock estimate in gC/m².

$$S_{total} = \sum_j \left(\overline{K_j} \cdot 0.001m \right) \qquad \sigma S_{total} = \sum_j \left(\overline{\sigma K_j} \cdot 0.001m \right)^2$$

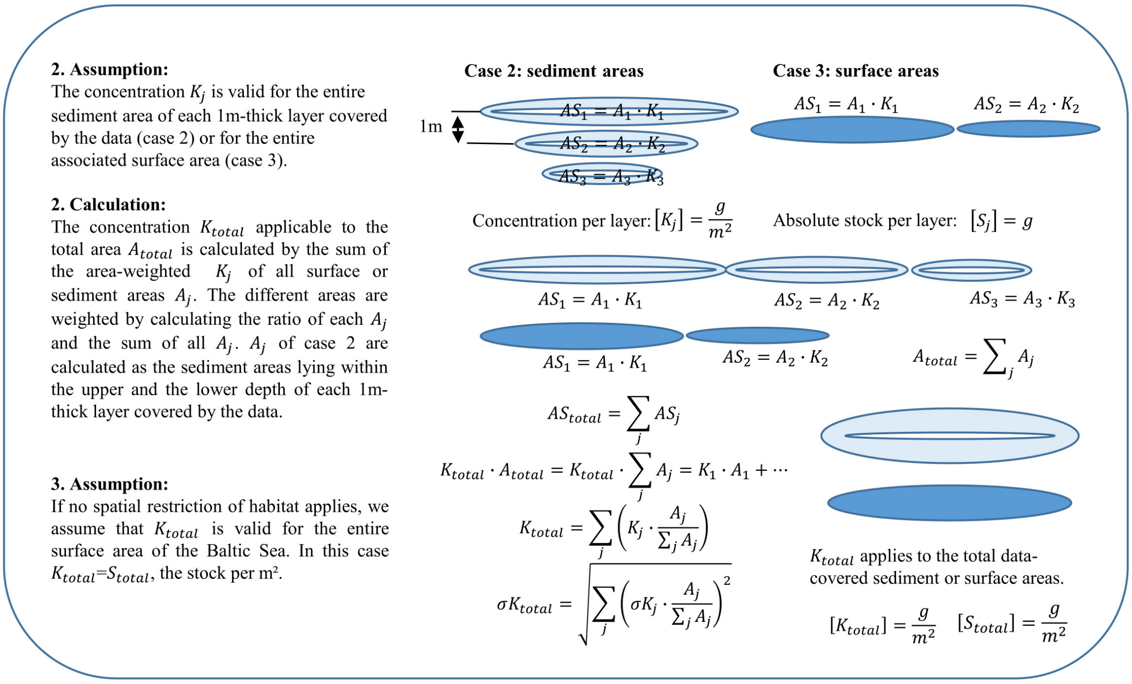
Figure 2.2.3: Calculation of the weighted mean concentration per 1 cm-thick sediment layer for the sediment stock. EB, Erosion Bottom; TB, Transport bottom; AB, Accumulation bottom; K_j^i, concentration for the 1 cm-thick layer j and the basin-specific area of different sediment types A_j^i; σK_j^i, uncertainty of the concentration for j and A_j^i; $\overline{K_j}$ mean weighted concentration for j; $\overline{\sigma K_j}$, uncertainty of the weighted mean concentration for j; and S_{total}, total sediment stock in g/m^2.

Case 3 concentrations, given for a certain location or basin, apply to the entire surface extent of the associated area. K_j is the mean of all concentrations given for each sediment or surface area (Figure 2.2.1). For benthos (case 2), associated areas for the considered depth ranges in different basins are given. We thus weight K_j for benthos ($\overline{K_j}$) similar to the weighting of the bottom types for the sediment stock (Figure 2.2.3) before calculating K_{total} (Figure 2.2.4, 2. Calculation).

To calculate K_{total} for case 2 and 3 we proceed similarly to case 1, we weight the mean concentrations K_j or $\overline{\sigma K_j}$ with area ratios (Figure 2.2.4, 2. Calculation). We assume that the mean concentration K_{total} in g/m^2 is the resulting stock estimate and if no spatial restriction applies, the stock is used for the entire Baltic Sea area (Figure 2.2.4, 3. Assumption).

Finally, we convert wet weight to carbon units by applying the conversion factors we aggregate from the literature (Appendix II, Table 4.1). We use specific carbon conversion factors if available, as it is the case for benthos (depth depending carbon conversion factors by Carman and Cederwall (2001), Appendix II, Table 4.2). We determine the associated uncertainties by propagating the standard deviations of each layer.

Some of the case 2 and 3 pools do not occur in the entire Baltic Sea. The stocks of these pools, calculated as described above, thus only apply to their habitat. To project these stocks to the entire Baltic Sea, we multiply the values with spatial limitation factors, the ratios between the areas where the stocks occur and 420,000 km^2, thus artificially "diluting" them. Macrophytes only grow on light exposed coastal seabed (mostly above 10 m). This



2. Assumption:
The concentration K_j is valid for the entire sediment area of each 1m-thick layer covered by the data (case 2) or for the entire associated surface area (case 3).

2. Calculation:
The concentration K_{total} applicable to the total area A_{total} is calculated by the sum of the area-weighted K_j of all surface or sediment areas A_j. The different areas are weighted by calculating the ratio of each A_j and the sum of all A_j. A_j of case 2 are calculated as the sediment areas lying within the upper and the lower depth of each 1m-thick layer covered by the data.

3. Assumption:
If no spatial restriction of habitat applies, we assume that K_{total} is valid for the entire surface area of the Baltic Sea. In this case K_{total}=S_{total}, the stock per m².

Concentration per layer: $[K_j] = \frac{g}{m^2}$

Absolute stock per layer: $[S_j] = g$

$$A_{total} = \sum_j A_j$$

$$AS_{total} = \sum_j AS_j$$

$$K_{total} \cdot A_{total} = K_{total} \cdot \sum_j A_j = K_1 \cdot A_1 + \cdots$$

$$K_{total} = \sum_j \left(K_j \cdot \frac{A_j}{\sum_j A_j} \right)$$

$$\sigma K_{total} = \sqrt{\sum_j \left(\sigma K_j \cdot \frac{A_j}{\sum_j A_j} \right)^2}$$

K_{total} applies to the total data-covered sediment or surface areas.

$[K_{total}] = \frac{g}{m^2}$ $[S_{total}] = \frac{g}{m^2}$

Figure 2.2.4: Calculations and assumptions for case 2 and case 3 stocks. AS$_j$, absolute stock of layer j; AS$_{total}$, total absolute stock of the entire area A$_{total}$; S$_{total}$, total stock in g/m^2; A$_{total}$, total area; A$_j$, sediment (case 2) or surface area (case 3); K$_j$, mean concentration of the area in g/m^2; σK$_j$, standard deviation of the mean concentration per area; K$_{total}$, weighted concentration of all areas covered by data; and σK$_{total}$, standard deviation of the mean concentration.

coastal stripe is further restricted by a combination of sediment types, salinity, wave exposure, temperature and ice cover (Al-Hamdani and Reker, 2007). We use a mean area of 2,020 ± 410 km^2 of seagrass beds reported by Green and Short (2003) and Boström et al. (2014) as macrophytes habitat and a spatial limitation factor of 0.0048. We further assume that benthos do not live in areas with permanent oxygen concentration below 2 mlO$_2$/l and dilute our benthic stock using a spatial limiting factor of 0.83 (83%), based on the mean anoxic and hypoxic areas by Hansen et al. (2007), Carstensen et al. (2014b,a), and Hansson et al. (2017). Populations of harbour seals and ringed seals occur in selected areas only. We calculate spatial-limiting factors of 0.30 for harbour and 0.46 for ringed seals based on the reported habitats. We do not use spatial limitations of the chosen fish species in the Baltic Sea, although some fish species might favour specific habitats and occur in some areas more frequently.

Validity and limitations of our estimates

One limitation of our estimates is our assumption of a homogeneous Baltic Sea. We temporally and spatially average the carbon concentration and overwrite heterogeneous signals, meridional gradients and area-specific properties. The assumption of homogeneity is very simplified but we consider it sufficient because we include heterogeneous signals in our uncertainty estimates where possible and are interested in the magnitudes rather than concrete numbers of the Baltic organic carbon stocks. However, our estimated distribution and size of the organic carbon stocks apply to the Baltic Sea ecosystem as a whole and sub basins might show very different magnitudes and distributions of organic carbon stocks.

The main limitation of our estimates is the lack and inhomogeneity of data in space and time. Although the Baltic Sea is well monitored, there are large data gaps and few comparable data and reported uncertainties. In addition, sampling data is inhomogeneous in space and time. To work with such a dataset, we have to assume that the data represent the actual state of the Baltic Sea and are "perfect" (i.e., we do not take the frequency nor the spatial clustering of observations into account).

Even if our estimate represents the most comprehensive estimate of total organic carbon (TOC) in the Baltic Sea, we could not quantify the stocks of all pools in the Baltic Sea due to lack of data (e.g., for some fish species and sediment DOC) and to avoid double counting (e.g., for macrophytes associated sediments and benthic bacteria). Further data and research are needed to complete the estimate of TOC in the Baltic Sea.

Our stock estimates reflect orders of magnitude. The estimates apply to the selected groups on the scale of the entire Baltic Sea ecosystem and the area of the Baltic Sea (420,000 km^2). Our estimates can be used to evaluate and compare the carbon stocks in the Baltic Sea for the selected pools, as they are all calculated under the same assumptions. Any comparison with historical data sets or other regions must take into account our assumptions and resulting limitations. Comparisons should not overestimate the accuracy of our estimates and should take into account the risks ofnon-quantifiable uncertainties sensu Hauge (2011).

Results and discussion

Non-living carbon stocks

We summarise results and associated uncertainties in gC/m^2 in Table 2.5 and in Mt in Figure 2.2.5. The estimated TOC stock in the selected pools valid for the entire Baltic Sea area (420,000 km^2) amounts to 1,050 ± 90 gC/m^2. The non-living organic stocks are by far the largest, contributing about 98.8%. The largest singular stock is sediment carbon with 830 ± 90 gC/m^2 (79.1% of TOC), followed by a DOC stock of 196 ± 4 gC/m^2 (18.7% of TOC) and a POC stock of 10.8 ± 1.2 gC/m^2 (1% of TOC).

Our estimate of the sediment carbon stock of the upper 5 cm (410 ± 60 gC/m^2) is of similar magnitude as basin-specific estimates of previous studies (Table 2.6) although they differ in some respects.

There is no estimate of the organic sediment carbon stock for the upper 10 cm for the entire Baltic Sea yet. To assess whether our estimate of 830 ± 90 gC/m^2 is appropriate, we compare our result with the sediment carbon stock of the Northwest European (NWE) continental shelf by Diesing et al. (2017). Our estimate is above the estimated range of 206–793 gC/m^2 by Diesing et al. (2017) (10 cm) and twice the estimated mean of 476 gC/m^2. The most likely explanation for the difference lies in the higher carbon contents (POC%) of the Baltic Sea sediments used in this study (0.44–11%) compared to POC% of the NWE shelf of 0.03–2.74% used by Diesing et al. (2017). Higher sedimentary POC% values are reasonable, since the Baltic Sea sediments show generally higher TOC contents compared to global values (Bunke et al., 2019). This is also reflected in Atwood et al. (2020) describing the Baltic Sea as a carbon hotspot (high carbon stock per unit area). Based on this assessment of Atwood et al.

(2020) and the similarity of our estimate to previous basin-specific assessments, we conclude that our estimate is appropriate.

In contrast to many studies using average POC% or at least average dry bulk densities (DBD) for the sediment profile, we incorporate DBD and POC% changes with sediment depth. Although this method is more accurate since POC%, DBD and thus POC concentrations are known to change with sediment depth, our approach is subject to uncertainties as we use correlations for POC% below 2.5% (for erosion and transport bottoms) that are not specific for the Baltic Sea. To account for the uncertainty of our approach, we set the uncertainty of sediment POC concentrations associated with POC% below 2.5% to ±30 gC/m^2, based on the variability of the POC%-POC concentration correlation given by Leipe et al. (2011). However, the coarse resolution of sediments (erosion, transport and accumulation bottoms) is another source of uncertainty and more research on depth-depending DBD, POC% and POC concentrations for all relevant sediment types in different depths and distances from the shore are needed.

Our DOC stock is of similar magnitude but lower than most of the basin-specific stock estimates (Table 2.6). The difference to our stock estimates is probably due to the fact that these estimates are based on a higher DOC concentration (4.5 gC/m^3 by Sandberg et al. (2000) than ours. We can only assume that this higher DOC concentration is due to a higher data proportion of surface water and/or of the growing season.

Compared to the stock estimate for the entire Baltic Sea of 75 ± 2 TgC corresponding to 179 ± 4 gC/m^2 by Gustafsson et al. (2014), our estimate of 196 ± 4 gC/m^2 is of similar magnitude. The estimated DOC concentration by Legge et al. (2020) used for the mean depth of the study area of Diesing et al. (2017) results in 40–88 gC/m^2. Our estimate is about 2–5 larger than the estimate of the NWE shelf. This is close to reported 3–4 higher DOC concentrations in the Baltic Sea compared to open ocean systems (Hagström et al., 2001) due to high riverine DOC inputs (Kulinski and Pempkowiak, 2011; Deutsch et al., 2012) and to high residence times of water (Savchuk, 2005) and refractory DOC (Seidel et al., 2017). Besides, our average DOC concentration of 3.88 ± 0.07 gC/m^3 (before depth integration)is within the estimated concentrations for the Baltic Sea of 3.2– 4.6 gC/m^3 (Hagström et al., 2001; Nausch et al., 2002; Hoikkala et al., 2015). These similarities suggest that our DOC stock estimate is reasonable.

Among previous studies on organic carbon stocks of the Baltic Sea (Table 2.6), a basin-specific POC stock estimate is only available for the Baltic Proper by Wulff and Ulanowicz (1989). Our estimate of 10.8 gC/m^2 is very similar to their result. A more detailed comparison is not possible as data and method description in Wulff and Ulanowicz (1989) is missing.

The model-based estimate of the POC of the Baltic Sea by Gustafsson et al. (2014) suggests much smaller values of 1.71 ± 0.17 gC/m^2(0.72 ± 0.07 TgC). Kulinski and Pempkowiak (2012) report surface water concentrations of 0.2–0.8 gC/m^3 for shelf seas and 0.1–1.0 gC/m^3 for the Baltic Sea. Our concentration estimate of 0.214 gC/m^3 (before depth integration) is at the lower limit of these ranges, probably because we include deeper water layers with lower POC concentrations. In addition, our estimate fits POC concentrations of 0.08–0.48 gC/m^3 (Legge et al., 2020) for the NWE shelf and a POC stock of 5.6–32.1 gC/m^2 for the study area of

Diesing et al. (2017).

A possible source for our relatively high POC stock is the used proportion of living particles in POC based on Andersson and Rudehäll (1993), who estimated the plankton content of POC in the northern part of the Baltic Sea. As the northern part of the Baltic Sea is less productive than the rest of the Baltic Sea, the planktonic contribution to POC of these parts might not be applicable for the entire Baltic Sea. However, since the mean contribution of phytoplankton to the POC of 25 ± 12% (based on Andersson and Rudehäll (1993)) is very similar to the estimated contribution of 10–30% given by Arteaga et al. (2016) for high latitude (>40°N) and productive marine ecosystems, we consider the planktonic content of POC of 25% as non-critical.

However, the proportion of living particles based on Andersson and Rudehäll (1993) does not include bacteria and zooplankton. To account for these living particles, we recalculate the POC stock with a living content of 50% as lower limit, following the estimate of Hagström et al. (2001) that less than 50% of the particulate organic matter is alive. The resulting POC stock is 9.6 ± 0.6 gC/m^2. With a more realistic living content of 36% (ratio of the sum of all estimated pelagic stocks and the sum of all pelagic stocks plus POC), the POC stock is 10.4 ± 0.7 gC/m^2. If we additionally include living bacteria below the surface waters by applying a bacterial content of 7% below 20 m depth (ratio of estimated bacteria and bacteria plus POC), the POC stock is 10.2 ± 0.6 gC/m^2. All three stocks are smaller (–11%, –4%, and –6%) than our estimate using the percentages of Andersson and Rudehäll (1993) but of similar magnitude. Hence, the proportion of living particles does not lead to a strong overestimation and cannot explain the difference to the estimate of Gustafsson et al. (2014). Due to the small differences and the lack of measured seasonal and mean bacterial and zooplankton content of POC, we keep our original estimate. However, we set the uncertainty of our POC stock at ± 1.2 gC/m^2 to include our estimate of the lower limit (with 50% living content).

The relative variability of the POC stock is higher than, for example, of the DOC stock (Kulinski and Pempkowiak, 2012). Seasonal and spatial signals are more pronounced and our spatially limited data could influence the outcome disproportionally leading to an overestimation. However, our mean POC concentrations/stocks of the growing (0.286 gC/m^3/ 14.4 gC/m^2) and non-growing season (0.109 gC/m^3/ 5.5 gC/m^2) for the entire water column are similar to previous values (Nausch et al., 2005; Naumann et al., 2018). In addition, the mean of these two concentrations of 0.198 gC/m^3 (10.0 gC/m^2) is close to our estimate including seasonal and mean data. We conclude that seasonal signals do not skew our estimate disproportionally.

Our DOC:POC ratio of ~18 further supports the reasonability of our POC estimate, as it is within the global range of 10–20 given by Kulinski and Pempkowiak (2012). The ratio of 100 by Gustafsson et al. (2014) is well above this global mean ratio. One could argue that this is reasonable due to the higher DOC stocks of the Baltic Sea. However, our DOC estimate agrees well with the one of Gustafsson et al. (2014) and thus the discrepancy is not due to differences in the DOC stocks. Besides, productive systems generally have higher POC stocks and lower DOC:POC ratios (Biddanda et al., 2001). Thus, our estimated DOC:POC ratio and consequently the POC stock are reasonable.

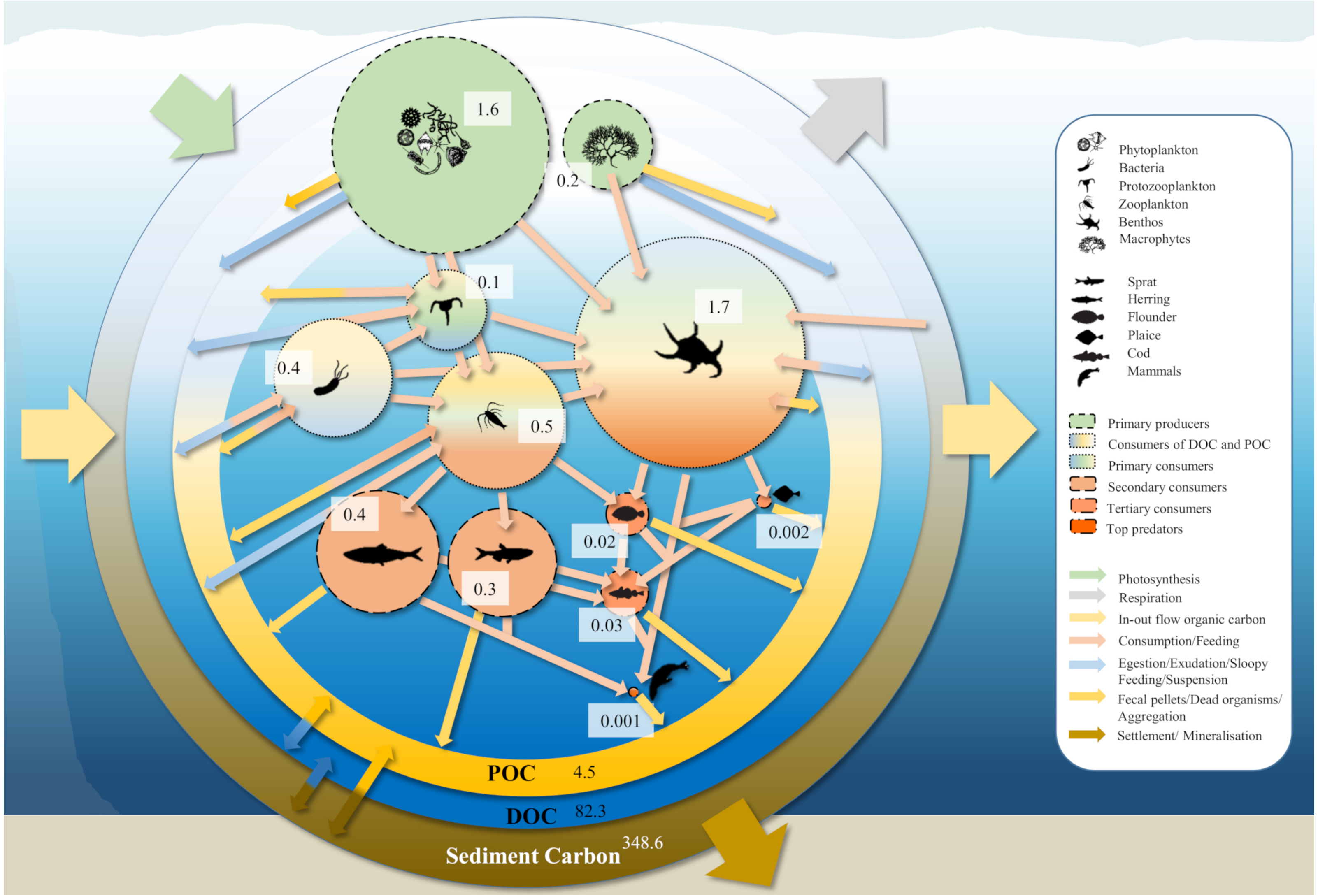


Figure 2.2.5: The carbon cycle of the Baltic Sea with the relevant living and non-living organic carbon stocks in Mt. Carbon stock estimates of the living pools are scaled and indicate their magnitudes. Colours of bubbles indicate diet preferences. Fluxes between the pools are not quantified.

Table 2.5: Organic carbon concentration and stock estimates with the associated uncertainties in gC/m^3 and gC/m^2 for the identified organic carbon pools with references volumes and areas and explanatory aspects.

OC pools	Results and relevant explanatory aspects		
DOC water column	Data covered depth: 0–459 m		
	Conversion factor: no conversion factor used as original data came in carbon units		
	Average concentration	**Reference volume**	**Comments**
	3.88 ± 0.07 gC/m^3	water volume of 21,177 km^3	Unintegrated mean over the water column of 459 m depth.
	Average stock	**Reference area**	Multiplied with the volume of 21,177 km^3 and divided by 420,000 km^2**.
	196 ± 4 gC/m^2	entire Baltic Sea area 420,000 km^2	
POC water column	Data covered depth: 0–459 m		
	Conversion factor: no conversion factor used as original data came in carbon units		
	Average concentration	**Reference volume**	**Comments**
	0.214 ± 0.014 gC/m^3	water volume of 21,177 km^3	Unintegrated mean over the water column of 459 m depth.
	Average stock	**Reference area**	Multiplied with the volume of 21,177 km^3 and divided by 420,000 km^2**.
	10.8 ± 1.2 gC/m^2	entire Baltic Sea area 420,000 km^2	
Sediment organic carbon carbon	Data covered depth: 0–10 cm		
	Conversion factor: no conversion factor used as original data came in carbon units		
	Average stock per bottom type	**Reference area**	**Comments**
	Accumulation bottom	138,600 km^2	Share of accumulation, erosion and transport bottom are 33, 50, and 17% (Almroth-Rosell et al., 2011).
	425 ± 12 gC/m^2 (5 cm)		
	979 ± 12 gC/m^2 (10 cm)		
	Transportation bottom	210,000 km^2	
	440 ± 60 gC/m^2 (5 cm)		
	790 ± 90 gC/m^2 (10 cm)		
	Erosion bottom	71,400 km^2	
	370 ± 60 gC/m^2 (5 cm)		
	710 ± 90 gC/m^2 (10 cm)		
	Average stock	**Reference area**	Weighted mean of the sediment carbon concentration of different bottoms types in different basins. Areas of bottom types are taken from Carman and Cederwall (2001) Table 11.1.
	410 ± 60 gC/m^2 (5 cm) **830 ± 90 gC/m^2 (10 cm)**	entire Baltic Sea area 420,000 km^2	
Phyto-	Data covered depth: 0–40 m		

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Table 2.5 – continued from previous page

OC pools	**Results and relevant explanatory aspects**		
plankton	Conversion factor: 0.16 ± 0.03 gC/gWW		
	Average concentration	**Reference volume**	**Comments**
	0.13 ± 0.05 gC/m^3	water volume of 12,115 km^3	Unintegrated mean over the water column of 40 m depth.
	Average stock	**Reference area**	Multiplied with the volume
	3.7 ± 1.5 gC/m^2	entire Baltic Sea area 420,000 km^2	of 12,115 km^3 and divided by 420,000 km^2.
Bacteria	Data covered depth: 0–271 m		
	Conversion factor: no conversion factor used as original data came in carbon units		
	Average concentration	**Reference volume**	**Comments**
	0.017 ± 0.002 gC/m^3	water volume of 21,173 km^3 km^3	Unintegrated mean over the water column of 271 m depth.
	Average stock	**Reference area**	Multiplied with the volume
	0.85 ± 0.09 gC/m^2	entire Baltic Sea area 420,000 km^2	of 21,173 km^3 and divided by 420,000 km^2.
Proto-zoo-plankton	Data covered depth: 0–40 m		
	Conversion factor: 0.07 gC/gWW		
	Average concentration	**Reference volume**	**Comments**
	0.010 ± 0.003 gC/m^3	water volume of 12,115 km^3	Unintegrated mean over the water column of 40 m depth.
	Average stock	**Reference area**	Multiplied with the volume
	0.29 ± 0.09 gC/m^2	entire Baltic Sea area 420,000 km^2	of 12,115 km^3 and divided by 420,000 km^2.
Zoo-plankton	Data covered depth: 0–400 m		
	Conversion factor: 0.09 ± 0.02 gC/gWW		
	Average concentration	**Reference volume**	**Comments**
	0.024 ± 0.009 gC/m^3	water volume of 21,177 km^3	Unintegrated mean over the water column of 40 m depth.
	Average stock	**Reference area**	Multiplied with the volume
	1.2 ± 0.5 gC/m^2	entire Baltic Sea area 420,000 km^2	of 21,177 km^3 and divided by 420,000 km^2.
Macro-phytes	Data covered depth: 0–10 m		
	Conversion factor: 0.4 ± 0.1 gC/gDW		
	Average stock	**Reference area**	**Comments**
	Aboveground	reported seagrass areas of	Area after
	50.9 ± 1.6 gC/m^2	2,020 ± 410 km^2	Green and Short (2003) and
	Belowground		Boström et al. (2014)
	38.6 ± 2.4 gC/m^2	8,400 km^2	About 2% of the Baltic Sea
	Total: 89.5 ± 2.9 gC/m^2		area.
	Aboveground	entire Baltic Sea area	Using spatial limitation factor
	0.3 ± 0.4 gC/m^2	420,000 km^2	0.0048 (reported areas 2,020
	Belowground		km^2 divided by the area of

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Table 2.5 – continued from previous page

OC pools	**Results and relevant explanatory aspects**		
	0.19 ± 0.29 gC/m^2 **Total** **0.4 ± 0.5 gC/m^2**		the entire Baltic Sea 420,000 km^2). Sum of below- and aboveground stocks.
	Aboveground 1.02 ± 0.04 gC/m^2 Belowground 0.77 ± 0.05 gC/m^2 Total 1.79 ± 0.06 gC/m^2	entire Baltic Sea area 420,000 km^2	Using spatial limitation factor 0.02 (8,400 km^2 divided by the area of the entire Baltic Sea 420,000 km^2). Sum of below-and aboveground stocks.
Benthos	Data covered depths: 0–30, 30–70, 70–120, and 120–350 m Conversion factor: depth and basin depending conversion factors based on Carman and Cederwall (2001) (see Appendix II, Table 4.2)		
	Average stock	**Reference area**	**Comments**
	5.3 ± 1.1 gC/m^2	area of 349,349 km^2, excluding areas $<$2 mlO$_2$/l	Areas of permanently $<$ 2 mlO$_2$/l estimated based on Hansen et al. (2007), Carstensen et al. (2014b,a) and Hansson et al. (2017) (70,651 ± 4,300 km^2).
		area of 295,105 km^2, excluding areas $<$3 mlO$_2$/l	Areas of permanently $<$ 3 mlO$_2$/l estimated based on Hansen et al. (2007) (124,896 km^2).
	4 ± 1 gC/m^2	entire Baltic Sea area 420,000 km^2	Using spatial limitation factor 0.83 (oxic areas of 349,349 km^2 divided by the area of the entire Baltic Sea 420,000 km^2 for $<$ 2 mlO$_2$/l).
	3.7 ± 0.8 gC/m^2	entire Baltic Sea area 420,000 km^2	Using spatial limitation factor 0.70 (oxic areas of 295,105 km^2 divided by the area of the entire Baltic Sea 420,000 km^2 for $<$ 3 mlO$_2$/l)***.
Sprat	Data covered depth: not applicable Conversion factor: 0.15 ± 0.04 gC/gWW		
	Average stock	**Reference area**	**Comments**
	0.649 ± 0.299 gC/m^2	entire Baltic Sea area 420,000 km^2	As no other data were applicable, sprat carbon per square meter estimated for ICES management units 22–32 is assumed to be valid in the entire Baltic Sea.
Herring	Data covered depth: not applicable Conversion factor: 0.15 ± 0.04 gC/gWW		

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Table 2.5 – continued from previous page

OC pools	**Results and relevant explanatory aspects**		
	Average stock	**Reference area**	**Comments**
	0.9 ± 0.5 gC/m^2	entire Baltic Sea area 420,000 km^2	Weighted mean using area ratios of the ICES management units 20–24, 28.1, 25, and 29–32*.
Flounder	Data covered depth: not applicable Conversion factor: 0.14 ± 0.04 gC/gWW		
	Average stock	**Reference area**	**Comments**
	0.058 ± 0.019 gC/m^2	entire Baltic Sea area 420,000 km^2	As no other data were applicable, flounder carbon per square meter estimated for ICES management units 24–25 is assumed to be valid in the entire Baltic Sea.
Plaice	Data covered depth: not applicable Conversion factor: 0.14 ± 0.04 gC/gWW		
	Average stock	**Reference area**	**Comments**
	0.005 ± 0.003 gC/m^2	entire Baltic Sea area 420,000 km^2	Weighted mean using area ratios of the ICES management units 21–23 and 24–32*.
Cod	Data covered depth: not applicable Conversion factor: 0.16 ± 0.04 gC/gWW		
	Average stock	**Reference area**	**Comments**
	0.08 ± 0.03 gC/m^2	entire Baltic Sea area 420,000 km^2	Weighted mean using area ratios of the ICES management units 22–24 and 25–32*.
Gray Seal	Data covered depth: not applicable Conversion factor: 0.15 ± 0.03 gC/gWW		
	Average stock	**Reference area**	**Comments**
	0.050 ± 0.007 ind./km^2 ual: 4.7 ± 0.8 kg/km^2	entire Baltic Sea area 420,000 km^2	Average weight per individ- 94 ± 8 kg/ind. after Lundstedt-Enkel et al. (2008) and Kauhala et al. (2012). Covered area: about 365,191 km^2.
	0.00066 ± 0.00022 gC/m^2		As no other data were applicable, weighted gray seal carbon per square meter estimated for covered areas is assumed valid in the entire Baltic Sea.
Ringed Seal	Data covered depth: not applicable Conversion factor: 0.14 ± 0.04 gC/gWW		
	Basin stocks	**Reference area**	**Comments**

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Table 2.5 – continued from previous page

OC pools	Results and relevant explanatory aspects		
	0.07 ± 0.05 ind./km^2 4.2 ± 2.5 kg/km^2 0.0006 ± 0.0004 gC/m^2	area with sightings 192,619 km^2	Average weight per individual: 58 ± 11 kg/ind. after Holst et al. (2006) and Krafft et al. (2006). Covered area: about 192,619 km^2.
	Average stock **0.00027 ± 0.00018 gC/m^2**	entire Baltic Sea area 420,000 km^2	Using spatial limitation factor 0.46 (area of 192,619 km^2 divided by the area of the entire Baltic Sea 420,000 km^2).
Harbour Seal	Data covered depth: not applicable Conversion factor: 0.15 ± 0.03 gC/gWW		
	Basin stocks	**Reference area**	**Comments**
	0.0028 ± 0.003 ind./km^2 1.18 ± 0.19 kg/km^2 0.00018 ± 0.00005 gC/m^2	area with sightings 125,280 km^2	Average weight per individual: 42 ± 5 kg/ind. after Härkönen and Heide-Jørgensen (1990) and Härkönen et al. (1999). Covered area: about 125,280 km^2.
	Average stock **0.000053 ± 0.000014 gC/m^2**	entire Baltic Sea area 420,000 km^2	Using spatial limitation factor 0.298 (area of 125,280 km^2 divided by the area of the entire Baltic Sea 420,000 km^2).
Harbour Porpoise	Data covered depth: not applicable Conversion factor: 0.15 ± 0.02 gC/gWW		
	Average stock	**Reference area**	**Comments**
	0.05 ± 0.02 ind./km^2 3.2 ± 1.6 kg/km^2	entire Baltic Sea area 420,000 km^2	Average weight per individual: 65 kg/ind. after Miller and Wahlberg (2013) and Kauhala et al. (2012). Covered area: about 118,335 km^2.
	0.00048 ± 0.00025 gC/m^2		As no other data were applicable, weighted harbour porpoise carbon per square meter estimated for the Belt and the Baltic Proper is assumed valid in the entire Baltic Sea*.

*Further basin-specific estimates can be found in Appendix II, Table 4.3.

**Further season-specific estimates can be found in Appendix II, Table 4.4 .

***Further basin- and depth-specific estimates can be found in Appendix II, Table 4.5.

Living organic carbon stocks

Living pools contribute about 1.2% (12.6 ± 1.9 gC/m^2) to the TOC stock.

Phytoplankton and macrophytes are the major primary producers of the Baltic Sea, providing the energy basis for the food web. The carbon stock of the primary producers accounts for 4.2 ± 1.6 gC/m^2 [0.39% of TOC and 33% of living total organic carbon (lTOC)].

Even though phytoplankton concentrations vary significantly in time and space, our stock estimate of phytoplankton of 3.7 ± 1.5 gC/m^2 is very similar to the basin-specific estimates (Table 2.6). In addition, our mean phytoplankton concentration value of 0.13 ± 0.05 gC/m^3 (before depth integration) agrees well with the mean biomass concentration values of 0.12 gC/m^3 and 0.13 gC/m^3 based on Wasmund et al. (2000) and Wasmund et al. (2016).

Macrophytes stock estimates are not available for the entire Baltic Sea. Our estimated stock of 89.5 ± 2.9 gC/m^2 for the reported seagrass areas in the Baltic Sea (2,020 km^2) (Table 2.5) is similar to estimated 85 gC/m^2 for macrophytes areas in the North Atlantic by Fourqurean et al. (2012). It also fits well within the reported dry weight range of ∼ 50–300 gDW/m^2 (20–120 gC/m^2) for vegetated areas with phytobenthos (Kautsky et al., 2017).

However, Kautsky et al. (2017) estimate an absolute macrophytes stock of ∼ 0.99 Mt (for BB, BS plus BP), while our estimate for the entire Baltic Sea is only 0.2 ± 0.2 Mt, which is about 5.5 times smaller. The difference lies in the selection of areas covered with macrophytes. In our estimate, we use ∼ 0.5% of the entire Baltic Sea based on Green and Short (2003) and Boström et al. (2014) as a reference area. If we use 2% of the Baltic Sea area instead, similar to the share of vegetated areas in the NWE shelf (see supplement of Legge et al. (2020) and to 1–2% of global coverage presented in Krause-Jensen et al. (2018) and Attard et al. (2019), our undiluted stock of 89.5 gC/m^2 is valid for 8,400 km^2. The diluted and the absolute stock for the entire Baltic Sea consequently amount to 1.79 ± 0.06 gC/m^2 and 0.75 ± 0.02 Mt. Since these 2% are not verified for the Baltic Sea, we keep our estimate. Nevertheless, it is likely that we underestimate the vegetated areas and thus the macrophytes stock of the Baltic Sea. We use the stock estimate with 2% coverage as an upper limit.

Macrophytes may locally enhance carbon contents of sediments compared to the not vegetated state and are associated with sediment carbon stocks of 251–4,324 gC/m^2 for the upper 25 cm (Jankowska et al., 2016; Röhr et al., 2016). To avoid double counting, we do not consider macrophyte-covered sediments separately, but when assessing macrophyte losses, the consequences for the associated sediment stocks must be considered.

The primary consumers, herbivores and detrivores, make up 7 ± 1 gC/m^2 (0.64% of TOC and 53% of lTOC). Interestingly, benthos, including meio- and macrobenthos, shows the highest living carbon stock (0.42% TOC and 35% lTOC). The estimate of benthos is of similar magnitude as the basin-specific estimates (Table 2.6), although the heterogeneous signals for the different basins are strong. The large carbon stock of benthos implies a strong benthic-pelagic coupling with productivity-controlled export fluxes of organic material that feed the benthos. The eutrophic Baltic Sea has strong export fluxes, due to its high bottom surface to volume ratio, high benthic-pelagic connectivity (Kopp et al., 2015; Tamelander et al., 2017; Ehrnsten et al., 2019) and temporarily decoupled zooplankton and phytoplankton peak biomass (Dahlgren, 2010). These fluxes lead to high food supply for benthos but also, if

Table 2.6: Basin-specific estimates from previous studies compared to our stock estimates.

	Baltic Proper (BP)										BP*	Bothnian Sea (BS)				Bothnian Bay (BB)						
	Wulff and Ulanowicz (1989)	Baird et al. (1991)	Jarre-Teichmann (1995)	ICES (2005a), BP 1990	ICES (2005a), BP 1990	Kautsky and Kautsky (2000)	Sandberg et al. (2000)	Tomczak et al. (2012)	Niiranen et al. (2013)	Bauer et al. (2018)	Harvey et al. (2003)	Kuparinen et al. (1996)	Sandberg et al. (2000)	Kautsky and Kautsky (2000)	Sandberg et al. (2004)	Kuparinen et al. (1996)	Sandberg et al. (2000)	Kautsky and Kautsky (2000)	Sandberg et al. (2004)	Weighted mean previous estimates	Uncertainty previous estimates	**This study**
DOC	266	266					280						280				190			264	5	196
POC	11	11																		11		10.8
SOC (5cm)							400	465					310				290			440	70	410
SOC (10cm)																						830
SOC (NA)	609	609																				
P	1.07	1.07	1.06	4.00	4.00	1.65	1.01	1.07	1.35	1.13	6.40	3.39	0.73	0.18	4.00	1.23	0.17	0.06	1.56	3.7	0.6	3.7
Bac	0.21	0.21	0.20	0.42	0.42		0.21				0.34	1.03	0.14		0.98	0.74	0.04		0.68	0.4	0.1	0.85
PZP	0.09	0.07	0.07		0.14		0.07	0.31	0.31		0.34		0.05		0.89		0.01		0.35	0.26	0.06	0.29
ZP	0.21	0.21	0.58	4.18	9.21		0.21	1.36	1.43	1.19	0.68	0.07	0.21		0.08	0.05	0.10		0.05	1.1	1.2	1.2
MP	0.021	0.021	0.019	0.020	0.020	0.485*	0.020						0.010	0.153*			0.010	0.053*		0.08	0.05	0.4
Benth	5.639	5.639	5.523	5.520	5.520	0.359	4.580	3.210	2.980	8.976	7.032	3.360	5.120	0.089		0.360	0.110	0.044		5.3	0.7	4.0
Sprat	0.293	0.293	0.700	0.275	0.991			0.513	0.546	0.915	1.158									0.73	0.11	0.649
Herr	0.293	0.293	1.010	0.725	0.516			0.959	0.962	0.200	1.703									0.99	0.13	0.9
Flound										0.126										0.126		0.058
Plaice																						0.005
Cod	0.505	0.505	0.120	0.640	0.197			0.178	0.111	0.055	0.341									0.26	0.08	0.08
Seals				0.00005	0.00005			0.00006	0.00006	0.00090	0.00007									0.00012	0.00014	0.00983
GS										0.00090										0.00122		0.00066
RS																						0.00027
HS																						0.000053
HP																						0.00048
Pel.AT	*1.07*	*1.07*	*1.06*	*4.00*	*4.00*	*1.65*	*1.01*	*1.07*	*1.35*	*1.13*	*6.40*	*3.39*	*0.73*	*0.18*	*4.00*	*1.23*	*0.17*	*0.06*	*1.56*	*3.7*		*3.7*
Pel.HT	*0.51*	*0.49*	*0.85*	*4.60*	*9.77*		*0.49*	*1.67*	*1.74*	*1.19*	*1.36*	*1.11*	*0.40*		*1.95*	*0.79*	*0.15*		*1.08*	*1.76*		*2.34*
Pel.HT: Pel.AT	*0.5*	*0.5*	*0.8*	*1.2*	*2.4*		*0.5*	*1.6*	*1.3*	*1.1*	*0.2*	*0.3*	*0.5*		*0.5*	*0.6*	*0.9*		*0.7*	*0.5*		*0.6*
B:P	*0.2*	*0.2*	*0.2*	*0.1*	*0.1*		*0.2*				*0.1*	*0.3*	*0.2*		*0.2*	*0.6*	*0.2*		*0.4*	*0.1*		*0.2*
B:PZP	*2.3*	*3.0*	*2.9*		*3.0*		*3.0*				*1.0*		*2.8*		*1.1*		*4.0*		*1.9*	*1.3*		*2.9*
B:ZP	*1.0*	*1.0*	*0.3*	*0.1*	*0.1*		*1.0*				*0.5*	*14.7*	*0.7*		*12.3*	*14.8*	*0.4*		*13.6*	*0.4*		*0.7*

We further provide a weighted mean of the previous estimates and the associated uncertainty. All stocks are given in gC/m^2. Dark-blue-hatched fields are sums of the stocks of several species. Benthos includes meio- and macrobenthos. The stock estimates of Harvey et al. (2003) and Bauer et al. (2018) were converted to carbon units using literature-based carbon conversion factors (S1). Italic rows contain information not displayed in the original data. *Estimates of Kautsky and Kautsky (2000) were given in 10^5 kgC. We divide these absolute numbers by the areas of the associated basins lacking other area information. Abbreviations: SOC = Sediment organic carbon, P = Phytoplankton, PZP = Protozooplankton, ZP = Zooplankton, MP = Macrophytes, Benth = Benthos, Herr = Herring, Flound = Flounder, GS = Gray seal, RS = Ringed seal, HS = Harbour seal, HP = Harbour porpoise, Pel. AT = Pelagic autotrophs, Pel. HT = Pelagic heterotrophs and B = Bacteria.

in oversupply, to decreasing oxygen concentrations in bottom waters. Allochthonous organic material can provide an additional energy resource that supports such a high benthic stock (Wikner and Andersson, 2012).

One source of uncertainty for the benthic stock is the extent of the estimated anoxic and hypoxic areas. With an estimated mean area of ∼ 17% of the Baltic Sea with oxygen concentrations below 2 mlO_2/l [according to Hansen et al. (2007), Carstensen et al. (2014b,a), and Hansson et al. (2017)] our diluted stock is 4 ± 1 gC/m^2. If we use the ∼ 30% of the Baltic Sea area below 3 mlO_2/l [according to Hansen et al. (2007)], the diluted benthic stock is 3.7 ± 0.8 gC/m^2. Since the hypoxic threshold in the Baltic Sea is generally defined as oxygen concentration below 2 mlO_2/l (Diaz and Rosenberg, 1995) and the mean lethal oxygen concentration for benthos is ∼ 1.54 mlO_2/l (Vaquer-Sunyer and Duarte, 2008), we use an area of 348,600 km^2 (73%) as mean area with sufficient oxygen ratios. The estimated value associated with <3 mlO_2/l is well suited as a lower limit of the benthos stock to account for sublethal oxygen concentrations.

Of the other consumer stocks, the protozooplankton stock fits best with the basin-specific estimates, while the bacteria are about three times larger. Estimates of zooplankton, protozooplankton and bacteria vary strongly between the basins (Table 2.6), due to inter alia the productivity gradient from the eutrophic southwest to the more oligotrophic northern part of the Baltic Sea. This also means that our estimated distribution and size of the planktonic carbon stocks, valid on the scale of the entire Baltic Sea, are not per se valid on a basin-scale since the Baltic Sea exhibits very different planktonic systems in its basins.

Our estimated ratio of pelagic autotrophs and heterotrophs supports the accuracy of our estimates. In contrast to some basin-specific studies (Table 2.6), the pelagic plankton system of the entire Baltic Sea shows a “bottom-heavy” pyramidal biomass distribution, with biomass decreasing with increasing trophic level. Phytoplankton have a larger biomass compared to their consumers (heterotrophic/autotrophic ratio of 0.6). This is consistent with the finding that eutrophied planktonic systems are dominated by phytoplankton biomass (Dortch and Packard, 1989) and support lower heterotrophic: autotrophic ratios (H:A ratios) than systems with lower phytoplankton biomass (Gasol et al., 1997). Accordingly, our H:A ratio of 0.6 fits reported H:A ratios for comparable phytoplankton biomasses by Gasol et al. (1997).

Our estimates of zooplankton and bacteria are in the same order of magnitude as other estimates for similar phytoplankton stocks (see Figure 2 in Gasol et al. (1997)). Our zooplankton stock is about 1.4 times larger than that of bacteria fitting a zooplankton to bacteria ratio of 1.4 estimated for coastal systems by Gasol et al. (1997). In contrast to open ocean systems, coastal systems have a higher proportion of zooplankton biomass and a stronger coupling of primary production to the grazing chain than to the microbial loop. As most of the Baltic Sea resembles a coastal system rather than an open ocean system with its shallow water depth, the proximity of the coast and strong terrestrial influence, it is dominated by higher zooplankton than bacteria stocks (Gasol et al., 1997).

Interestingly, the unusually high DOC stock compared to open ocean systems does not lead to bacterial dominance in the planktonic system. The bacterial stock seems to be limited to some extent and unable to use the entire available DOC. Probable but not exclusive causes could be a high proportion of refractory DOC (Kuliński et al., 2016), light or temperature limited bacterial growth and/or competition between phytoplankton and bacteria for nutrients (Church, 2008). The large surface-to-volume ratio of bacteria is advantageous in nutrient-limited systems but does not bring any advantage in productive systems (Azam et al., 1983; Cotner and Biddanda, 2002). On the contrary, in areas with periodic nutrient input like the Baltic Sea, larger cells like phytoplankton are advantageous, as they can store nutrients (Cotner and Biddanda, 2002).

Protozooplankton play only a minor role in coastal systems and protozooplankton stock is on average 2–4 times smaller than that of zooplankton (Gasol et al., 1997). In our case, the protozooplankton stock is 4 times smaller. Since our protozooplankton stock is at the lower limit, this might indicate a stock limitation, such as top–down regulation by zooplankton. The ratio and the small difference to the mean of the basin-specific estimates suggest a reasonable protozooplankton stock.

The standing stock of secondary consumers (sprat, herring, flounder, plaice) and tertiary consumers (cod) amount to 1.6 ± 0.5 gC/m^2 (0.002% TOC and 13% lTOC) and 0.08 ± 0.06 gC/m^2 (<0.001% TOC and 0.6% lTOC). Our stock estimates of sprat and herring are smaller than the mean of the basin-specific estimates but within the uncertainty range. Similar to the weighted mean of the basin-specific estimates, our sprat stock is lower than the herring stock. This is further supported by the temporal development of the clupeid stocks (sprat and herring) reported by HELCOM, which are on average of similar size, with a recent trend toward higher herring stocks (HELCOM, 2017).

Due to different salinity tolerances, flounders are more abundant in the Baltic Sea than plaice (Ojaveer et al., 2010), which is reflected in our stock estimates. Further, the cod stock is significantly smaller than the clupeid stocks. This ratio is consistent with the Baltic Sea regime change from a cod-dominated to a clupeid-dominated system (Österblom et al., 2007). However, apart from these similarities, our estimates for flounder and cod are much smaller than the basin-specific estimates for the Baltic Proper. We can only assume that the reasons for these differences are limited data (i.e., for flounder only ICES units 24–25) and/or the high interannual and spatial variability of fish stocks, which is reflected in the broad range of basin-specific estimates (i.e., for cod 0.055–0.640 gC/m^2, Table 2.6) and in the high uncertainties of our fish stock estimates. Although our fish-stock estimates are subject to considerable uncertainty, we use them nevertheless as they are the only available estimates for the entire Baltic Sea.

The Baltic Sea is home to about 230 species of fish. Due to lack of data, we cannot estimate the stocks of most of these species. Stocks of these fish species could be around 0.09–0.40 gC/m^2 (including flounder and plaice), assuming that clupeids and cod represent 80% (Elmgren, 1984) to 95% (Thurow, 1980) of all fish stocks.

The standing stock of the highest trophic level accounts for 0.0015 ± 0.0004 gC/m^2 (<0.001% TOC and <0.001% lTOC). The few basin-specific estimates given do not allow for a comparison and a discussion about the accuracy of our estimates. However, our overall estimates remain reasonable, as these stocks, due to their small size, do not significantly alter the TOC stock. Their importance for this stock quantification is small. However, this does

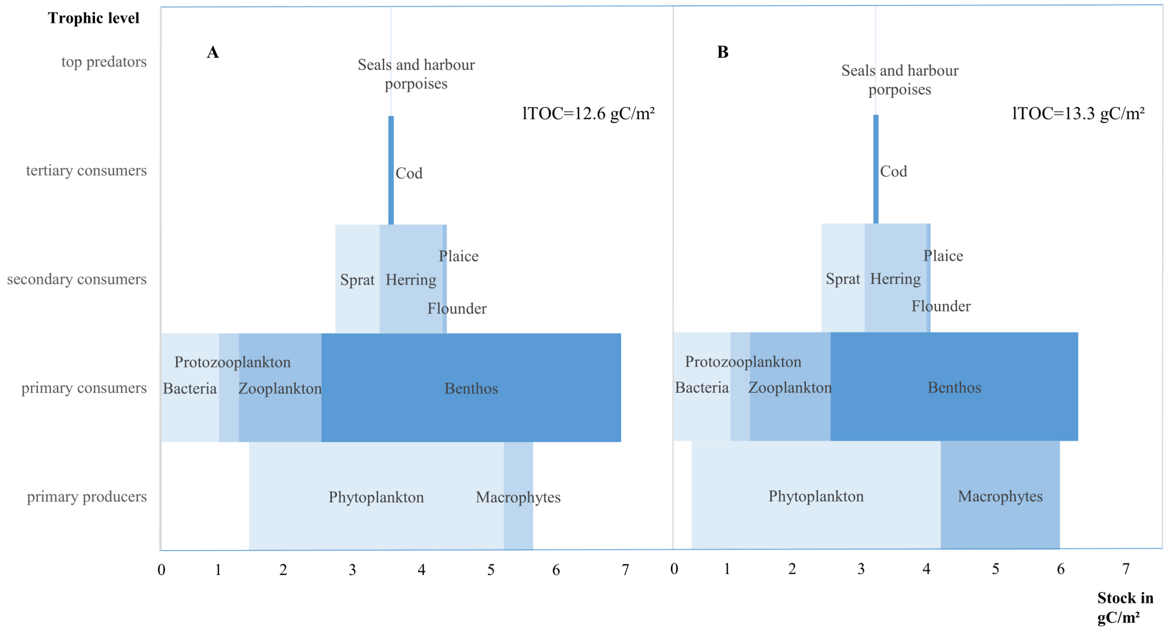

Figure 2.2.6: Carbon stocks per trophic level valid for the entire Baltic Sea area. **(A)** With the macrophytes covering 2,020 km^2 and benthos 349,349 km^2 (areas $<$ 2 mlO_2/l) and total living carbon (lTOC) of 12.6 gC/m^2. **(B)** With macrophytes covering 8,400 km^2 (2% of entire Baltic Sea area) and benthos 295,105 km^2 (areas $<$ 3 mlO_2/l) and lTOC of 13.3 gC/m^2.

not necessarily mean that their influence on carbon fluxes and their contribution to the carbon cycle (see Figure 2.2.5) is insignificant (Schmitz et al., 2014).

One of the most interesting results concerning all living stocks is that our estimated stocks form a partially inverted biomass pyramid with a higher stock of primary consumers than primary producers (Figure 2.2.6). This distribution is consistent with most basin-specific estimates (Table 2.6) and remains consistent if we add the upper limit of macrophytes of 1.79 gC/m^2 (2% areal coverage) and the lower limit of benthos of 3.7 gC/m^2 (30% lethal area).

Recent studies suggest that inverted pyramids or some kind of top-heaviness may be more common than previously thought, even in environments with which they were not originally associated (Trebilco et al., 2016; Bar-On et al., 2018; Woodson et al., 2018). Responsible for the non-Eltonian/partly inverted biomass distribution in the Baltic Sea, and in the basin-specific studies, is the magnitude of the benthic biomass. While not all benthic species belong to the second trophic level, the majority of benthic species feed on primary producers or detritus and thus belong to the primary consumers (Sokołowski et al., 2012). We assume that the huge stock of benthos and the partly inverted biomass pyramid are consequences of allochthonous subsidies of riverine organic material (Bartels et al., 2018), lower turnovers rates of benthos, access to different resources due to moderate morphological complexity and omnivores feeding modes [as described for other systems by Trebilco et al. (2013, 2016) and McCauley et al. (2018)].

Contemporary stocks and future changes

The quantification of organic carbon stocks is the first step. Analyses of inorganic carbon stocks, the interplay between inorganic and organic stocks and the processes governing the cycling of these stocks must follow to further define today's baseline of carbon stocks in the Baltic Sea. With the help of such a baseline, the impact of measures on carbon stocks can be assessed. Such carbon impact assessments are a prerequisite for identifying losses of carbon stocks, discussing possible strategies to increase total carbon stocks as a mitigation measure and increasing incentives to leave natural resources untouched (Ajani et al., 2013). However, the value of carbon stocks to society has not yet been taken into account and needs to be defined. How socio-economic objectives and the conservation of carbon stocks can be reconciled or balanced against each other remains to be discussed.

Conclusion

We present the first detailed quantification of all relevant living and non-living organic carbon stocks for the entire Baltic Sea ecosystem. In addition, we describe in detail data sources, methods and the associated uncertainties that allow reproduction and critical evaluation of our estimates.

Apart from the estimates themselves, some interesting aspects stand out. Our estimated POC stock is higher than some previous studies suggest. Whether this potential difference in magnitude has consequences for the carbon cycle of the Baltic Sea remains to be investigated. Some earlier basin-specific studies in the Baltic Proper show a higher zooplankton than phytoplankton biomass. We cannot confirm this for the entire Baltic Sea ecosystem. Besides, productive, coastal and eutrophic systems are generally not associated with inverse biomass distributions. However, we do find such a partially inverse biomass distribution if benthos is considered. Therefore, we need to rethink biomass distribution and investigate the mechanisms that can lead to such a partially inverse biomass distribution in eutrophic systems such as the Baltic Sea.

Challenges for the quantification of carbon stocks are uncertainties and data limitations. Although the Baltic Sea is well monitored, the differences in the available data are enormous and limit our estimates. In particular, data on planktonic, microbial, benthic and fish biomass as well as on macrophytes-covered areas and sediment properties need to be improved. For benthic bacteria and macrophytes-associated sediments, not sufficient data are available to avoid double counting with the sediment stock. In addition, we need to improve carbon-concentration estimates, find common reporting and calculation methods and communicate uncertainties to avoid misinterpretation of the accuracy of carbon stock estimates. Because of the variability and scarcity of data and the resulting wide range of assumptions and calculations, we do not aim for concrete numbers, nor do our estimates represent concrete numbers, but rather orders of magnitude.

The present study provides estimates of the contemporary organic carbon stock. This quantification can be seen as a baseline for further studies focusing on the stability of these stocks and their response to ongoing environmental changes. Given the ongoing anthropogenic activities and management strategies in the Baltic Sea, carbon stocks and their responses need to become more relevant for impact assessments.

2.3 Study III: The Central Baltic Sea organic carbon cycle with or without cod

Same same, but different:
How a cod collapse might change organic carbon cycling and stocks in the Central Baltic Sea

Maike Scheffold & Inga Hense

The Baltic Sea is a unique ecosystem characterised by a relatively simple food web and a few key species, one of which is the piscivorous cod. Due to anthropogenic influences and climate change-induced alterations in, for instance, salinity, there have been several regime shifts in the Baltic Sea over the last decade, including a sharp decline in the formerly dominant stock of cod. While the reasons for this change have been studied in detail, the consequences of the declining population of cod for the organic carbon (OC) cycle and stocks, specifically in the Central Baltic Sea (CBS) with its deep-lying sediments, are still unclear. One reason for this knowledge gap is that it is not yet conclusively clear whether cod only control the population size of their main prey, sprat, or whether they also control populations that occupy a lower position in the food web, such as phytoplankton, through a trophic cascade. Tackling that gap, we describe how a cod collapse can theoretically change the OC cycle in the CBS. To this end, we compare a CBS reference state with a healthy cod stock (BREF) with a state with a dominant sprat and a depleted cod population. To account for the different extent of top-down control, we distinguish two variants in the CBS with the collapsed cod population: one with top-down control (BNoCodTD) down to phytoplankton and one variant with trophic control down to sprat (BNoCodBU) only. Based on the general concept of the OC cycle and process knowledge, we describe which pathways and loops transport more or less OC and how the living and non-living stocks of the two variants could change compared to BREF. In BNoCodTD, all loops in the water column recycle OC less efficiently. As a result, more OC sinks and is buried. BNoCodTD can thus be a carbon sink, especially if anoxic bottom conditions prevail. In contrast, BNoCodBU can be a carbon source, as all loops in this variant work more effectively and less OC reaches the sediment. Although our descriptions are theoretical, they show conditions under which a collapse of the cod population can have a significant impact on the OC cycle and storage of the CBS. Building on these results, quantification and modelling, must follow to refine the conditions and thus support or falsify the hypothesised alterations in the OC cycle of the CBS.

Keywords: fish carbon, top-down control, remineralisation loops, burial, carbon source, carbon sink, benthic-pelagic coupling

Hitherto unpublished

Introduction

The Baltic Sea is a unique brackish ecosystem characterised by a significant Southwest-Northeast salinity and biodiversity gradient and by a relatively simple food web driven by a handful of keystone species. Surrounded by nine highly industrialised countries with intensive agriculture, the Baltic Sea is is at the centre of numerous human activities, such as tourism and fishing, and experiences exploitation, eutrophication and continuously changing abiotic factors. The combination of these drivers have led to several well-known regime shifts (as defined by Scheffer et al. (2001) and Biggs et al. (2009)) in the last century.

The Baltic Sea changed from an oligotrophic, seal-dominated ecosystem with relevant benthic components to a eutrophic, cod-dominated one with a weak benthic-pelagic coupling after a drastic decline of flatfish, seals, and harbour porpoises and the onset of human-induced eutrophication after the 1920s (Österblom et al., 2007; Tomczak et al., 2021). In the 1980s, a sharp decline in the cod stock in the Baltic Sea and changes in abiotic factors caused the ecosystem to evolve from one dominated by cod to one dominated by planktivores, predominantly sprat (Casini et al., 2009; Möllmann et al., 2009). The Western Baltic Sea cod likely passed a tipping point and practically collapsed as a result (Möllmann et al., 2021). The remaining cod stock is in poor conditions (ICES, 2021b,a) and at risk of disruption or collapse below a recovery potential due to climate change-induced warming, mainly as a result of hypoxia (Orio et al. 2021; Casini et al. 2016) and decreasing salinity (Köster et al., 2005), combined with unsustainable fishing practices (Svedäng and Hornborg, 2017) and other factors, such as infections (ICES, 2021a). Elements of the regime shifts in the Baltic Sea fit well into the decline of higher trophic levels - even of apex predators - already observed in many marine ecosystems worldwide and mainly attributed to overfishing (Myers and Worm, 2003; Jackson et al., 2001; Estes et al., 2011).

Regime shifts associated with changes at higher trophic levels influence organic carbon (OC) stocks and the carbon cycle by, among other things, altering the abundance of lower trophic levels via so-called trophic cascades (Baum and Worm, 2009; Paine, 1980); as observed in kelp systems (Wilmers et al., 2012) and in the Black Sea (Daskalov, 2002), for instance. Although research on food web dynamics in the Baltic Sea is very advanced, there is still no consensus on how changes at higher trophic levels affect lower trophic levels, i.e. how far top-down control and trophic cascades extend. For example, Casini et al. (2008) found that cod control the food web down to zooplankton and possibly even phytoplankton, while Bernreuther et al. (2018) and Möllmann and Köster (1999) showed that cod only control sprat, one of the planktivores in this system, as the abundance of sprat and mesozooplankton is decoupled. Further, there are less clear either/or results indicating mixed or species-dependent forms of trophic control. For example, Möllmann et al. (2008) found a species-dependent trophic cascade in which planktivores determine individual species rather than total zooplankton abundance, and Casini et al. (2009) described that top-down or bottom-up control of zooplankton are dominant in the Baltic Sea, depending on whether a threshold of 17×10^{10} planktivores is reached. This result resembles the discussion of Pershing et al. (2015) that the Baltic Sea may be subject to both trophic cascades and bottom-up factors.

Since we do not know exactly how changes at higher trophic levels affect lower levels, trophic cascades and their consequences for the carbon cycle in the Baltic Sea and the Central Baltic Sea (CBS), which has the highest potential for longer-term burial of OC in the Baltic Sea due to its high proportion of deposition bottoms (Carman and Cederwall, 2001), are still uncertain and have also not yet been studied.

Our aim is to describe theoretical effects of a cod stock collapse on the OC cycle and stocks of CBS under different degrees of top-down control in a first systematic discussion. To this end, we compare literature-based hypothetical OC cycles of a CBS state with a healthy cod stock and one with a collapsed cod stock. Based on the question of how far top-down control extends, which remains to be clarified, we distinguish between two versions of CBS with a collapsed cod stock; one with extensive top-down control and one with a mixture of bottom-up and top-down control. For the comparison, we use the concept described in chapter 2.1 (see Scheffold and Hense (2022)) to systematically present and discuss the OC pathways and their overarching structures (loops) in the CBS. The result of the comparisons are first hypotheses on how a cod collapse can influence the OC cycle in the CBS under different conditions.

The used concept

We use the OC cycle concept by Scheffold and Hense (2022) introduced in chapter 2.1 to illustrate OC pathways and loops in the CBS in different ecosystem states and under different assumptions of top-down control. The concept condenses and synthesises OC pathways into higher-level structures by defining these through unique combinations of sequences of functional segments and spaces (see Box 2.3.1). The concept resolves structures of closed and open loops according to whether the OC pathways close inside or outside the marine system (outside: in the atmosphere or deeper sediments involved in the geological carbon cycle). Using at least four spaces for pelagic systems and seven functional segments (see chapter 2.1 or Scheffold and Hense (2022) for a complete description), the concept defines five closed loops (three remineralisation and two refractory dissolved organic carbon (rDOC) loops) that describe the marine OC cycle completely. The open loops comprise atmosphere inorganic carbon (IC) and OC loops as well as lower sediment OC and IC loops. Apart from these overarching loops, the OC cycle concept differentiates OC pools, processes,

Box 2.3.1

Structure: A structure is a superordinate generalisation/ condensation of multiple pathways. A structure is defined by a unique combination of a sequence of functional segments and the involved spaces. The combination describing a structure must be true for all pathways of that structure.

Closed loop: A structure that comprises all pathways returning to the initial position (OC in the SLS). Closed loops are the most overarching structure in the marine OC cycle.

Functional segment: The condensed function of processes that have the same general functionality. For instance: 'OC position change' including sinking and biota-induced transport.

Spaces: Spatially bounded volumes with very different environmental conditions, for instance the surface layer space (SLS).

and organisms that initiate processes (agents) embedded in the closed loops. This additional information can be used to define structures hierarchically below the defined loops. For instance, one can define 'Fish remineralisation loops' belonging to the remineralisation loops by focusing on pathways involving fish.

Specifications for the CBS

We focus on the pathways that start with particulate organic carbon (POC) produced in the CBS. We do not consider loops involving rDOC and volatile organic compounds (VOC) (see Table 2.7 for loops considered).

Although a simplification, we regard this limitation sufficient to illustrate the potential impact of a cod collapse on the OC cycle. However, we recognise that the dissolved organic carbon (DOC) and rDOC pathways may be significant for the carbon storage of the CBS.

Table 2.7: Functional segments, spaces and loops used for the CBS based on Scheffold and Hense (2022). The functional segments 'Burial' and 'Outgassing of dissolved inorganic carbon (DIC)' are not common to all pathways of the closed loops and not given a capital letter in the original concept. Acronyms: OC position change = A, OC remineralisation = D, DIC upward position change= E, DIC uptake by primary producers =F, Surface layer space= SLS[1], Water column space = WCS[2], Upper sediment space= USS[3], Lower sediment space= LSS[5], Atmosphere space = AS.

Loop	**Sequence of functional segments and involved spaces**
Surface layer remineralisation loop (SLRL)	D[5] [SLS] → F [SLS]
SL atmosphere inorganic carbon loop (SLAICL)	D [SLS] → Outgassing of DIC [AS]
Water column remineralisation loop (WCRL)	A [WCS] → D [WCS] → E [SLS]→ F [SLS]
WC atmosphere inorganic carbon loop (WCAICL)	A [WCS] → D [WCS] → E [SLS]→ Outgassing of DIC [AS]
Upper sediment remineralisation loop (USRL)	A [USS] → D [USS] → E [SLS]→ F [SLS]
US atmosphere inorganic carbon loop (USAICL)	A [USS] → OC [USS] → E [SLS]→ Outgassing of DIC [AS]
Lower sediment organic and inorganic carbon loop (LSOCL and LSICL)	A [LSS][6] → Burial [LSS] or A [USS] → D [USS] → Burial [LSS]

Notes:

[1] SLS= Upper mixed and sunlit water layer.

[2] WCS= Water column below the well-mixed surface layer.

[3] USS= Uppermost part of the sediment that is still actively involved in OC cycling in the marine system.

[4] LSS= Lower sediment not actively involved in OC cycling.

[5] If pathways with multiple remineralisation steps are assigned to the loops, the last remineralisation before uptake by primary producers defines the loop.

[6] This also included OC being transported to the WCS pausing there until finally reaching the lower sediment.

We further focus on 'OC position change', 'OC remineralisation', 'Fragmentation' and

Table 2.8: Focus on the functional segments A, D, fragmentation and burial plus the displayed embedded processes and process-executing organisms (agents).

Functional segment	**Processes**	**Agents**
OC position change (A)	Direct biota-induced transport	Migrating organisms
	Sinking	
OC remineralisation (D)	Bacterial remineralisation	Bacteria
	Phytoplankton respiration	Phytoplankton
	POC_L consumer-based respiration	POC_L consumer (including migrating organisms)
	POC_D consumer-based respiration	POC_D consumer (including migrating organisms)
Fragmentation	Bacterial hydrolysis	Bacteria
	Phytoplankton exudation	Phytoplankton
	POC_L consumer fragmentation	POC_L consumer (including migrating organisms)
	POC_D consumer fragmentation	POC_D consumer (including migrating organisms)
Burial	Burial	

'Burial' (Table 2.8). We thus do not distinguish whether pathways belong to the open atmosphere IC or closed remineralisation loops, as we do not resolve the functional segments 'DIC upward position change' and 'DIC uptake by primary producers' that are necessary to differentiate these loops. Furthermore, for simplicity, we only consider direct biota-induced transport and sinking without resolving biota-induced upward transport, though. We regard this simplification as sufficient for theoretically describing pathway changes in the CBS.

To resolve the food web dynamics, we add carbon pools and distinguish between DOC (produced by fragmentation processes) and living (POC_L) and detrital POC (POC_D), which is either produced in situ, sunken, or transported by mixed processes. POC_L comprises a simplified and trimmed CBS food web consisting of small and large phytoplankton, pelagic bacteria, protozooplankton, zooplankton, herring, sprat, cod, and mammals. We further assume that the oxygen concentration in the system still allows benthic life. Hence, we resolve a benthic food web with nektobenthic mysids, meiobenthos, sediment bacteria, and macrobenthos (isopods). Pools comprise grouped species or individual species if they are managed independently (sprat, herring, cod) or if they are used as representatives of a larger pool due to their dominance in the stock or in the literature (mysids, isopods). We define the feeding habits of the different organism groups and species based on Kiljunen et al. (2020), Harvey et al. (2003), Takahashi (2004), Englund et al. (2008) and Šiaulys et al. (2012).

Comparison of cod- and sprat-dominated system states

We compare a reference system state, the CBS with a cod stock (BREF), with one with a collapsed cod stock (BNoCod) to show how a complete collapse of the cod stock in the CBS could change carbon pathways and stocks. For BNoCod, we distinguish two equally likely versions by changing only the extent of top-down control. While the decline of cod affects the planktonic structures via trophic cascades in BNoCodTD, it only affects the sprat population in BNoCodBU, as the stocks of the underlying levels are decoupled from the sprat population.

We add semi-quantified assumptions based on a non-systematic literature review to hypothesise about changes in stocks and loops. For example, we indicate whether living stocks increase and whether a process, e.g. bacterial remineralisation, is enhanced, i.e. channels more absolute carbon when compared to BREF. We graphically represent stock changes by adjusting the size or number of symbols. Functional segments/ processes that channel more OC are visualised in purple and those that channel less in red (see Figures 2.3.1 and 2.3.2).

We do not quantify carbon stocks and the described changes in pool sizes are only relative to BREF. In addition, we only consider the role of the collapse of the cod stock. Hence, we do not consider other possible disturbances. In reality, the decline in cod has been accompanied by other processes and alterations, such as intensified fishing of herring and sprat and the spread of anoxia. For our consideration, we assume that these processes did not take place. Since most food webs, carbon cycles and ecosystem interactions are non-linear, our semi-quantified estimates and assumed changes are exemplary only. Since we want to systematically identify possible options for how a collapse of the cod population could change carbon pathways and OC cycling, this limitation is acceptable at this stage. However, we emphasise that our presented options are neither the only ones nor necessarily the most realistic, particularly in view of the interaction of multiple factors and perturbations. We point out where the literature supports our assumptions, but the entire discussion is exemplary.

The reference OC cycle of the CBS

The OC cycle in BREF, resembling the eutrophied pre-collapse CBS before 1980, is conceptually described in figures 2.3.1 and 2.3.2 in the left panel. Cod are the main piscivores in this system state, as mammals are only present in small numbers due to slow recovery from hunting and pollutants-related mass mortalities (Harding and Härkönen, 1999). The sprat stock is controlled by cod (Casini et al., 2008) and thus smaller than productivity in BREF would support. The herring stock, on the contrary, is comparatively high in BREF since cod control herring to a lesser extent (Harvey et al., 2003; Casini et al., 2008); herring are rarely predated by mammals; and experience weak food competition with sprat, which can limit the herring stock (Möllmann et al., 2004).

Zooplankton and mysids, both feeding on phytoplankton, characterise the planktonic food web. Zooplankton as a homogeneous group are reportedly high in biomass (see i.e., Tomczak et al. (2021)) and mysids feeding on it, too. Phytoplankton, fertilised by eutrophication, maintain a high abundance against grazing (Niiranen et al., 2013; Li et al., 2020). The smaller components of the planktonic food web are of lesser importance, as a higher share of large primary producers characterises eutrophied systems (Cotner and Biddanda, 2002; Biddanda et al., 2001). The microbial loop (the recovery of microbial OC to the classical food web) is not considerably involved in the OC cycle, as abundant zooplankton control the protozooplankton stock (Samuelsson et al., 2006). The protozooplankton, therefore, consume few small phytoplankton and bacteria and recover less of this small-sized carbon for the classical food web.

Cod top-down control macrobenthos (Harvey et al., 2003), in our example Saduria entomon, by feeding on it in the sediment boundary layer. Therefore, the macrobenthos population is comparatively small. Some studies discuss the possibility of an inverse relation of meio- and macrobenthos (e.g. Harvey et al. (2003)). However, the omnivorous feeding behaviour of all benthic organisms can decrease the direct regulation of meiobenthos biomass by macrobenthos (Polis and Strong, 1996; Eriksson et al., 2011). We assume that the meiobenthos stock is relatively large. Although cod and some mammals (Kiljunen et al., 2020) feed on benthic organisms, we do not consider them as pools in the USS because they do not live in the sediment or boundary layer or stay there longer than is required for feeding.

Direct biota-induced transport includes the movements of all migratory species between the SLS and WCS and of mysids between the WCS and USS. The upward transport of OC from the sediment to the upper spaces by cod and mammals is not considered in detail here (light grey upward-pointing arrows in Figure 2.3.1 and 2.3.2). Some potentially migrating organisms do not actually migrate (Hays et al., 2001). Therefore, the largest visualised pool of a migrating species in figure 2.3.1 and 2.3.1 represents the pool of the entire system, while the smaller ones represent the proportion that migrates to the respective space and not an additional stock of residing species. For example, not all zooplankton migrate into the WCS (smaller symbol in the WCS) (see Figure 2.3.1, left panel).

Sinking, the other process we consider within the functional segment ‘OC position change’, is mainly driven by primary producers and consumer products (sunken, mixed transported, or produced in-situ) such as faecal pellets and carcasses.

The fragmentation processes by POC consumers that convert POC into DOC involve sloppy feeding, excretion, and coprophagy. POC_D is fragmented by organisms that feed partly or mainly on non-living POC. Following the literature for diet-characteristics in the CBS (see specifications for the CBS), protozooplankton are POC_D consumers in the SLS and zooplankton in the SLS and WCS. Mysids, meio- and macrobenthos may feed on non-living POC in the USS.

Stocks of living pools

In BNoCodTD (Figure 2.3.1, right panel), the collapse of the cod stock causes an increase in sprat, and a sprat-dominated state emerges. The mammal stock is slightly higher compared to BREF due to reduced resource competition with cod. The herring stock is marginally lower than in BREF, since it is under slightly more pressure from an increase in mammals (Hansson et al., 2018) and greater competition with sprat (Möllmann and Köster, 2002). The sprat-controlled zooplankton stock decreases in this version due to top-down control as discussed by Casini et al. (2009). In turn, the decrease in zooplankton increases the abundance of large phytoplankton and protozooplankton (Samuelsson et al., 2006; Aberle et al., 2015). The increase of protozooplankton leads to a lower bacteria stock than in BREF. The abundance of small phytoplankton remains similar though, as the increased feeding pressure by protozooplankton is balanced by reduced predation by zooplankton.

A different picture emerges for BNoCodBU (Figure 2.3.2, right panel). The stocks of sprat, herring and mammals change in a similar way compared to BREF as in BNoCodTD. However, as the top-down control does not extend to organisms trophically below the zooplankton, the changes in the living pools of BNoCodBU are weaker; i.e. the zooplankton stock is only slightly lower and that of the phytoplankton only slightly higher. The planktonic and microbial populations of BNoCodBU thus resemble those of BREF more than those of BNoCodTD. Overall, the total living biomass in BNoCodBU is higher than in BREF, as described by Spiers et al. (2016) for a comparable ecosystem state.

The changes in the benthic communities due to the collapse of cod are similar in both versions: the decline in cod leads to a larger stock of macrobenthos (Harvey et al., 2003). The higher macrobenthos population intensifies predation pressure on meio- and nektobenthos, but does not lead to a significant decline in these populations, as all benthic organisms are omnivorous. The increased predation is distributed across multiple food sources and potentially weakens trophic cascades (Polis and Strong, 1996; Eriksson et al., 2011). However, the influence of omnivores on trophic dynamics is still very controversial as omnivores do not necessarily dampen trophic cascades (Kratina et al., 2012; Fahimipour et al., 2019).

Mysids can escape predation by upward migration, but the mysid stock is slightly lower in both versions due to enhanced benthic predation by isopods. Bacteria in the sediment are consumed by all benthic organisms, partly as by-products. Thus, there is a slight decrease in the bacteria stock due to the increase of the benthic biomass.

Loops in the SLS

Remineralisation pathways in the SLS in BNoCodTD change compared to BREF. Respiration and exudation of phytoplankton increase, since the phytoplankton biomass is higher than in BREF (stock of large phytoplankton is lager and of small ones of similar size). The higher phytoplankton abundance likely also enhances primary production as for example shown in Purina et al. (2018).

How a decrease in top-predators affect community respiration is still debated. Gilman et al. (2013) showed that the amount of carbon consumed for respiration per unit body mass is higher in smaller organisms. This size-based respiration ratio argues for a general increase in consumer respiration when larger populations of smaller organisms replace fewer larger organisms. However, this does not necessarily hold true for all systems depending among others on the number of trophic levels and the extent of top-down control. The results of Atwood et al. (2013) show that larger stocks of predators in an odd-numbered food chain accompanied by an increase in primary production decrease respiration in the system. The BNoCodTD is, assuming a continuing low mammalian population, more or less an odd-numbered food chain with an increase of the (new) top predator sprat and enhanced primary production. Thus, POC_L- based respiration decreases in BNoCodTD compared to BREF.

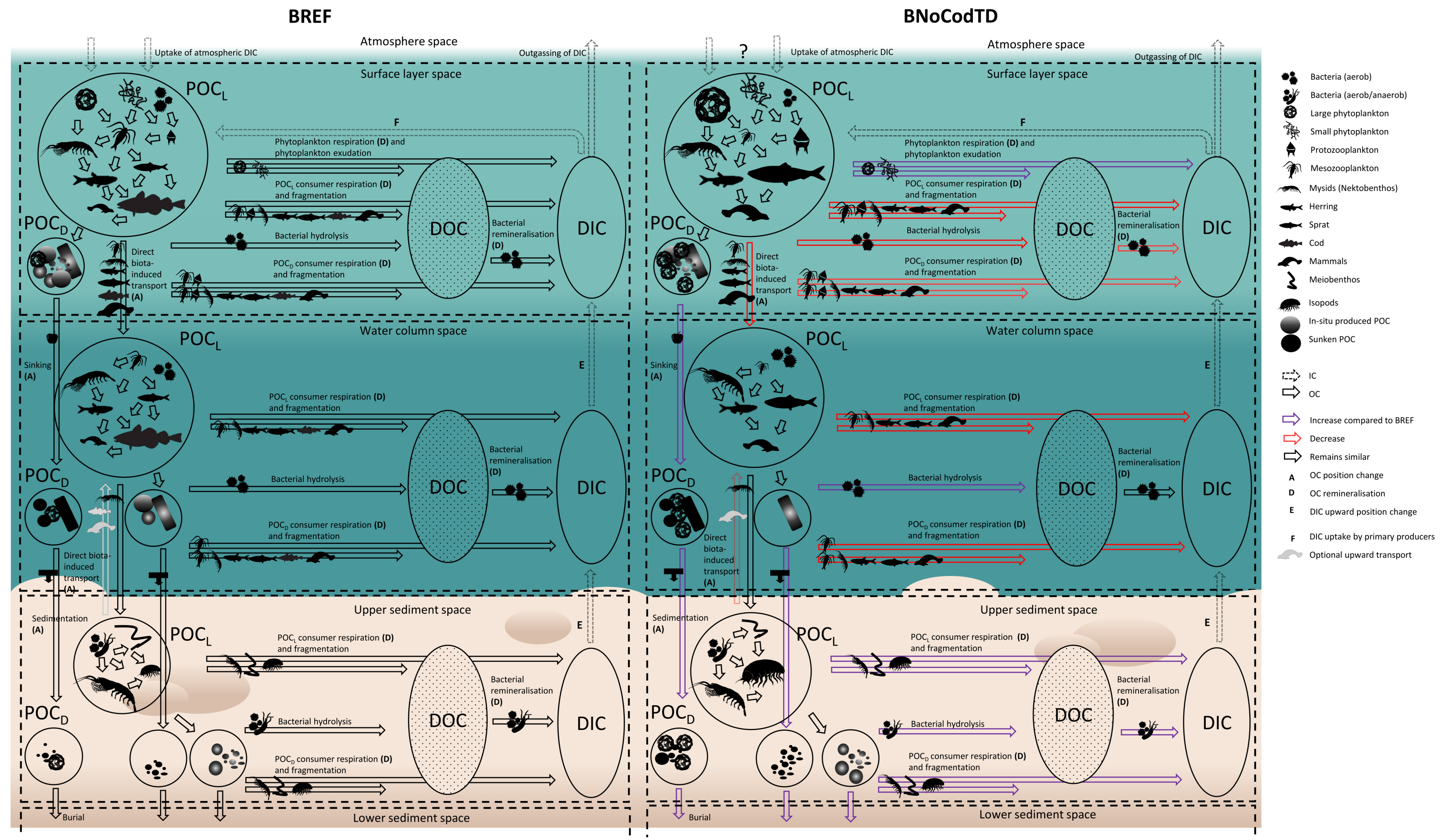

Figure 2.3.1: OC pathways and loops of BREF (left panel) and BNoCodTD (right panel). The illustration is based on the OC cycle concept presented in Chapter 2.1. Changes in pool sizes compared to BREF are displayed by increased symbol sizes or the number of symbols. Red/ purple arrows imply less/ more OC is channelled via this functional segment/ process. Note that for stocks of migrating species, the largest stock represents the stock of the entire system. Smaller stocks of these organisms are not residential stocks.

In addition, POC_D-based remineralisation in BNoCodTD drops because the biomass of consumers feeding on POC_D decreases, and more primary producers sink rapidly due to their larger size, thereby reducing the amount of available POC_D in the SLS. Bacterial hydrolysis and bacterial remineralisation decline, as the stock of bacteria, slow sinking POC_D and DOC decrease. The overall drop of remineralisation reduces the amount of carbon processed in the SLRL and associated AICL in BNoCodTD.

In BNoCodBU, phytoplankton biomass increases only slightly compared to BREF, and so their respiration, excretion and primary production remain similar. In contrast, the respiration of POC_L consumers rises in BNoCodBU compared to BREF, as the overall biomass is higher in BNoCodBU. A similar change of biomass and community respiration was described by Stafford et al. (2021) and Spiers et al. (2016) for comparable ecosystem states. However, more research on community respiration and its possible alterations in changing systems is needed to ground our assumption with field observations or modelling results for specific ecosystems such as the Baltic Sea.

Remineralisation based on POC_D consumption in BNoCodBU hardly changes, as the biomass of POC_D consumers stagnates. Although total biomass increases, fragmentation by POC_L consumers remains of a similar magnitude, as there is no evidence that larger stocks of more productive lower trophic levels increase POC consumer-induced fragmentation. Due to stable DOC production, bacterial remineralisation does not change significantly. Overall, the SLRL or the corresponding AICL in BNoCodBU channel more OC due to elevated POC_L consumer respiration.

Loops in the WCS

In BNoCodTD, more larger phytoplankton sink from the SLS. As large phytoplankton contribute substantially to OC export by sinking (Griffiths et al., 2017; Tamelander et al., 2017), and as sprat metabolites also increase, sinking is strengthened even though there are fewer faecal pellets of zooplankton. The assumption of increased sinking is also supported by the estimated ratios of pelagic heterotrophs to autotrophs (H:A probably < 1) and of bacteria to phytoplankton (B:P probably < 1) in the SLS. Such ratios usually correlate with higher organic matter export (Tamelander et al., 2017).

While sinking is enhanced, direct biota-induced transport in BNoCodTD decreases. Zooplankton and the nektobenthic mysids migrate due to abiotic factors, to optimise foraging (O'Malley et al., 2018) and to escape predators (Möller, 2013; Zaret and Suffern, 1976). There are two lines of argumentation for a decline in this migration. The first is that predation due to a higher sprat stock and consequently the need for migration increases, but the zooplankton stock is so low that overall migration decreases. The second argument is the other way around. Since there is evidence that some zooplankton migrate primarily to escape top-down control of sprat (Möller, 2013; Hänselmann, 2019), existing top-down control of sprat would argue for less accomplished migration. While mysids still migrate to feed in the SLS and escape predation from the increased macrobenthos, fewer organisms migrate into the WCS overall. The low predation pressure on sprat supports a weakening of migration-based OC transport, as sprat migrate among others to escape predation (Solberg et al., 2015).

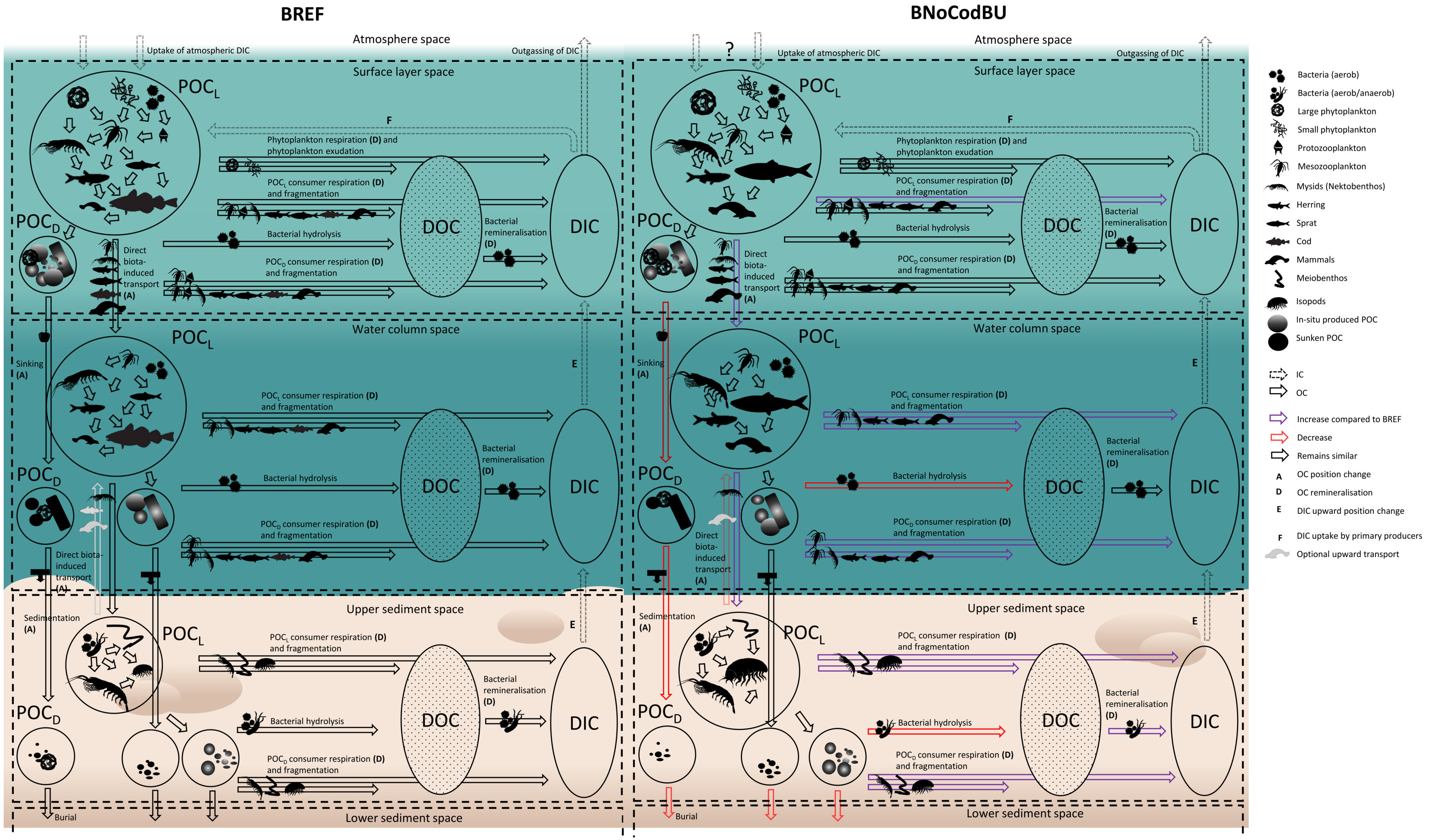

Figure 2.3.2: OC pathways and loops of BREF (left panel) and BNoCodBU (right panel). The illustration is based on the OC cycle concept presented in Chapter 2.1. Changes in pool sizes compared to BREF are displayed by increased symbol sizes or the number of symbols. Red/ purple arrows imply less/ more OC is channelled via this functional segment/ process. Note that for stocks of migrating species, the largest stock represents the stock of the entire system. Smaller stocks of these organisms are not residential stocks.

POC consumer-based remineralisation in the WCS in BNoCodTD drops as we assume that there is less migration and no resident POC consumer community in the WCS to compensate for the lower migration. Analogous, POC_D based respiration and fragmentation decreases, since e.g. coprophagy and indirect particle destruction via swimming (Goldthwait et al., 2004) decline. Bacterial hydrolysis is increased by higher sinking fluxes. However, as more fast sinking particles are available in BNoCodTD and these particles reach the sediment more likely than slow-sinking particles, bacterial hydrolysis cannot compensate for the lower fragmentation of POC consumers. Overall, DOC production is reduced or remains the same. The bacteria stock and bacterial remineralisation behave analogously and stagnate.

However, how much POC consumers contribute to DOC production by fragmentation is still largely unquantified for distinct ecosystems, although the general mechanisms have been described. Studies suggest that POC fragmentation is a significant contributor to DOC production, about 50% in temperate oxic waters (Giering et al., 2014), but there are no comparable estimates for the Baltic Sea. Further research is needed to understand how organisms in the Baltic Sea drive or alter DOC production and bacterial remineralisation. For this study, we assume that POC consumer provide a comparable share of DOC via fragmentation as bacterial hydrolysis.

In BNoCodBU, direct biota-induced transport increases with higher predation pressure of sprat on a high stock of zooplankton. It may even be that the lower top-down control allowing higher zooplankton abundance is due to increased and successful migration to avoid predation. With the exception of cod, the stocks of all migrating species are larger or only marginally smaller, so that migration is elevated in BNoCodBU compared to BREF.

Sinking, on the other hand, decreases in BNoCodBU, similar to the ecosystem state discussed by Stafford et al. (2021). As described in their study, sinking decreases when remineralisation and direct biota-induced transport increase but primary production stagnates.

In BNoCodBU, all remineralisation processes connected to migrating POC consumers increase since more organisms migrate. At the same time, bacterial hydrolysis decreases due to the reduced sinking. Assuming, as with BNoCodTD, that bacterial hydrolysis and other POC fragmentation processes are comparable in magnitude, bacterial remineralisation stagnates as DOC production is in a similar range as in BREF.

Overall BNoCodBU shows a strong increase in the remineralisation in the WCS that could increase DIC pools in the WCS and enhance the WCRL and the respective AICL. In BNoCodTD, in contrast, remineralisation processes channel less OC via the WCRL and the WC atmosphere inorganic carbon loop (WCAICL).

Loops in the USS and burial

In BNoCodTD, more POC reaches the USS, mainly by sinking out of the surface and less by mixed processes such as migration plus sinking or cascading migration (Bollens et al., 2011). Migration into the USS is similar and sinking of WCS-produced POC is similar or slightly higher compared to BREF. However, changes in the migration behaviour of mysids are not well known and could change due to abiotic factors, enhanced predation of macrobenthos and changes in pelagic POC subsidies (Ogonowski, 2012; O'Malley et al., 2018).

The increased benthic biomass enhances respiration and fragmentation in BNoCodTD. Bacterial hydrolysis and fragmentation also rise as more POC reaches the sediment. Although remineralisation is enhanced, burial in BNoCodTD increases since the amount of OC reaching the USS is very high. We assume that the input of OC to the USS in BNoCodTD resembles times of high productivity in the Baltic Sea that reportedly lead to increased burial (Maciejewska and Pempkowiak, 2014). In addition, the increased respiration in the USS might promote anoxia. This anoxia in turn could dampen benthic activities and increase anoxic bacterial remineralisation, enhancing burial even more, as remineralisation is positively connected to bioturbation by benthic species (Middelburg, 2019).

In BNoCodBU, less carbon enters the USS compared to BREF, since less OC sinks as overall remineralisation in the SLS and in the WCS is increased.

Similar to BNoCodTD, respiration of POC consumers increases in BNoCodBU as the benthic biomass is larger than in BREF. At the same time, bacterial hydrolysis decreases as the bacteria stock is lower compared to BREF and a greater proportion of the reduced POC sinking flux is readily consumed by the higher POC consumer stock. However, the increased DOC production associated with the higher benthic stock likely counteracts the losses from bacterial hydrolysis. Thus, bacterial remineralisation remains constant or decreases slightly. In contrast to BNoCodTD, burial is reduced as less OC reaches the sediment and more of it is consumed. If the reduced POC input leads to starvation of the benthos, this could lead to even more burial.

Mysids likely react to the reduced input of POC as food resource by migrating more to feed on pelagic resources (Rudstam, 2009; O'Malley et al., 2018). The migration of mysids to the WCS and the SLS is not only necessary for their OC needs but might be a significant link of OC to the sediment. It is well established that organisms change the distribution of carbon and nutrients by breathing, feeding and defecating in different positions in the water column. For instance, the nutrient transport by upward pumps via reverse migration (Pinti et al., 2019; Roman and McCarthy, 2010) can alter the productivity of primary producers and the plankton stock (Allgeier et al., 2017) with consequences for the food web and carbon pathways. In our example, we only consider the direct biota-induced transport of organic material to deeper spaces. Thus, we neglect, for example, upward transport by migrating organisms that alters carbon stocks by reinforcing loops in the upper spaces. To account for migration and its full impact on carbon and nutrient distribution, further research is needed to understand migration in the Baltic Sea, especially as migration patterns vary greatly e.g. inter- and intraspecifically (Hays et al., 2001).

Overall, remineralisation via POC_D consumers increases in both versions and thus increases the USRL or the respective AICL. Depending on the input of OC, BNoCodTD potentially buries more OC, while BNoCodBU will likely exhibit decreased burial. In both cases, benthos might be endangered either by anoxia or starvation.

Summary and conclusion

The results of our theoretical excursus into possible changes in OC pathways and stocks show that the existence or non-existence of cod can change the OC through-put of loops and the size of standing stocks depending on the extent of top-down control (summarised in Table 2.9).

Table 2.9: Summary of the changes in functional segments and loops in BNoCodTD and BNoCodBU compared to BREF and the assumptions and conditions necessary for these outcomes.

	BNoCodTD	**Assumptions/ conditions**	**BNoCodBU**	**Assumptions/ conditions**
Fragmentation [SLS]	⬇	More fast sinking POC_D as more larger phytoplankton, smaller stocks of bacteria and zooplankton	➡	Similar basal production and no significant changes in living stocks sizes relevant for fragmentation
POC_D remineralisation [SLS]	⬇	Decrease in POC_D consumer respiration, the bacteria stock and fragmentation	➡	Similar basal production and similar POC_D consumer stocks
POC_L remineralisation [SLS]	⬇	Increase in primary production and higher trophic level biomass	⬆	Increase of living stocks, similar basal production and a stagnating stock of large phytoplankton
SLRL or respective AICL	⬇	All above	⬆	All above
Sinking [WCS]	⬆	More primary production, less OC channelled through SLRL and more larger phytoplankton	⬇	Direct biota-induced transport and POC_L remineralisation enhanced plus primary production similar

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Table 2.9 – continued from previous page

	BNoCodTD	Assumptions/ conditions	BNoCodBU	Assumptions/ conditions
Direct biota-induced transport [WCS]	⬇	Non-effective migration by low zooplankton stock to avoid higher predation pressure	⬆	Effective migration by similar zooplankton stock to avoid higher predation pressure
Fragmentation [WCS]	➡	Decreased migrated POC consumer stocks and more bacterial hydrolysis balanced	➡	Increased migrated POC consumer stocks and less bacterial hydrolysis balanced
POC_D remineralisation [WCS]	⬇	Increased fast sinking POC and lower POC_D consumer stocks due to less migration	⬆	Increase in in-situ POC_D and higher stocks of POC_D consumers due to enhanced migration
POC_L remineralisation [WCS]	⬇	Decreased POC_L consumer respiration due to less migration and overall less community respiration	⬆	Increase POC_L consumer respiration due to more migration
WCRL or respective AICL	⬇	All above	⬆	All above

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Table 2.9 – continued from previous page

	BNoCodTD	Assumptions/ conditions	BNoCodBU	Assumptions/ conditions
Sinking [USS]	⬆	Decreased remineralisation in the WCS and enhanced sinking to the WCS, in-situ produced POC$_D$ readily remineralised in the WCS	⬇	Increased remineralisation in the WCS and reduced sinking to the WCS, in-situ produced POC$_D$ readily remineralised in the WCS
Direct biota-induced transport [USS]	➡	Enhanced POC availability and predation pressure on mysids are balanced	⬆	Low POC availability and increased predation pressure enhance migration
Fragmentation [USS]	⬆	More benthic POC$_L$ stocks	⬆	More benthic POC$_L$ stocks
POC$_D$ remineralisation [USS]	⬆	Increase in in-situ produced POC$_D$, higher benthic stocks, more sunken POC$_D$	⬆	Increase in in-situ produced POC$_D$ and higher benthic stocks
POC$_L$ remineralisation [USS]	⬆	Increase POC$_L$ consumer respiration due higher benthic stocks	⬆	Increase POC$_L$ consumer respiration due higher benthic stocks
USRL or respective AICL	⬆	All above	⬆	All above
Burial	⬆	Very enhanced POC input	⬇	Decreased POC input and enhanced remineralisation in USS

The BNoCodTD variant is characterised by a starvation of the loops in the SLS and the WCS with simultaneously higher primary production. More OC is introduced into the system via primary production, but a high proportion of this additional OC is rapidly transported to the benthic stocks via sinking, enhancing pathways with physical OC position change. Migration and benthic-pelagic coupling by living organisms is of less importance. Burial is increased compared to BREF. If bacterial remineralisation increases strongly, anoxia and increased burial may follow (Baroni et al., 2020). The pelagic OC cycle is less efficient than in BREF because more OC is less remineralised. Remineralisation in the USS is enhanced, but is not necessarily more efficient, as much more OC (the additional primary production plus the non-remineralised OC sinking out of the SLS and WCS) reaches the USS. Changes in living stocks are difficult to estimate. In the WCS, they are probably declining, while they are increasing in the USS. Overall, living stocks are probably somewhat smaller than in BREF. Hence, the transfer efficiency within the food web may be higher than in BREF, reflected in the low respiration losses. Whether BNoCodTD is a sink or a more or less balanced system state is not easy to answer. Under anoxic conditions, it would probably be a sink, as more OC would be buried. Under oxic conditions, it would depend on the difference between burial, DIC outgassing, and DIC uptake from the atmosphere.

In BNoCodBU, the collapse of the cod population strengthens the remineralisation in all spaces and the pathways with direct biota-induced transport, but reduces purely physically induced transport pathways and burial. Increased migration, reduced sinking, and the possibility of starvation of benthic organisms characterise BNoCodBU. Mysids and migration play a more significant role in distributing carbon compared to BREF. More OC is remineralised in each loop while fewer OC reaches deeper spaces than in BREF. This relation implies that all loops in BNoCodBU are more efficient than in BREF. BREF is dominated by the functional segment A and loses a share of OC in every loop to burial. In BNoCodBU, the loops, especially the biota-driven loops and functional segment 'OC remineralisation' are strengthened, while the loss processes are weakened. The standing stocks of living organisms increase. Due to the constant primary production, a simple budget shows that either less atmospheric carbon dioxide is taken up or more DIC is outgassed. Both lead to the same result: BNoCodBU is a source of carbon dioxide. The variant BNoCodBU is a source, although living standing stocks in the system increase. This is possible since the living stocks are much smaller than the non-living OC stocks (Scheffold and Hense, 2020b) and the DIC pool.

What can we learn from our considerations for the real CBS? As described above, due to the limitations of our study (e.g. the semi-quantitative approach, the homogeneity of the pools, the ignorance of the timing and ongoing nutrient trends), the non-linear correlation (e.g. feedbacks and indirect effects) and research gaps (e.g. response of the community respiration), the variants are only exemplary results. Both variants present end-members and were chosen as such intentionally. Between these end-members there are countless hybrid variants. However, the theoretical and systematic description shows how a cod collapse could affect the carbon cycle, the standing OC stocks, and the potential burial capacity of the CBS. The theoretical possibility of such changes alone is a basis for further research on the influence of higher trophic levels on OC in the Baltic Sea.

2.4 Study IV: Leverage management of fish - a perspective

Leverage management of fish for climate, biodiversity, and society

Angela Helen Martin, **Maike Scheffold** & Bethan C. O'Leary

Bold measures addressing multiple goals for planetary and human health simultaneously are now critical. Marine fish store carbon, provide habitats, fertilise oceans, and facilitate adaptation to climate change, but current policies focus only on fish as a commodity. Leveraging management of fish would deliver co-benefits for climate, biodiversity, and society.

Keywords: fish carbon, blue carbon, fish as habitat providers, fish carbonates, ecological functions of fish, co-benefits of healthy fish, new perspective on fish

Hitherto unpublished

Introduction

Climate change and the accelerating deterioration of nature are the defining crises of our time; creating wide scale disruption to ecological functioning which underpins societies and economies. The trajectory of change already embedded in planetary systems from past and present inaction requires bold measures to address multiple goals for planetary and human health simultaneously, in addition to immediate large-scale reduction of greenhouse gas emissions and decarbonisation of economies. Given the scale of the crises, novel perspectives are necessary to extend our toolbox of possible actions. Here, we present one such perspective; that management actions to protect and rebuild wild marine fish populations contribute toward the achievement of international climate, biodiversity, and sustainable development goals.

The ocean regulates climate, supports biodiversity, and provides essential resources including food and protein for billions of people, a source of livelihoods, and an economic base for coastal and island nations (Duarte et al., 2020). Yet rates of ocean defaunation and degradation are increasing, and many fish populations have declined substantially in abundance and range. Given this, we highlight the critical need for fish to be better managed, beyond their value as a commodity, to secure wider co-benefits for climate, biodiversity, and society. In support, we outline the key roles fish play in carbon storage, ocean fertilisation, habitat provision, and climate change adaptation.

Agents in addressing the climate and ecological crises for a sustainable future

Carbon storers

Fish contribute to the carbon storage capacity of the ocean by two dominant mechanisms (see Martin et al. (2021) and references therein). First, like all animals they are made up of organic molecules and thus act as a temporary carbon store while alive. Long-lived fish can store carbon on timescales from decades to hundreds of years, much like trees, and, through reproduction, fish populations may represent a perpetual carbon store. Secondly, fish contribute to the transfer of carbon to ocean depths and sediment, where the timescale for the release of carbon back into the atmosphere can be centuries to millennia. For example, mesopelagic fish that feed in shallower water and then migrate deeper release ingested carbon at depth through respiration, defecation, or death. It is estimated that at current biomass levels, fish are responsible for 16% of the carbon flux in the oceans globally (Saba and Steinberg, 2012).

Ocean fertilisers

Fish recycle the nutrients they eat and release them back into the ocean through faeces and urine, thereby providing nutrients to other species through coprophagy, i.e., ingestion of faeces, and to plants, i.e. providing natural fertiliser (Martin et al., 2021). As with carbon, fish transfer nutrients through food webs when they are eaten, and across habitats and vertically through the water column by migration or in their carcasses as they sink or drift with currents. These nutrient-transfer mechanisms enable productivity in the open ocean; coastal habitats; rivers; and terrestrial forests, thereby supporting the ecological and societal benefits of those ecosystems (Martin et al., 2021).

Habitat providers

Fish transform habitats as they move through and between them, influencing plant and animal life. In the open ocean, they provide structuring biomass and define habitats (O'Leary and Roberts, 2017), while population control of grazers and digging animals by predatory fish enables biodiverse vegetated habitats, and the animals that live within them, to persist and thrive (e.g. Hammerschlag et al. (2019)). Removal of predatory fish can degrade vegetated coastal habitats and, in extreme cases, turn them into barren seascapes. Removal of smaller fish lower in the food web impacts the ability of ecosystems to support predatory species. Healthy and diverse fish populations are thus critical for ocean and coastal ecosystem functioning (O'Leary and Roberts, 2017).

Adaptation specialists

By maintaining ecosystem health, stability, and function, fish enhance the adaptive capacity of marine ecosystems to various impacts of climate change. For example, as ocean fertilisers, fish can counteract some of the projected increase in nutrient-depleted waters; as habitat providers, some fish contribute to maintaining coral reefs, kelp forests, and salt marshes, and therefore the protection they provide to coastal areas against sea level rise and increased wave and storm intensity; and, by excreting carbonates, fish can increase local alkalinity and buffer climate-induced acidification (Roberts et al. 2017). Furthermore, larger fish populations can help alleviate some of the projected declines in fisheries catches as, with greater genetic diversity, higher reproductive output, and a larger size structure, large populations are more resilient to, and recover better after, stress than depleted populations.

More than food

There is a constant stream of new evidence on the ecological role (Glossary, Box 2.4.1) of fish and other marine life (Martin et al., 2021; Hammerschlag et al., 2019) (Figure 2.4.1); qualitative and quantitative studies of carbon sequestration or perpetual carbon stores of whole ecosystems at regional scales (Bianchi et al., 2021; Trebilco et al., 2020; Scheffold and Hense, 2020b); and new management and policy approaches (Williams and Rangel-Buitrago, 2019; Roberts et al., 2017). Despite this, international policy measures that seek to secure ocean ecosystem services to tackle climate change, address biodiversity loss, and secure marine resources overlook the role of fish beyond food security or as a commodity (Duarte et al., 2020). For example, in Nationally Determined Contributions submitted by countries under the United Nations (UN) Framework Convention on Climate Change, all mentions of fish focus on climate threats to fishery resources and fishery-based livelihoods; fishery adaptation strategies; and sector-based emission reductions. The role of fish in maintaining ecosystem health is absent in commitments to restore and protect coastal habitats and their benefits, including blue carbon storage. Likewise, fish targeted as a commodity look likely to be excluded from the new UN instrument for the conservation and sustainable use of marine biodiversity beyond national jurisdiction currently being developed (UNGA 2019, Article 8 of the draft text). At best, such policies may fail to reach their full potential, including achieving co-benefits and synergies that management of fish could achieve across such policies; at worst, neglecting the links between fish and ecosystem services may damage the ability of fish and their habitats to deliver their essential functions (Martin et al., 2021; Sala et al., 2021).

Box 2.4.1: Glossary

Areas Beyond National jurisdiction: areas outside of 200 nautical miles of a coastline or the median line between adjacent countries, where exclusive rights are claimed by the country.

Carbon sequestration: carbon kept within the ocean for over 100 years

Carbon storage: carbon kept within the ocean for up to 100 years

Ecological functioning: describes the collective life activities of all organisms in an ecosystem that help sustain the ecosystem and affect the physical and chemical conditions of their environment.

Ecological role: function of an organism in an ecosystem.

Precautionary principle: risk management framework used to identify policy actions required to avoid or reduce potentially serious or irreversible threats to health or the environment in situations of scientific complexity, uncertainty, or ignorance.

To mobilise the function of fish in support of achieving goals on climate action, biodiversity protection and sustainable development, we first need a perception shift, such that the environmental, cultural, societal, and economic benefits of fish are similarly valued. When viewed only as a commodity, the continued degradation of fish populations, while alarming, does not incite the same urgency for their sustainable management as when the planetary wide implications for carbon cycling, habitat loss, ecosystem collapse, and food security are considered simultaneously. The importance of fish across all aspects of life, the current state of ocean defaunation, and the narrow focus of today's fisheries management necessitates a change: fish need to be managed for more than just their commodity value.

During the UN Decades of Ocean Science and Ecosystem Restoration, further research on the function, importance, and optimal management of fish for ocean ecosystem services is to be expected, should be encouraged, and will help develop new approaches to policy and management. However, with climate change likely to exacerbate accelerating ocean defaunation and ecosystem restructuring, there is an urgency to act now and act fast to safeguard the roles of fish, even before they are wholly understood. While there will always be gaps in our knowledge, there are strong arguments to manage fish differently now. Therefore, where research is still emerging, following the precautionary principle is critical. At a time when measures must work harder towards safeguarding planetary health for the wellbeing of humans and nature, re-evaluating the purpose of ocean stewardship, and in particular fisheries

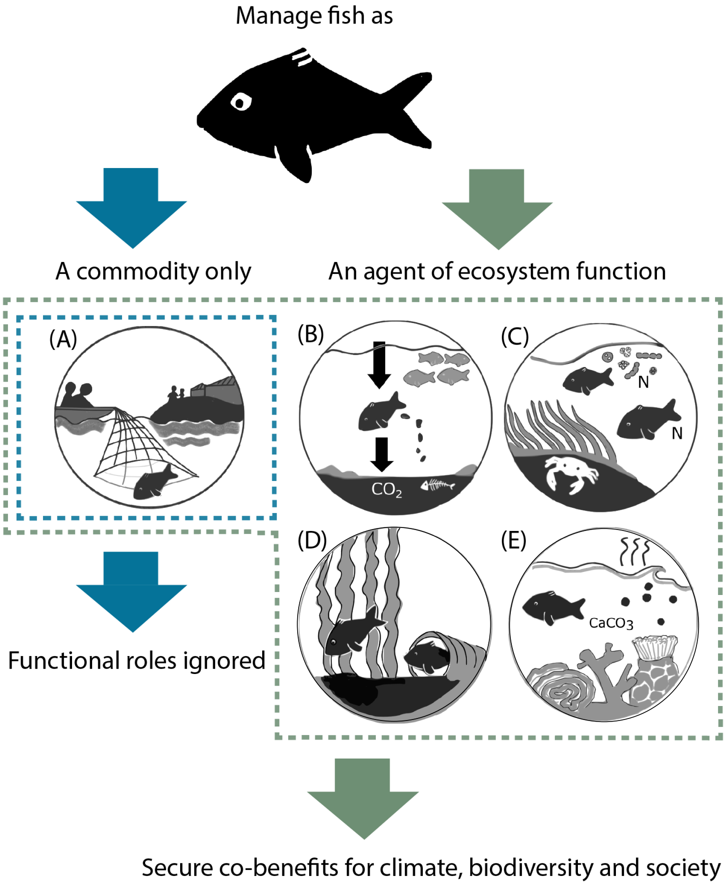


Figure 2.4.1: Concept of the different management perspectives on fish. The arrows and dashed line in blue represent the traditional management perspective with a focus on the value of fish in fisheries. The arrows and dashed line in green denote fish management that takes into account the different roles of fish as A) resource of food and livelihood, B) carbon storers, C) ocean fertiliser, D) habitat provider and E) adaptation specialist.

management, to secure multiple co-benefits seems like a low-risk, achievable strategy.

There is a wealth of evidence and experience on how to sustainably manage, rebuild, and protect fish populations on which to build (Duarte et al., 2020); harnessing these existing tools for better climate, biodiversity and sustainable development outcomes is thus a realistic target. Furthermore, legal structures, policy frameworks, and international agreements already exist to manage fish as a commodity. Implementing these existing approaches for additional goals could be quicker than starting with nothing. One strategy to achieve multiple goals is likely to incentivise implementation and be more cost-efficient and effective than multiple strategies to achieve single goals, even if the full transformation of governance systems will require time, effort, and a stepwise process (e.g. Brodie Rudolph et al. (2020)).

Recognising the multiple and complementary climate, biodiversity, and societal benefits of healthy fish populations will only maximise the effectiveness and efficiency of measures to safeguard planetary and human health. With this holistic perspective of fish, more could be achieved for society, at low cost and with few regrets.

3 | SYNTHESIS

Not only food, and now what?

There is a growing global consensus that fish and marine mammals have been neglected unjustly and that these organisms, like lower trophic level organisms, play significant roles in e.g. food web dynamics (Otto et al., 2008), blue carbon storage (Atwood et al., 2015), export fluxes (Trebilco et al., 2020; St. John et al., 2016) and nutrient trends (Burkepile et al., 2013). Therefore, these organisms will increasingly play a role in quantification and modelling studies. We provide a new general concept (**Study I**) that reflects these new findings and developments, comprises all organisms and differentiates them not by species but by their functions/roles. Being the first concept to generalise overarching structures of all OC pathways, the concept provides a framework for sub-concepts such as the biological carbon pump and allows more structured comparisons of different ecosystems and a consistent visualisation and communication. It can be used for carbon considerations related to all organisms and processes in ecosystems of all scales.

In the Baltic Sea, carbon considerations related to higher trophic levels have not yet been addressed comprehensively. The question arises whether higher trophic levels such as fish/marine mammals are relevant for the OC cycle of the Baltic Sea. Despite the partly theoretical and exemplary nature of studies II and III, there are some findings and hypotheses that we put forward to answer this question.

In **Study II**, we provide a first quantification of OC stocks in the Baltic Sea. These estimates are valid for the whole Baltic Sea, can be compared among each other, and represent the baseline of contemporary OC stocks in the Baltic Sea. Non-living OC stocks are by far the largest in the Baltic Sea (98.8%) with the sediment stock leading the ranking. Interestingly, benthos and not phytoplankton comprises the largest of the living OC stocks. The top-heavy trophic pyramid that results from this large benthic stock is an undescribed feature of the Baltic Sea that needs to be further investigated. OC stocks of the higher trophic levels in the Baltic Sea are relatively low and contribute only marginally to the total OC stock of the Baltic Sea today. However, the Baltic Sea could contain more living biomass, as mammal and fish populations have been depleted over the last century (Österblom et al., 2007). An increase in biomass would not necessarily translate into higher carbon storage capacity of the Baltic Sea since, for example, a decrease in other carbon pools such as DIC could buffer this increase and thus reduce or stabilise the total carbon in the system.

Despite the low importance as carbon stocks, we have shown in **Study III** that a collapse of the cod stock can affect the carbon cycle and carbon stocks in the CBS so that the system functions in a very different way to become either a source or a sink. Higher trophic levels, discussed here using the example of cod, can therefore influence the carbon cycle and storage of the Baltic Sea under certain conditions. This influence may even be more pronounced, since we have not considered the indirect effects of fish and marine mammals, such as their contributions to fertilisation and the lateral connection of habitats. Consequently, in the Baltic Sea, fish are not just food. Nevertheless, fish are considered mainly a fishery commodity. Therefore, the scientific understanding and the management relying on it may have a blind spot regarding the impact of e.g. fisheries on the carbon cycle.

What follows from our considerations for science and marine management? We have highlighted that we need more research on trophic interactions to understand the consequences of drastic changes in the abundance of higher trophic levels. Approaches combining experiments to determine e.g. respiration rates and community respiration, with food web models such as Ecopath, or qualitative network models such as the model developed by Melbourne-Thomas et al. (2012) are needed. In addition, we need to quantify the carbon in the system that is at risk when the system changes. First basic estimates have been provided in this thesis (Study II) for the OC pools of the entire Baltic Sea, but these need to be complemented by quantifications on smaller scales and of IC pools to allow complete budgeting of carbon in the CBS. Based on the complete budgeting of carbon stocks in the Baltic Sea, the carbon storage capacity and stocks of the system could then be modelled under different conditions.

In terms of future ocean governance and management, we argue that potential changes of the carbon cycle and budget that result from fisheries management and policies must no longer be ignored. Even though there are still major scientific uncertainties and gaps, all human actions ought to include a perspective of climate impacts, following the precautionary principle, as also argued in **Study IV**. In particular, as there is increasing insight that ill-considered fisheries management can impact the carbon storage capacity of ecosystems (Mariani et al., 2020; Bianchi et al., 2021), while healthy fish populations promote several other benefits alongside safeguarding food provision.

We acknowledge that the carbon perspective is only one of many that marine management must consider. A scenario compared to BNoCodTD would increase OC in the CBS sediments, but the consequences for the benthos, the living stock, fish productivity, and thus for the fishing industry and its associated societies would likely be ambivalent. Decisions on what to prioritise have to be reached in a societal debate and cannot be based on just one aspect, and one perspective. However, the risk of a reduction or loss of carbon stocks due to ill-considered impacts on the carbon cycle is too high to not, at least, monitor and understand these potential impacts, simply because they could complicate decisions. On the contrary, the multiplicity of demands on ecosystems makes it necessary to examine management options in more detail concerning their sustainability, risk liability, and impacts. Since the presence or absence of cod in the CBS likely impacts its carbon budget and cycling, fisheries management needs to adopt a carbon perspective. A new challenge for policy and marine planning will be to find new structures or test existing instruments for their adaptability for such a carbon perspective.

4 | APPENDICES

4.1 Appendix I

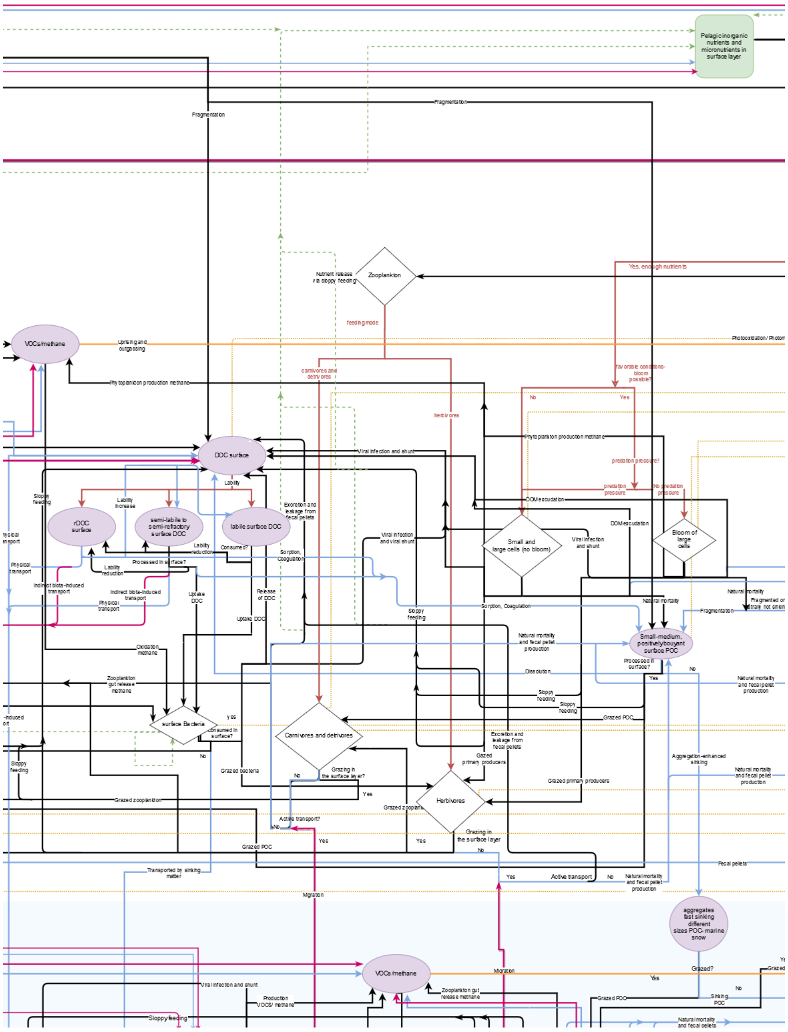
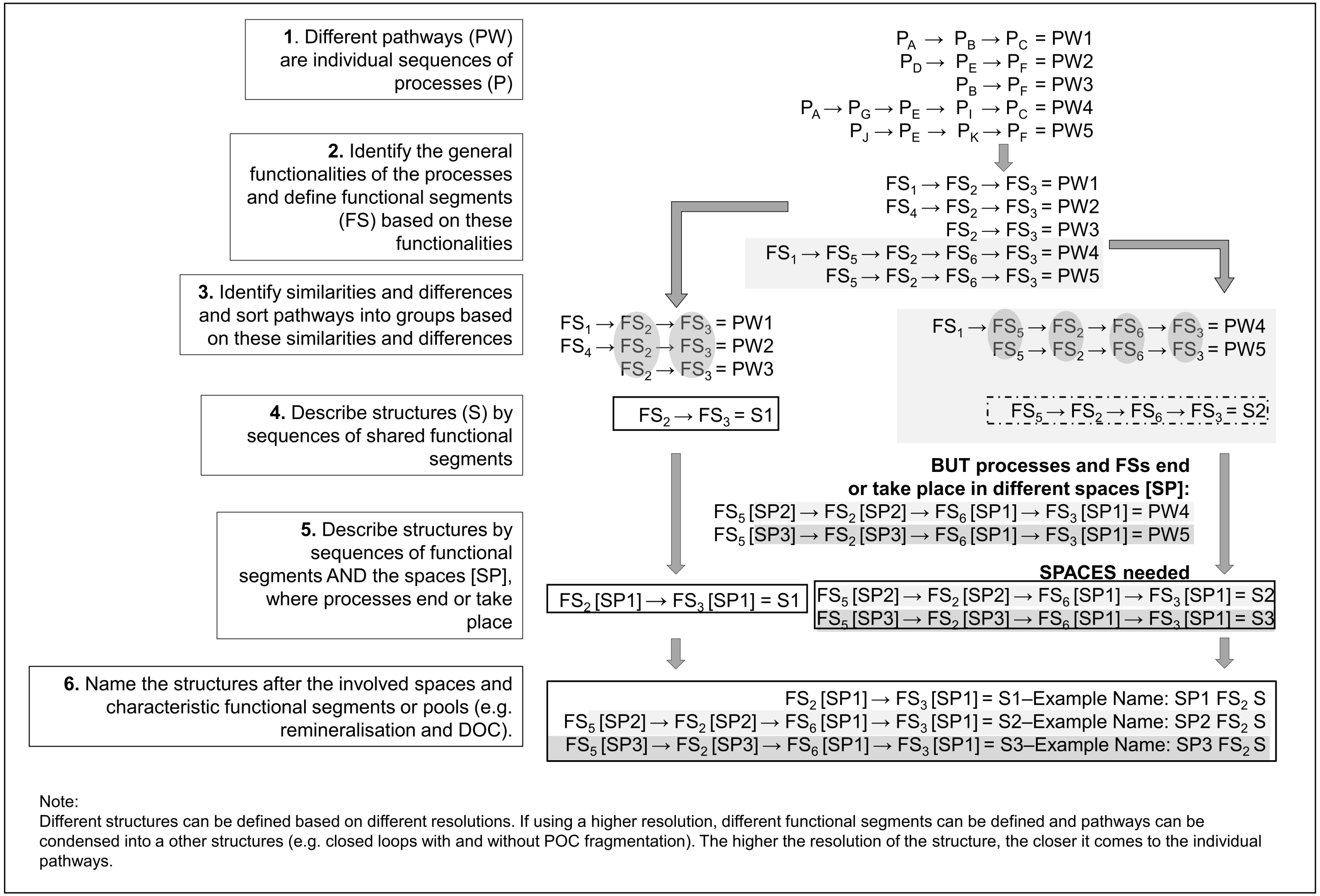


Figure 4.1.1: A section of the literature-based pathway concept. Due to the large size and the interactive nature of the literature-based pathway concept, we cannot display the full concept here. In the original version, short descriptions and references are linked to each functional segment and process.

Please find the original version and the used references with this short URL https://t1p.de/dcrsa, by scanning the QR code or as a supplement of the study I currently published as a preprint in Ocean Science (DOI: 10.5194/os-2021-75).



Note:
Different structures can be defined based on different resolutions. If using a higher resolution, different functional segments can be defined and pathways can be condensed into a other structures (e.g. closed loops with and without POC fragmentation). The higher the resolution of the structure, the closer it comes to the individual pathways.

Figure 4.1.2: Methodology of comparing pathways and defining higher-level structures.

4.2 Appendix II

Table 4.1: Carbon conversion factors from wet weight to carbon.

Pool	**C/WW**	**References**
Phytoplankton	0.16 ± 0.03	Yacobi and Zohary (2010) and references therein
Macrophytes	0.04 ± 0.01	Based on Duarte et al. (1986), Röhr et al. (2016) and Kautsky (1995)
Bacteria*	0.08 ± 0.03	Based on Virtanen (1985) and Hecky and Kling (1981)
Protozooplankton	0.07	Fenchel and Finlay (1983)
Zooplankton	0.09 ± 0.02	Based on Kiørboe (2013), Vinogradov and Shushkina (1987), Harris et al. (2000), Mauchline (1998) and Båmstedt (1986)
Benthos* **	0.12 ± 0.06	Based on Carman and Cederwall (2001)
Sprat	0.15 ± 0.04	Based on Grosslein et al. (1980), Horn and de La Vega (2016), Bar-On et al. (2018), Andersen et al. (2016), Jarre-Teichmann (1995) and Kautsky (1995)
Flounder	0.14 ± 0.04	see above
Herring	0.15 ± 0.04	see above
Plaice	0.14 ± 0.04	see above
Cod	0.16 ± 0.04	see above
Grey Seals	0.14 ± 0.04	Based on Horn and de La Vega (2016), Bar-On et al. (2018), Andersen et al. (2016) and Sandberg (2007)
Harbour Seals	0.15 ± 0.03	see above
Ringed Seals	0.14 ± 0.04	Based on Horn and de La Vega (2016), Bar-On et al. (2018) and Andersen et al. (2016)
Harbour Porpoise	0.18 ± 0.03	Based on Bar-On et al. (2018) and Andersen et al. (2016)
Mammals	0.15 ± 0.02	Based on Horn and de La Vega (2016), Bar-On et al. (2018), Andersen et al. (2016) and Sandberg (2007)
Sediment detritus*	0.09	Tomczak et al. (2012)
Water column detritus*	0.09	see above

* The carbon stocks of this study are estimated without these conversion factors, as data are already available in carbon units.

** Meio- und Macrobenthos are not distinguished.

Table 4.2: Carbon conversion factors for benthos. Conversion of g/m^2 to gC/m^2 for different basins and depths after Carman and Cederwall (2001).

Depth zone in m	**Biomass in g/m^2**	**Biomass in gC/m^2**	**Conversion factor in C/WW**	**Standard deviation in C/WW**
Bothnian Bay and the Quark				
0-30	3.25	0.38	0.12	
30-70	0.61	0.18	0.30	
70-100	2.69	0.77	0.29	
Bothnian Sea and Åland Sea				
0-30	96.90	5.74	0.06	
30-70	57.84	6.57	0.11	
70-100	16.95	3.31	0.20	
120-250	14.03	2.33	0.17	
Gulf of Finland				
0-30	93.69	5.97	0.06	
30-70	82.07	5.97	0.07	
70-100	4.00	0.80	0.20	
Baltic Proper				
0-30	117.2	5.50	0.05	
30-70	57.83	4.24	0.07	
70-100	1.87	0.18	0.10	
120-350	0.10	0.00	0.02	
Average all basins				
0-30			0.07	0.03
30-70			0.14	0.09
70-100			0.19	0.07
120-350			0.09	0.07

Table 4.3: Basin OC stocks of some fish species and harbour porpoises based on the ICES (2013, 2017, 2018b), Sveegaard (2011) and Benke et al. (2014).

Pool	**Basin OC stock** in gC/m^2	**Uncertainty** in gC/m^2	**Areas**
Plaice	0.033	0.004	ICES units 21-23 (area 42,248 km^2)
	0.0017	0.0004	ICES units 24-32 (area 358,584 km^2)
Herring	0.57	0.27	ICES units 20-24 (area 64,788 km^2)
	1.2	043	ICES units 28.1 (area 16,108 km^2)
	1.0	0.4	ICES units 25 and 29-32 (area 228,453 km^2)
Cod	0.75	0.12	ICES units 22-24 (area 43,434 km^2)
	0.46	0.08	ICES units 25-32 (area 336,044 km^2)
Harbour	0.003	0.001	Area with sightings Belt (7,820 km^2)
Porpoise	0.000002	0.000003	Area with sightings Baltic Proper (102,695 km^2)

Table 4.4: Seasonal carbon stocks of POC and DOC in the water column based on Donali et al. (1999), Schneider et al. (2003), Gustafsson et al. (2014), Maciejewska and Pempkowiak (2014), Hoikkala et al. (2015), Szymczycha et al. (2017), Nausch et al. (2006), Winogradow et al. (2019), and Andersson and Rudehäll (1993).

Pool	**Seasonal carbon stock** in gC/m^3	**Uncertainty** in gC/m^3	**Water volume** in km^3
DOC	Growing season		water volume of 21,177 km^3
water	4.37	0.06	
column	Non-growing season		water volume of 21,177 km^3
	3.57	0.05	
POC	Growing season		water volume of 21,177 km^3
water	0.286	0.028	
column	Non-growing season		water volume of 21,177 km^3
	0.109	0.009	

Table 4.5: Basin and depth depending benthos carbon stocks based on Carman and Cederwall (2001) and Gogina et al. (2016). Please note, that the high uncertainty of the biomass estimate of the Bothnian Sea is related to the strong variability of the underlying data. The reliability of this estimate is thus comparably low.

	Depth range in m	**Carbon stock** in gC/m^2	**Uncertainty** in gC/m^2	**Areas** in km^2
Bothnian Bay, Quark	0-30	0.8	0.5	19,049
	30-70	1.3	1.6	8,689
	70-120	1.1	0.4	5,262
	>120			
	total	1	1	33,000
	total in 10^4 t	3	4	
Bothnian Sea, Åland Archipelago Sea	0-30	20	30	24,022
	30-70	8.64	1.98	21,744
	70-120	6	5	21,721
	>120	4	5	5,479
	total	11	16	72,966
	total in 10^4 t	80	120	
Gulf of Finland	0-30	4.3	1.6	17,650
	30-70	3.80	1.98	13,777
	70-120	2.1	1.3	4,388
	>120			
	total	3.86	1.96	35,815
	total in 10^4 t	11	7	
Baltic Proper	0-30	6	4	69,374
	30-70	4.9	2.5	57,645
	70-120	1.3	1.5	72,264
	>120	0.12	0.22	21,575
	total	3.48	2.97	220,858
	total in 10^4 t	80	70	
South Western Baltic	0-30	11	5	28,586
	30-70	15.90	0.25	5,386
	70-120	12		404
	>120			
	total	12	5	34,376

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	Depth range in m	**Carbon stock** in gC/m^2	**Uncertainty** in gC/m^2	**Areas** in km^2
	total in 10^4 t	40	16	
Gulf or Riga	0-30	5.6		9,959
	30-70	7.6		6,357
	70-120			
	>120			
	total	6.4	1.1	16,316
	total in 10^4 t	10.0	1.6	
Baltic Sea	0-30	7	13	147,020
	30-70	6	4	113,598
	70-120	2.2	2.4	104,039
	>120	1	4	27,054

NOTE:

Further additional material, such as compiled data, documented R codes and methodical descriptions can be found in the PANGAEA repository under the DOI: 10.1594/PANGAEA.925062 or by scanning the included QR code.

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Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare upon oath that I have written the present dissertation independently and have not used further resources and aids than those stated.

Maike Scheffold

Hamburg, 03.03.2022