Rühl, S. (2020) " Temporal variability in benthic-pelagic exchanges: Seasonal cycles, inter-and multiannual variability, and long-term climate driven trends", University of Southampton, Faculty of Natural and Environmental Sciences, School of Ocean and Earth Science, PhD Thesis, pp 1 - 267.

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University of Southampton

Faculty of Natural and Environmental Sciences

School of Ocean and Earth Science

Temporal variability in benthic-pelagic exchanges: Seasonal cycles, inter-and multiannual variability, and long-term climate change driven trends

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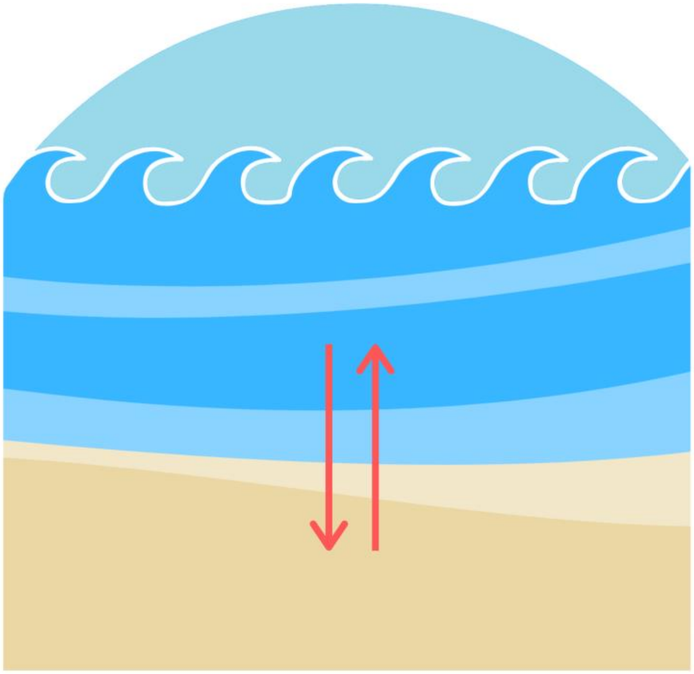

Thesis for the degree of Doctor of Philosophy

June, 2020

University of Southampton

Abstract

Faculty of Natural and Environmental Sciences
Ocean and Earth Science
Doctor of Philosophy

Temporal variability in benthic-pelagic exchanges: Seasonal cycles, inter-and multiannual variability, and long-term climate driven trends

By Saskia Rühl

Exchanges of solutes and solids between the sea floor (benthic) and water column (pelagic) are a vital component of ecosystem functioning in marine habitats around the globe. Various drivers affect these exchanges interdependently, and are in turn affected by them. While some individual driver-process relationships are well known, spatial or temporal ecological context to accurately assess the relative importance of the various drivers, is often missing. The work presented in this thesis explores benthic-pelagic exchange drivers and processes on three different temporal scales. First, short term intra-annual cycling is investigated in a temperate coastal environment. Results showed that there were distinct phases of upward and downward fluxes of significant magnitude throughout the year, in both dissolved and particulate matter fluxes. Timings and cause-effect relationships to direct and indirect drivers however differed between the two. As multi-year climatic influences and the stochastic occurrence of extreme events cause deviation from typical seasonal patterns in the natural environment, the second objective was to characterise medium term inter- and multiannual temporal variability. Decomposition of a decadal temperate time-series data set showed, that the main causes of inter-annual variability were extreme meteorological and biological outlier events, as well as global-scale climatic fluctuations. In order to investigate true long-term temporal variability such as climate change induced trends, the final investigations take place in the Arctic, where the effects of climate change can be observed at a fast pace. Results showed, that there is a clear divide between southern, Atlantic dominated, and northern, Arctic water dominated, environments under present conditions. In the South, there is a net downward flux of dissolved matter and a net upward flux of particulates, while the North exhibits the opposite trend. Based on the driver-process relationships identified in this chapter, it is likely that there will be a change to the dominant direction of seafloor-water exchanges in the northern Barents Sea under future conditions. Overall this thesis provides a novel and fundamental temporal ecological context for important ecosystem processes, evidences the utility of transdisciplinary data analyses and could be used to inform ecosystem models, management decisions, and future studies of similar processes in other environments in the future.

Table of Contents

Table of Tables

Table of Figures

Table of Figures

List of Accompanying Materials

1. Data sets

Rühl, S. (2020), L4 benthic pelagic seasonal data set, *University of Southampton repository*, doi.org/10.5258/SOTON/D1337

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2. Appendices

A) Chapter 2 appendices
  - 2a: Sources of supplemental data sets
  - 2b: Sampling campaign of data collection throughout the 2017/2018 seasonal cycle

- 2c: Flume programmes
- exchange drivers and processes
- 2d: Results of the OPLS models
- 2e: VIP scores of the OPLS models

B) Chapter 3 appendices
  - 3a: Selection of driving factors for each direct driver of DM and PM exchange, as well as the overall exchange processes
  - 3b: Seasonal time-series decomposition figures of individual variables (Supplemental figures 1-14)
  - 3c: Results of the OPLS models
  - 3d: VIP scores of the OPLS models

C) Chapter 4 appendices
  - 4a: Exact locations of replicate box cores
  - 4b: Locations and depths of the CTD bottom water samples and distances between replicate box cores
  - 4c: Dates and times of arrival and departure at each station in both cruises
  - 4d: OPLS models significant VIP scores

D) Published papers associated with sections of this thesis
  - Rühl, S., Thompson, C., Queirós, A., Widdicombe, S. (2020), Missing links in the study of solute and particle exchange between the sea floor and water column, *ICES Journal of Marine Science*, doi: 10.1093/icesjms/fsaa060

Research Thesis: Declaration of Authorship

Print name: Saskia Rühl

Title of thesis: Temporal variability in benthic-pelagic exchanges: Seasonal cycles, inter-and multiannual variability, and long-term climate driven trends

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:-

    - Rühl, S., Thompson, C., Queirós, A., Widdicombe, S. (2020), Missing links in the study of solute and particle exchange between the sea floor and water column, *ICES Journal of Marine Science*, doi: 10.1093/icesjms/fsaa060

Signature: Date:

Acknowledgements

I would like to formally thank the Natural Environmental Research Council for funding this research, and Plymouth Marine Laboratory for hosting and supporting me. I would also like to thank the University of Southampton, and specifically the SPITFIRE team, for offering me opportunity to carry out this degree and also gain further training in skills to which I would not have had access otherwise. Furthermore, I am much obliged to the Plymouth Marine Science and Education Foundation and the Estuarine and Coastal Sciences Association, for financially supporting my studies, with the PlyMSEF Grant in Aid and the Charles Boyden Award respectively.

To my supervisors, I am very grateful for the high degree of freedom and independence I was granted throughout the course of my PhD. The trust they placed in me, to have the self-discipline and time-management to work autonomously, has allowed me to grow as a researcher and improve my independent problem solving skills.

First, I would like to thank Prof Steve Widdicombe, my primary supervisor. Thank you for being an inspiring source of fresh ideas and suggestions, I really enjoyed our discussions and brainstorming sessions. Your repeated generous offers allowed me to be included in work on projects and participate in cruise work that I otherwise would have never even known about. The unique experiences and new skills I gained this way will always be with me. Thank you for having faith in me.

To Dr Charlie Thompson, thank you for always having an open ear and offering me practical advice. Despite that fact that you were supervising me remotely, you were always quick and happy to help when needed; in many ways it didn’t feel like there was any distance at all. Thank you for making the way down to Plymouth on several occasions to show me the ropes in practical work, or even just to meet up in person. And finally, thank you for always welcoming me at the NOC, and for opening your ears, your labs and your freezer to me.

Last but not least, Dr Ana Queirós, who has not only offered me practical help and constructive feedback on so much of my work but also built me up and raised my confidence on occasions when I doubted myself. Thank you for supporting me academically as well as emotionally, and offering me advice I sometimes didn’t even know I needed. I immensely appreciate the time and effort all three of you have put into helping me become the researcher I am today.

During my time at Plymouth Marine Laboratory, both staff and student communities have been truly welcoming, and while I cannot mention everyone personally, there are some individuals who have specifically helped me with my work in the field and the laboratory. Thank you to Andy, Gary, Andrew and Jim, who have worked tirelessly aboard the PML Quest to get me the samples I needed, including a number of back-breaking box cores so large, I better not mention it here… Thank you to Mark Wilson, Tony Staff and Andy Dunn for driving me and my gear around Plymouth, facilitating my sampling efforts, and helping me around the lab. I probably would have given myself a hernia by now if it wasn't for your help and continued insistence to carry things for me. Thank you to Amanda Beesley, Dr Rachel Coppock, Dr Liz Talbot, Franki Perry, and many more, who have freely donated their time to accompany me to L4 during my seasonal sampling campaign. A special thanks also goes to Joana Nuñes, who has helped me countless times in the field and in the lab, during cruise preparations and everyday work. Jo, I try to take your positive attitude and ever helpful actions as an example to live by. Dr Paul Somerfield, Dr Tim Smyth, Patrick Downes, and the various members of the MEB and MEMP groups whose expertise and feedback helped me develop the methods used in this thesis are thanked for their time, advice and help.

From my time involved in the Changing Arctic Ocean Seafloor (ChAOS) cruises, I would like to specifically thank Dr Liz Talbot, Chris Walkinshaw, Thomas Mesher, Prof Martin Solan, Ellie Ward, Christina Wood, Dr Adam Reed, Dr Laura Grange and Dr Jasmin Godbold, Joana Beja, Emmeline Broad, Natalie Ensor, Dr Emily Venables, and Robyn Owen. Thanks for helping me to collect, extract and carry to and from the CT lab, what I calculated to be a rough total of 1395 kg of mud and water! I am further indebted to the crew and engineering team of the RSS James Clark Ross and the National Marine Facilities scientific engineers who provided technical assistance and advice throughout both cruises. Thank you also to Dr Christian März for supporting the inclusion of my PhD work in the ChAOS project, and all the ChAOS scientists who have happily and openly discussed their work with me to help me understand their aspect of the Arctic ecosystem.

Throughout this PhD, I used not only data collected by myself, but also data from open sources, prior publications and some data that was only available to me through the work and generosity of the scientist around me. For the latter, I would like to especially thank Prof Martin Solan, Dr Ruth Airs, Dr Birthe Zänker, Dr Sian Henley, Dr Joanne Hopkins, Dr Claire Widdicombe, Caroline Louise McNeill and Tomas Mesher, Christine Pascoe, Dr Karen Tait, Dr Vassilis Kitidis, Dr Angus Atkinson, Dr Pierre Cazenave and Dr Yuri Artioli.

Privately, I would like to first and fore-most thank my partner, Tom, who has supported me not only throughout this PhD, but through life for almost ten years now. Thank you for keeping me grounded, reminding me to take enough time for myself away from work, and for supporting me when I most need it. I know I can count on you now and in the future to stand by me and broaden my horizon.

To my friends, the new and the old, thank you for great times playing games, exercising, doing crafts, gardening, eating and drinking, quizzing and discussing books and many other things. You have enriched my life, and I hope to stay in touch with as many of you as possible in the future.

Thank you to the Lenton’s, Marks’ and Towers’ for welcoming me to your family as one of your own and being ever supportive and interested in myself and my work. I entrust my continued education in British music, media and specialty baked goods to you.

Last but not least, I would like to thank my family for always being supportive of my plans and dreams. Auch wenn wir uns weniger oft sehen konnten als erhofft, habt ihr mich stets unterstützt! Dank euch Mama und Papa, ihr habt immer dafür gesorgt dass ich mich sofort wieder zuhause gefühlt habe wenn ich auf Heimatbesuch war, und euch dafür interessiert, was ich denn jetzt genau erforsche, auch wenn ich es auf Deutsch manchmal nicht so super erklären konnte. Ich bin so froh, dass wir in einer Zeit leben in der man sich auch auf Distanz nahe sein kann, vor Allem wo ihr jetzt sogar beiden mobil und online seid! Danke an meine lieben Geschwister, Carina und Nicolai, die immer für einen Videoanruf zu haben waren und an deren Leben ich somit auch teilhaben konnte. Es tut immer gut sich mit euch aus zu tauschen, hoffentlich können wir uns schon bald mal wieder im echten Leben wiedersehen.

Thank you one and all for your support, I would not have been able to carry out this PhD without you!

Definitions and Abbreviations

ADCP	Acoustic Doppler Current Profiler
ADV	Acoustic Doppler Velocimeter
AIS	Automatic Identification Systems
ANOSIM	Analysis Of SIMilarity
B/P	Benthic-Pelagic
B13	Station B13 of the Barents Sea Transect
B14	Station B14 of the Barents Sea Transect
B15	Station B15 of the Barents Sea Transect
B16	Station B16 of the Barents Sea Transect
B17	Station B17 of the Barents Sea Transect
BIPc	Community Bioirrigation Potentials
BPc	Community Bioturbation Potentials
C	Carbon
CDOM	Coloured Dissolved Organic Matter
CMF	Core Mini Flume
CT lab	Controlled Temperature Laboratory
CTD	Conductivity, Temperature, Depth
d_{50}	Mean Sediment Grain Size
DIN	Dissolved Inorganic Nitrogen
DM	Dissolved Matter
DOM	Dissolved Organic Matter
eDNA	environmental DNA
EPS	Extracellular Polymeric Substances
GFF	Glass Fibre Filters
h	water depth
ICES	International Council for the Exploration of the Sea
IPCC	Intergovernmental Panel on Climate Change

IQR	Interquartile Range
JR17007	2018 Barents Sea Cruise
JR18006	2019 Barents Sea Cruise
L4	Station L4 of the Western Channel Observatory
LOESS	Locally Estimated Scatterplot Smoothing
MBA	Marine Biological Association
N	Nitrogen
NAO	North Atlantic Oscillation
O_2	Oxygen
OBS	Optical Backscatter Sensors
OC	Organic Carbon
OM	Organic Matter
OM	Organic Matter
OPLS	Orthogonal Partial Least Squares Discriminant Analyses
OSPAR	Oslo-Paris (Convention for the Protection of the Marine Environment of the North-East Atlantic)
P	Phosphorous
PAR	Photosynthetically Active Radiation
PM	Particulate Matter
PML	Plymouth Marine Laboratory
POC	Particulate Organic Carbon
POM	Particulate Organic Matter
PON	Particulate Organic Nitrogen
SPM	Suspended Particulate Matter
STL	Seasonal Decomposition of Time Series
TEP	Transparent Exopolymer Particle
TOC	Total Organic Carbon
TPC	Total Particulate Carbon
T_{peak}	Wave period
TPN	Total Particulate Nitrogen
T_z	Wave duration

$\bar{U}$	Depth-averaged current speed
u_{*crit}	Critical Erosion Velocity
U_z	Velocity at height z
VIP	Variable Influence on Projection
WCO	Western Channel Observatory
z	Height above seabed
ρ	Fluid density
τ_{0crit}	Critical Shear Stress

Chapter 1

Introduction

Note: The literature review in this section was published in the ICES Journal of Marine Science (Rühl, S., Thompson, C., Queirós, A., Widdicombe, S. (2020), Missing links in the study of solute and particle exchange between the sea floor and water column, *ICES Journal of Marine Science*, see Appendix D). Author contributions: SR wrote the manuscript; CT, AQ and SW helped in conceptualising and dissecting the processes this review focuses on, as well as providing feedback and improvements to the manuscript throughout the writing process and while it was under review for publication. I would like to acknowledge Dr Joanna Norkko in her role as editor for the ICES Journal of Marine Science, as well as the two reviewers for providing us with insightful and helpful comments which have improved the structure and readability of this review.

1.1 Literature Review

More than 70% of the Earth's surface is covered by water. If the water were to be removed, marine sediments would cover more global surface area than all other ecosystems combined (Snelgrove *et al.*, 1999). This marine benthos (sea floor) can have extremely varied geological, physical and chemical characteristics and is now known to support a diverse range of life forms. It also acts as an important source and sink of energy and matter which are exchanged with the overlying water (Morris and Howarth, 1998). Thanks to new technologies, tackling formerly inaccessible areas of the ocean, it is now known that the benthos is an important asset of marine ecosystems globally, which is tightly coupled with other marine environments (*e.g.* Marcus and Boero, 1998; Navarrete *et al.*, 2005). In this review, this connection of benthic and pelagic (water column) environments will be explored by assessing exchange processes between the two.

A wide diversity of physically and biologically mediated benthic-pelagic solute and particle exchanges (hereafter "B/P exchanges") exists. The potential for, and nature and magnitude of, B/P exchanges depends strongly upon the physical characteristics of the sediment, such as its grain size, cohesion, permeability and porosity (Kalnejais *et al.*, 2010). A sediment bed may be described as cohesive when it contains at least 10 - 30 % clay and / or silt content, particles which are less than 63 µm in grain size; and non-cohesive otherwise (Winterwerp, 2011). While non-cohesive sediment erodes following simple linear physical laws, the dynamics of cohesive environments are more complex. Permeable sediment can be defined as having a permeability of greater than 10^{-12} m^2 (see Huettel *et al*., 2014, after hydraulic diffusivity methods described in Klute and Dirksen, 1986). While cohesion mostly affects particle exchange processes, more permeable environments have larger solute exchange potentials. Sediment properties may in turn be modified through physical and biologically mediated sediment mixing and ventilation, thereby passively and actively altering exchange rates (Volkenborn *et al.*, 2010). In many cases the effects of biological processes are particularly influential in the absence of large-scale physical disturbances (*e.g.* Widdows *et al.*, 1998; Andersen and Pejrup, 2002; Paarlberg *et al.*, 2005). For instance, the degree of cohesion and fluidisations of sediments may fundamentally reflect the activity of its biological community (Widdicombe and Austen, 1999). In turn, biological communities are often shaped by their physical and chemical environment as many organisms occupy specific niches (Snelgrove, 1999), which will be explained in more detail in later sections of this review.

In addition to biogenic and physical influences on B/P exchanges, anthropogenic (human) interventions can also play an important role. The effects of anthropogenic interaction with the marine environment are often synchronous and can act additively, making it difficult to put preventative and counter-active measures in place (Caddy, 2000). Impacts are not only concentrated in coastal shelf areas where anthropogenic activity is prevalent, but can be spread further (Martín *et al.*, 2008). For example, the form and extent of effects of bottom trawling on benthic communities is also dependent on the respective sediment types they occur in, which also in themselves affected by this activity (Hiddink *et al.*, 2006;

Queirós *et al.*, 2006; Hale *et al.*, 2017).The relative impact of anthropogenic interferences compared to naturally occurring processes on B/P exchanges can thus be hard to quantify, as the two can have similar consequences (Pusceddu *et al.*, 2005) but cause different effects on different types of organisms (*e.g*. on meiofauna: Schratzberger *et al.*, 2009; and macrofauna: Fang *et al.*, 2019).

In the course of this review, the complexity of particle and solute B/P exchange processes, as well as particular driver interactions will be explored. Solute and particle exchanges will be reviewed individually, with solute exchange subsections designed to highlight the main drivers of exchange, and particulate exchange subsections structured to highlight downward and upward directed exchange processes. Interdependencies between solute and particle specific processes will be explored using the example of organic matter cycling, which is a biologically vital process that crucially depends on both types of exchange. Knowledge gaps in the current research will be highlighted throughout each section and finally reviewed in combination with recommendations for future research.

1.1.1 Solutes

Solutes in the marine environment can broadly be defined as substances dissolved in sea water. Throughout the water column, solutes may be transported through eddy and molecular diffusion (Boudreau 2001), as well as convection (Webster *et al.*, 1996). When biologically important elements such as oxygen (O_2), carbon (C) and nitrogen (N) are in solution, they are readily available for processes such as respiration, photosynthesis, calcification, diagenesis, and direct nutrient uptake, which is why their transport across the pelagic and the benthic environments, and exchange between the two, are essential.

O_2 is perhaps the most biologically important solute moving across the sediment-water interface. The depth to which O_2 penetrates the sediment controls the depth-distribution of O_2-dependent biogeochemical oxidation reactions, such as nitrification and sulphide oxidation (Rysgaard *et al.*, 1994), as well as the oxidisation of organic matter (OM; Cai and Sayles, 1996). On the whole, the availability of dissolved Oxygen in sediment drives aerobic OM degradation rates, a reduction of the concentration of dissolved organic C, and can decrease molecular dissolved OM diversity (Seidel *et al.*, 2015). O_2-driven diagenesis (mineralisation, dissolution and geo-polymerisation during burial; Lindqvist, 2014) is intensified in the presence of marine organisms, which produce enzymes that catalyse those reactions (Lindqvist, 2014). In the absence of biological interactions, the penetration depth of O_2 in the sediment has been shown to depend on the O_2 concentration in the overlying water (Revsbech and Jorgensen, 1980; Rasmussen and Jorgensen, 1992). Anthropogenic disturbance, such as trawling, can cause a reduction in dissolved O_2 in bottom-near water and surface-near sediments, through promotion of more deep-reaching sediment oxygenation (Tiano *et al.*, 2019). The displacement of the oxygenated sedimentary surface layer through trawling equipment lessens biogenic O_2 consumption and causes deeper O_2 penetration depths in the affected areas, thereby effectively changing the sedimentary biogeochemical environment (Tiano *et al.*, 2019).

Nutrients are another ecologically important solute group in the marine system, as their availability and cycling throughout the environment can be limiting to many organisms (*e.g.* Howarth, 1988). Intermittence in nutrient concentrations in the water column, and thus at the sediment water interface, is driven, among other processes, by seasonal changes in temperature (Pomeroy and Deibel, 1986), fluvial and terrestrial input (Justic *et al.*, 1995; Burnett *et al.*, 2003; Milliman and

Farnsworth, 2013), water column mixing, and sea bed resuspension. The latter can be initiated by stochastic storm events (Corte *et al.*, 2017). Temporal patterns of denitrification and nutrient flux dynamics also depend upon the sediment type, as sandy sediments exhibit seasonal changes primarily driven by temperature and irradiation, while silty sediments are additionally influenced by aforementioned stochastic resuspension events (Seidel *et al.*, 2015) and meteorologically induced upwelling events (MacIntyre, 1998). The resulting supply of nutrients from the benthos to the pelagic environment is a crucial factor controlling phytoplankton blooms at times of the year when the water column is not stratified in non-eutrophic systems, as the mixing of water from depth and surface layers can place nutrients from benthic sources within reach of the pelagic organisms (Barnes *et al.*, 2015). This, in turn, fuels zooplankton productivity and can give rise to knock-on effects throughout the entire marine food web (Eloire *et al.*, 2010). Increased pelagic productivity, on the other hand, leads to increased nutrient influx rates to the benthos from sinking OM, which is why the benthic community and its activity typically flourish in response to large seasonal plankton blooms (*e.g.* Queirós *et al.*, 2015; Tait *et al.*, 2015). Other nutrient sources to benthic sediment-water interactions include atmospheric input (Krishnamurthy *et al.*, 2010), anthropogenic terrestrial sources (Justic *et al.*, 1995; Burnett *et al.*, 2003), dredge-spoil dumps (*e.g.* Harvey, Gauthier and Munro, 1998), as well as the addition of dead cells and faecal pellets from pelagic organisms, sinking onto the sea floor (van Duyl *et al.*, 1992). The relative impact of each of these depends on factors such as proximity to the coast and the extent of local pelagic primary productivity, and lateral transport fuelled by circulation patterns can alter their relative importance (*e.g.* Walsh, 1991; Williams and Follows, 1998). Most of the organically available nutrients near the seafloor are extracted and processed diagenetically by the benthic microbial community, or directly consumed by deposit and suspension feeding fauna, degrading and mineralising their contents. The latter can generally be described as the return of N and Phosphorous (P) to inorganic forms after having been incorporated in organic molecules, or (re-)mineralisation (Williams and del Giorgio, 2005). Within the sediment, diagenesis is fuelled by the enrichment of the sediment matrix with O_2 (Emerson and Hedges, 2003).

The B/P exchange of not only O_2 and nutrients but of all solutes is governed by a number of direct and indirect drivers (Figure 1), and the current understanding of each in the literature will be detailed throughout this section.

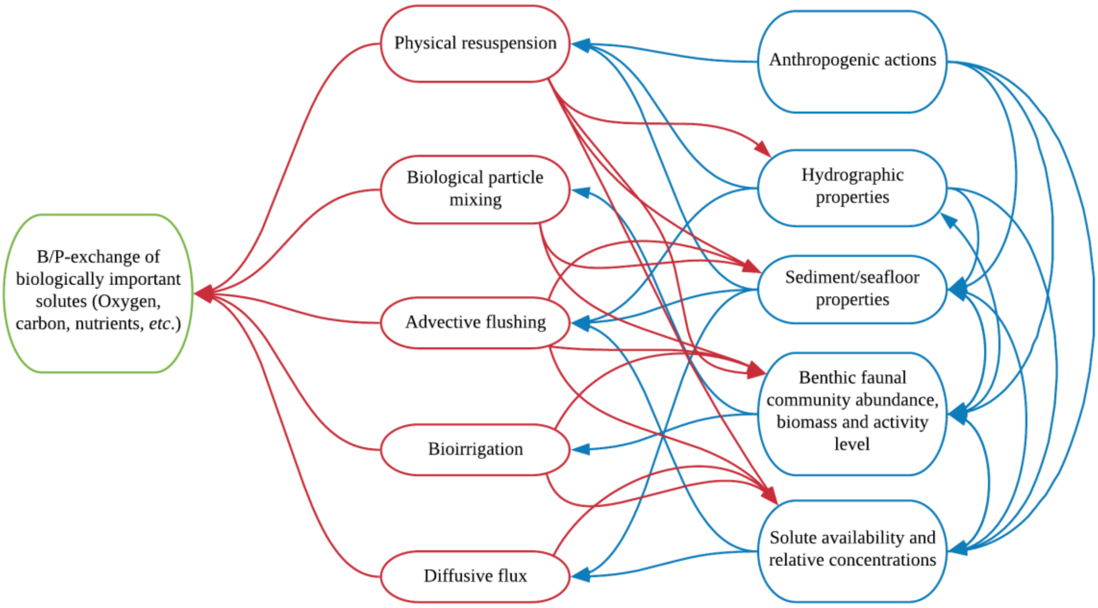

Figure 1: Flowchart of direct (red) and indirect (blue) drivers of solute B/P exchange (green); arrows indicate which factors affect others and are colour-coordinated with the driver group they originate from.

It is difficult to definitively determine the relative importance of the different driver groups and important factors within each on B/P, as they can be highly variable across spatial and temporal scales. Seasonal variation, for example, can cause shifts in the relative importance of biological and physical influences (Howarth *et* *al.*, 1993; Schlüter *et al.*, 2000); biogenically induced spatial variation in sediment properties can cause differences in the main drivers of solute B/P exchange on both small (Wethey and Woodin, 2005) and large (Fang *et al.*, 2019) spatial scales. This variability constitutes a knowledge gap which has to be filled on a situational basis, specific to the system, location and time period of each study within which such processes are investigated. For the purposes of this review, the main drivers of solute B/P exchange are therefore elaborated upon in no particular order.

1.1.1.1 Diffusive flux

Water close to the sediment surface within the benthic boundary layer (a layer of water immediately above the sediment which possesses different physical characteristics to the rest of the water column) is directly affected by friction at the seabed, which promotes solute transport *via* diffusion. Cohesive sediments, with high clay content, tend to be more difficult to percolate due to a generally smaller degree of permeability, thus impeding the flux of solutes (Yang and Aplin, 2010; though this is not necessarily true for cohesive environments with low clay content, see *e.g.* Winterwerp and Kesteren, 2004). In such conditions, molecular diffusion of pore-water solutes across the sediment-water interface prevails, leading to more gradual solute fluxes (Berner, 1980; Forster *et al.*, 1999) in the form of ion transfer between pore water and near-bottom water or as a result of the reactivity of solid surfaces (Kalnejais, Martin and Bothner, 2010). Other physical environmental variables, such as pressure differentials driven by tides, have been shown to lead to short-term temporal variability of diffusive fluxes (van der Kamp and Gale, 1983). The potential depth of diffusive processes is, theoretically, only limited by time. In some cases, however, diffusive distances can be altered, driven, and extended through an increase in sediment permeability, promoted by benthic biological activity. Sedimentary O_2 uptake, for instance, is only a function of physical penetration depth, which is determined by time in the absence of biological activity and organic matter (Revsbech and Jorgensen, 1980). What is hitherto unknown is whether there are ways in which biological or anthropogenic interactions may be directly inhibitive of solute diffusion across the sediment-water interface. As diffusion does not necessarily occur in isolation from other drivers of solute exchange, a differentiation between relative contributions of each driver would be of interest to correctly quantify each pathway. However, while the balance between, for example diffusive and advective solute B/P exchange, may be calculated in theory (Anderson and Cherry, 1979; Taigbenu and Liggett, 1986), in-situ measurements that take both into account and clearly differentiate between their respective contributions have so far not been successful.

1.1.1.2 Advection and physical resuspension

Abiotically driven fluctuations into (and out of) the sediment matrix can also occur through mechanically-driven water transfer into and out of the sediment pores. With increasing shear stress and turbulence, benthic boundary layer thickness typically decreases (though there are some exceptions) and with it the resistance of solute transfers into and out of the sediment (Lohse *et al.*, 1996). This decline continues into the top sediment layers (Ahmerkamp *et al.*, 2017). In turbulent conditions, under strong enough shear stress or in the presence of sediment surface obstacles, solute transport is prevalent through advection and physical resuspension. Obstacles can include protruding solid objects (rocks, shells, *etc*.), man-made structures, biogenic sediment structures (*e.g.* polychaete tubes) or simply a three-dimensional bedform, all of which lead to pressure differentials that drive water through the sediment and significantly enhance the exchange of solutes (Huettel and Gust, 1992; Ziebis *et al*., 1996; Hutchinson and Webster, 1998). The flushing action from advective processes can winnow smaller particles from the sediment matrix, leading to an overall coarser environment which can be percolated more easily (Malarkey *et al.*, 2015) and the less cohesive and more permeable the seabed is, the more likely is the occurrence of active ejections of solutes into the water column through physically driven advective currents (Lohse *et al.*, 1996; Cook *et al.*, 2007). Resuspension events, driven by either biological activity or abiotic interactions, can enhance solute exchange processes through an increase of the sediment surface area availability for dissolution through placement of particulates in the water column, re-oxygenation of formerly diagenised elements, and the direct flushing out of interstitial water (Morse, 1994; Morin and Morse, 1999; Saulnier and Mucci, 2000; Kalnejais *et al*., 2010). Turbulent hydrodynamic forces close to the sea bed thus catalyse the oxygenation of the surface sediment layers through partial resuspension as well as flushing action (Malan and McLachlan, 1991; Couceiro *et al.*, 2013). B/P solute exchange through physical processes, such as advection and resuspension, further contributes to the breaking down of OM and subsequent supply of biologically important solutes (Franke *et al.*, 2006). In intertidal sandy areas, for example, which typically contain low concentrations of particulate OM due to seasonal hydrodynamic removal (POM; Rusch, Huettel and Forster, 2000), pore-water nutrients may be supplemented through advective flushing (Seidel *et al.*, 2015).

Clearly, although there already is a large body of literature covering physically-driven solute exchange processes, there are still areas requiring further exploration. Temporal variability of advective transport, for instance, is poorly understood and has therefore so far not been taken into account in most studies (Cook *et al.*, 2007). As the hydrographic drivers of advection and resuspension may be consistent (*e.g.* currents), and/or regularly occurring (*e.g.* tidal flow), and/or stochastic in nature (*e.g.* storm events), even in-situ measurements only capture a snapshot of events, and the potential overlap between time-scales impedes our ability to differentiate between them. Long-term monitoring of physically-driven B/P solute exchanges may offer a solution to this, though so far this has not been undertaken. The extent to which boundary layer flow dynamics impact physically driven solute B/P exchange has also yet to be definitively quantified, especially in an in-situ context, including physical and biological interactions. It is unclear, to what extent this endeavour is even possible.

1.1.1.3 Bioirrigation and biological particle mixing

Biological mediation of solute exchange across the sediment-water interface is constant and inherent to sedimentary life, but in environments in which physically mediated transport is minimal, processes such as faunal flushing of pore waters can determine the rate and characteristics of B/P exchange of solutes (Mermillod-Blondin and Rosenberg, 2006; Volkenborn *et al.*, 2010). In addition, the sediment depth to which solutes are transported biologically can be multiple times that which may be reached through purely physical means (Volkenborn *et al.*, 2010). The biological exchange of solutes can take the form of bioirrigation, the active displacement of liquid and solutes by benthic organisms (Volkenborn *et al.*, 2007) linked to respiration, metabolite excretion, and other individual-based processes; or bioadvection, the induction of additional pore water through burrowing organisms' physical activity into the surrounding sediment (Volkenborn *et al.*, 2012). Biologically mediated exchange rates strongly depend on the characteristics of the associated faunal and microbial community (see *e.g.* Waldbusser *et al.*, 2004). Both bioirrigation and bioadvection are at least equally as important as, and often largely exceed, the rates of molecular diffusion in the upper sediment layers of biogenic environments (Berg *et al.*, 2001). The large spatial extent to which the hydraulic forces generated by bioadvectors and bioirrigators propagate through the sediment can lead to effects which far exceed the immediate vicinity of their burrows (Wethey and Woodin, 2005). This can in some instances have significant effects at the landscape scale (Fang *et al.*, 2019), though more often it leads to small-scale spatial variation with hot-spots of altered oxygenation nutrient and Carbon concentrations in the immediate vicinity of the bioirrigative activity. The release of O_2 from root systems in submerged macrophytes can even create three-dimensional spatial variability of variable diffusion potential and solute distribution (Sand-Jensen *et al*., 1982).

Pore-water O_2 content in particular is typically increased through bioadvection (Volkenborn *et al.*, 2010; Volkenborn *et al.*, 2012) as many burrowing animals actively oxygenate the surrounding sediment by ventilating their burrows with bottom water (Volkenborn *et al.*, 2007). Due to this, the thickness and volume of the sedimentary oxidising phase is largely extended, thus ameliorating conditions and promoting the occurrence of other aerobic life forms (Mermillod-Blondin and Rosenberg, 2006; Glud, 2008). This can in some cases lead to seasonal variations in O_2 availability linked to organisms' own seasonal life-cycle processes (Glud *et al.*, 2003). Significant variation is also observed between sediment types (Hicks *et al.*, 2017) . Through the particle movement and disruption of sediment layering, biogenic particle mixing (bioturbation) strengthens B/P coupling as it increases fluxes of nutrients, metals, C, O_2 and other micro-particles which would otherwise remain buried (Caliman *et al.*, 2007; Hale *et al.*, 2017). At the local scale, the presence of infaunal bioturbators has been shown to increase natural denitrification rates by at least 160% (Gilbert *et al*., 1998). Generally, N-mineralisation rates are faster in more permeable substrates and may be enhanced by macrofauna influence, irrespective of organic enrichments, due to the O_2 enrichment (Hansen and Kristensen, 1998; Huettel *et al.*, 2014). The associated modified supply of nutrients can also strongly affect microbial community structure (Yingst and Rhoads, 1980). This can be traced back to a combination of factors, one of which is the input of macrofaunal metabolic waste products which provides additional sources of nutrients to microbial communities (*e.g.* Reichardt, 1988) thereby adding to the overall flux and cycling of solutes, and their bio-catalysing effects on the microbial community (*e.g.* Yazdani Foshtomi *et al.*, 2015). The polysaccharide protein lining the burrows of many invertebrates has a filtering effect on the water flushing across and through it, affects exchange processes by preferentially selecting against anionic solutes due to their own net negative charge (Aller, 1983; Lalonde *et al*., 2010; Konhauser *et al.*, 2019). Burrowing macrofauna can in some cases actively culture the microbial community associated with their burrows which then in turn affects the rates and direction of solute exchange within the burrows (Kristensen, 1988; Kristensen & Kostka 2005). Fishing pressure can passively affect C and nutrient fluxes mediated by benthic macrofauna by altering the community composition, though these effects are mediated by sediment type and the kind of fishing gear deployed (Hale *et al.*, 2017). Changes in benthic community can also be induced through the installation of offshore wind farms (Coates *et al.*, 2014) and other solid substrates or through dredging (*e.g.* Thrush *et al.*, 1995). Sources of pollution can also affect benthic community diversity (*e.g*. Kingston, 1992) and thereby also passively lower biogenic B/P solute exchange rates.

Due to many organisms' temporally variable behaviours, rates of biologically mediated solute transport can vary on scales of minutes to seasons (*e.g.* Schlüter *et al.*, 2000). Despite this seasonality being a well-studied phenomenon, there is an important consideration that has thus far not been investigated: The assumption and assessment that in some areas physical pressures are strong enough to drown out the effects of biological processes (as assumed in *e.g*. Andersen *et al.*, 2002; Paarlberg *et al.*, 2005) may not be true at all times as the balance may swing the other way during biologically active seasons. This is a crucial knowledge gap which warrants further research. Spatial variability too should be considered more often when assessing the relative importance of physical *versus* biological drivers of B/P exchange, as small scale patchiness and large scale B/P exchange budgets may differ.

1.1.2 Particles

In contrast to solutes, particles are not transported uniformly as they occur in a variety of materials, sizes, shapes and concentrations. Particle exchange between benthic and pelagic environments may be driven by water flow, occurring regularly (such as through currents or tides); stochastically (such as through storm events and faunal activity); or *via* direct disturbance of the sea bed through biological activity or anthropogenic interference. Biologically and physically mediated particle transport processes often occur simultaneously and non-independently from one another, on separate or concurrent spatial and temporal scales. Within the sediment bed, particle reworking occurs mainly through sources of biotic and abiotic mixing rather than resuspension and deposition (though these processes too, are context-dependent). The main drivers of exchange between the seabed and the water column can be grouped into upward transport from the benthos to the pelagic environment, in the form of resuspension; and downward transport from the pelagic environment to the benthos through deposition (Figure 2). These two routes include various biological, physical and anthropogenic pathways, which will be elucidated in this section.

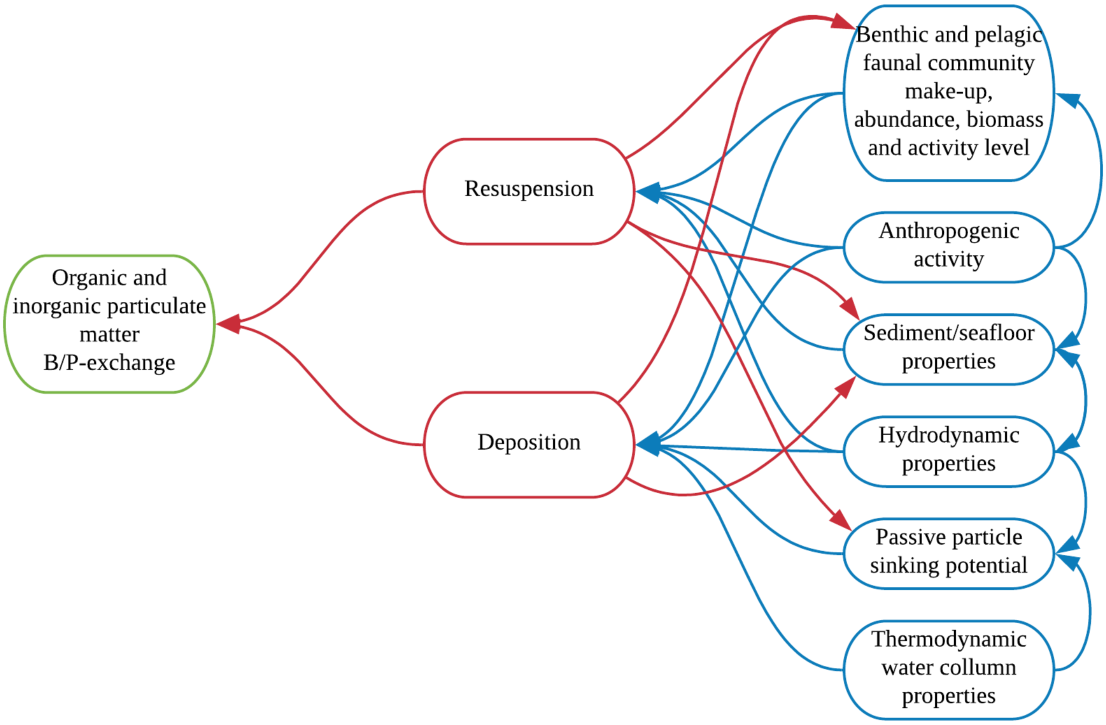

Figure 2: Flowchart of direct (red) and indirect (blue) drivers of particle B/P exchange; arrows indicate which factors affect others and are colour-coordinated with the driver group they originate from

As previously mentioned, the relative importance of individual drivers of B/P exchange is context dependent. The occurrence of large phytoplankton blooms (*e.g.* Zhang *et al.*, 2015) or dredge-spoil dumps (*e.g.* Moon *et al.*, 1994), for example, leads to an abundance of suspended material, the sinking of which is likely to locally dominate particle exchange processes. During extreme storm events and in periods during which frequent intermediate storm events occur, upward particle fluxes are likely to be dominant (*e.g* Madsen *et al.*, 1993). Outside of such extreme events, the relative importance of physical and biological drivers of B/P exchange is dependent on location (*e.g*. Dellapenna *et al.*, 1998). This situation and location dependence of the relative importance of B/P particle exchange drivers constitutes yet another gap in our knowledge of these processes. Past studies may be used to estimate each driver’s importance to warrant its inclusion in future studies, though this assessment has to be made in each instance, taking into account the scale, location and timing of the sampling effort, as well as the occurrence of extreme events close to the time of sampling (Hewitt *et al.*, 2007). Because of this complexity, and for the sake of simplicity, these drivers of particle exchange are reviewed subsequently, moving focus from the water column and towards the sediment, without necessarily reflecting their relative importance.

1.1.2.1 Downward flux and deposition

Throughout the water column, particles stay in suspension when the ascending vertical components of turbulent eddy velocity fluctuation are greater than the corresponding particle settling velocity (Komar, 1976b, 1976a). Physical and chemical barriers in the water column, for instance in the form of haloclines and thermoclines, can change and inhibit the rates at which matter is exchanged between the water column and the benthos (*e.g.* Biggs and Wetzel, 1968; Qiao *et al., 2011)*. While dissolved matter can still readily diffuse across the thermocline (*e.g.* Emerson *et al*., 1997), particulate matter up to a critical negative buoyancy threshold is unlikely to cross a thermodynamic barrier. In the majority of cases, the deposition of particles occurs in combination with other processes; turbulence and upward-mixing can make the settling process considerably unpredictable (Winterwerp and Kesteren, 2004). Mass settling flux may thus be defined as a product of matter concentration and settling velocity (Manning and Bass, 2006). The latter is mainly affected by the size and density in which flocs occur (Maa and Kwon, 2007) while PM concentration in the water depends not only on export but also on the rates at which particles are supplied through resuspension or release within the water column or from other sources (*e.g.* fluvial and terrestrial). In cohesive sediment settling conditions, high concentrations of suspended particles may flocculate while in suspension (Einstein and Krone, 1962; Stolzenbach and Elimelech, 1994). Flocculation is a constant yet dynamic balance of aggregation and disaggregation (Tsai *et al*., 1987) driven by physical or chemical attraction (Sun *et al.*, 2017). The typical primary source of cohesion and hence flocculation is the effect of salinity on charged clay particles through mass-attractive London-van der Waals forces and electrostatic bonding, though this may not be the most important factor driving flocculation in a biological context (Parsons *et al.*, 2016). Flocculated particles are relatively large in size and tend to settle more readily than primary particles, depending on their size and density, but may be broken up again easily by applied shear stress (Winterwerp, 2011). Regardless of particle size or nature, materials can be moved around the water column through turbulent water flow and trapped in biological (*e.g.* Gambi *et al*., 1990) or man-made (*e.g.* Simons and Şentürk, 1992) near-bottom structures such as mooring anchors. Lateral transport throughout water bodies can be hard to track and only some studies attempt to trace the origins of suspended matter collected in sediment traps (*e.g.* Narita *et al*. , 1990). There is much to discover yet about the sources of suspended particulates and the pathways they take through the water column.

Biological drivers of particle deposition can act both actively and passively. Some zooplankton groups, such as copepods, migrate vertically through the water column on a diurnal basis. The transport of organic matter through diel vertical migration constitutes an active downward transport, as organisms come towards the upper water layers to feed at night and return to deeper water where the organic matter is returned to the system in the form of excretions, or as decaying carcasses (Packard and Gómez, 2013). The presence of organic matter and associated microbes suspended in the water column (generally termed 'marine snow') can enhance benthic community metabolism rates and nutrient mineralisation (van Duyl *et al.*, 1992). Marine snow aggregates can include any combination of dead and living matter of highly variable spatial complexity, density and consequently, sinking rate (Alldredge and Gotschalk, 1988). It serves as a microhabitat and food source to pelagic organisms during its sinking (Lundgaard *et al.*, 2017) and is a source of organic matter to benthic organisms (*e.g.* Townsend *et al.*, 1992). In low turbulence, fluff-like organic matter which is not immediately incorporated into the sediment matrix may form a layer which rests on the sediment surface along with fine sediment particles (termed nepheloid layer; *e.g.* Durrieu De Madron *et al.*, 2017). Within this layer, particulates may be transported laterally across large distances and even exported off the continental shelf (Inthorn *et al.*, 2006). Particle residence times within the nepheloid layer can be vast, and warrant further study.

Deposition of particulate matter on the seafloor is catalysed by roughness elements which result in interfacial flow dynamics, and cause descending vertical sweeps (Huettel *et al*., 1996). Biogenic structures, such as bivalve byssal structures and seagrass blades, can trap suspended particles, reduce near-bed water velocity and increase turbulence in the benthic boundary layer (*e.g.* Widdows *et al*., 1998). In addition, filter feeders can actively move water, and the particles suspended in it, towards the sea floor, causing increased particle fluxes towards the benthos, preventing subsequent resuspension through ingestion, trapping in structures (such as tubes and gills), and pelletisation of the descended matter (*e.g.* Widdows *et al.,* 1998; Denis *et al*., 2007). Selective sediment particle processing, through the actions of biodiffusing bivalves for example, can lead to long-lasting changes in granulometry over large spatial scales, thereby changing the environment and creating specific habitats for other organisms (Montserrat *et al.*, 2009). Around mussel beds, biodeposition is further catalysed and accelerated through the production of pseudo-faeces, which leads to an increase in annual deposition of sediment, C and nutrients (Kautsky and Evans, 1987). Macroalgae and seagrasses have been shown to shield the sea bed from turbulence and lower water velocities, thereby increasing net deposition rates (Fonseca *et al.*, 1982; Gambi *et al.*, 1990). The rate at which this filtering of suspended material flowing through the fronds occurs depends strongly upon the morphology of the macrophytes (Hendrick *et al*., 2016). Obstacle-induced flow turbulence can effectively filter suspended particulate matter from the water column by driving parts of the flow through the sediment matrix, thus leading to their deposition within the sediment (Hutchinson and Webster, 1998). B/P exchange may further be affected by animals that increase sediment cohesion by building protruding tubes and byssal mats. These act similarly to sea grass and algal fronds by altering the flow and trapping sediments when they occur in high densities. *Lanice conchilega* presence for example, can lead to a reduction in erosion potential when occurring in high enough densities (Denis *et al*., 2007; Borsje *et al.*, 2014). The addition of small particles to the sediment matrix through active or passive filtering may lead to a change in sediment granulometry and, effectively, cohesion (*e.g.* Widdows *et al.*, 2000; Volkenborn *et al.*, 2007b). During the deposition of already cohesive sediments, though particles of all sizes may be deposited (Lau and Krishnappan, 1994), a sorting process can occur thus leading to vertical and horizontal particle size gradients due to the differences in sinking velocities between differently sized grains (Mehta, 1988).

The availability of depositable particulate material in the water column may also be affected by anthropogenic structures and actions, including dredge-spoil dumping (Moon *et al.*, 1994; Pilskaln *et al.*, 1998; Mikkelsen and Pejrup, 2000) and the installation of off-shore wind farms (Baeye *et al.*, 2011; Coates *et al.*, 2014;

Dannheim *et al.*, 2019). Although the former constitutes a rapid and intense input of non-native particulate matter to the water column, this does not always affect the benthic community or local sediment properties directly (Smith and Rule, 2001). It can however introduce additional organic Carbon and new species to the dredged site (Morton, 1977; Wildish and Thomas, 1985) which is likely to have knock-on effects on the biogeochemical composition of the affected environments and B/P exchange potentials. Although some monitoring studies have investigated short to medium term effects of dredge-spoil dumping on drivers of B/P exchange, few of these studies include an adequate assessment of the benthic environment prior to the commencement of the dumping and the number of long-term monitoring studies to date is insufficient to draw meaningful conclusions. Other activities, such as active bottom fishing practices (dredging, trawling), can also cause increases in suspended particulate matter (SPM). For instance, trawling can increase SPM concentrations up to six times that of the background levels (Tiano *et al.*, 2019). In the case of offshore wind farms, SPM plumes up to five times the background level in concentration have been shown to be generated through tidal resuspension of fine grained materials accumulated and produced by epifauna associated with the wind farms’ solid structures (Baeye and Fettweis, 2015). The changes in granulometry and organic matter content in the sediment (Coates *et al.*, 2014) are mostly attributable to the fauna’s filtering activity and the production of faeces and pseudo-faeces which can lead to a shift in microbenthic community structure and diversity. Additionally, the solid structures constituting the wind turbine’s foundations introduce roughness elements to the water column, thereby creating eddies, vortexes and turbulent flow dynamics and increasing the probability of resuspension (Grashorn and Stanev, 2016). Considering the extensive coverage of offshore wind farms in some areas, such as throughout the

North Sea, this change in circulation, seafloor community and sediment properties may constitute shifts in B/P exchange pathways at large spatial scales (tens of hectares).

In contrast to several well-studied offshore wind farms impacts, such as seabird collisions, settlement of encrusting fauna and flora, and electromagnetic disturbances, not much research has been carried out to test their effects on B/P exchange processes (Dannheim *et al.*, 2019). Furthermore, the investigation of anthropogenic impacts often happens in retrospect and the addition of more baseline studies would undoubtedly add much to our understanding of anthropogenic impacts on particle deposition.

1.1.2.2 Upward flux and resuspension

Particle deposition is rarely final, as particulates can be eroded away from the sediment surface. Generally speaking, the erosion of non-cohesive sediments is constant with applied shear stress and a product of fluid stresses and grain stresses only affected by the excess shear stress, bed roughness, grain size and orientation, particle sorting and packing and bed configuration (biological factors are considered subordinate to physicsal ones in this sediment type; Julien, 2010). On an exclusively physical basis, low level forces applied to the sediment lead to rolling or sliding of particles along its surface, medium levels prompt a hopping motion called saltation, and strong forces cause particles to be drawn from the bulk sediment into complete suspension. In turbulent environments, particles exchange momentum with the surrounding fluids and are thereby swept across or ejected from the sediment surface (Gordon, 1974; Kassem *et al.*, 2015). Physical erosion patterns in cohesive environments depend strongly upon the way in which the bed was originally formed (Ariathurai and Arulanandan, 1978). Erosion processes in cohesive environments are depth-limited and erosion rates are reduced in deeper layers, due to the consolidation of particles with depth (Aberle *et al.*, 2004). There are three different types of physical erosion (Amos *et al.*, 1992, 1997) and several may be displayed in parallel in cohesive sediments, making the process notoriously hard to model. Type Ia causes asymptotically decreasing surface erosion of cohesive sediment up to a depth of ≤ 0.5 cm, and mainly affects organic matter and small particles layered on or in the topmost sediment layer. Type Ib often follows type Ia and causes a similarly asymptotic erosion, which ceases as sediment shear strength increases with depth. While type Ib erosion typically reaches ≤ 2 cm in depth, type II is limited only by the strength of the applied force, and affects mainly non-cohesive sediment types. In type II, constant erosion of mass occurs independently of changes in shear strength with depth, typically under elevated current speed and turbulence conditions (Amos *et al.*, 1992).

An additional factor which complicates our understanding of the erosion process is the interference of biotic elements. The extracellular polymeric substances (EPS) produced by marine biofilms, for example, reduce the sediment surface roughness and frictional drag, and increase cohesion (Sutherland *et al*., 1998). EPS distribution throughout the sediment is one of the key components controlling bed form dynamics where it appears in high enough concentrations (Malarkey *et al.*, 2015). There are other biological mechanisms affecting sediment erosion and resuspension such as animal tracking, grazing, (Nowell *et al.*, 1981; Borsje *et al*., 2008; Kristensen *et al.*, 2012) and faecal pellet production (Andersen and Pejrup, 2002) affecting bed roughness as well as resuspension potentials.

Benthic organisms can also drive transport that counters gravimetric deposition by actively ejecting OM and sediment grains into the water column during feeding and other activities, as well as their gametes and larvae to initiate pelagic stages in their development (*e.g*. the polychaete burrowers *Nereis virens*; Bass and Brafield, 1972). Other organisms known as ecosystem engineers modify, maintain and create habitats by causing physical state changes in biotic or abiotic materials, thereby modulating resource availabilities directly and/or indirectly (*e.g*. reef-building bivalves and macrophytes; Jones *et al*., 1994). The extent to which different areas of the ecosystem in question are impacted depends upon the strength and nature of the respective engineering species (Bouma *et al.*, 2009; Meadows *et al.*, 2012). They may for example alter their environment and change flow dynamics around the sea bed, thereby altering erosion and deposition rates in various ways (Coleman and Williams, 2002) and thus dictating the sediment type present in an area (Ginsburg and Lowenstam, 1958). Increases in bulk sediment grain size and permeability caused by the bioengineers then promotes altered B/P exchange rates (Ziebis *et al.*, 1996). Erosion thresholds may also be affected, in some cases seasonally varying between increase and decrease (Grant and Daborn, 1994; Paarlberg *et al.*, 2005). These and other biologically mediated particle movements can affect particle distributions from micro to landscape scale (Van Hoey *et al.*, 2008; Montserrat *et al.*, 2009).

Bioturbation (the biogenic movement of particulate matter throughout the sediment matrix) can play an important role in localised particle displacement (Berg *et al.*, 2001) as well as landscape scaled effects on particle distributions by affecting sedimentary structure, biogeochemical gradients and fluxes, and the composition of associated communities of auto and heterotrophs (Van Hoey *et al.*, 2008; Bouma *et al.*, 2009; Montserrat *et al.*, 2009). Each bioturbating species may affect particle exchanges differently, depending on their functional traits, mediated by species performance in response to the environment in which they occur (*e.g*.

Mermillod-Blondin *et al.*, 2004; Solan *et al.*, 2004; Maire *et al.*, 2006; Braeckman *et al.*, 2010; Ouellette *et al.*, 2012), sediment characteristics (Bernard *et al.*, 2019) and temporal patterns such as seasonal cycles (Que*irós et al*., 2015). The main impacts bioturbation activity has on upward B/P exchange processes, are a) that it generally destabilises the sediment, lowering critical erosion and resuspension thresholds in the process (Widdows *et al.,* 1998; de Deckere *et al.*, 2001) and b) the biogenic physical ejection of particulate matter into the water column (Davis, 1993). Co-occurrence of bio-stabilising and destabilising organisms is known to have variable effects on sediment matrix properties (Queirós *et al.*, 2011). Such duality may even exist within the effects of a single species, such as has been shown in the deposit-feeder *Peringia ulvae*, which destabilises sediment surfaces through grazing whilst simultaneously excreting pellets with increased settling velocity compared to the original sediment, thereby having both destabilising and stabilising effects (Andersen and Pejrup, 2002). In some cases, an organisms' effect on sediment erosion thresholds may even reverse in sync with seasonal environmental changes, leading to alternating stabilisation and destabilisation of the surrounding sediment (*e.g.* Grant and Daborn, 1994). Overall, the magnitude at which biological processes affect sediment transport and solute exchange is tightly dependent upon the density of active organisms and the magnitude of their effects relative to that of ecosystem attributes or processes also affecting transport of sediment and solutes (Queirós *et al.*, 2011; Kristensen *et al.*, 2012). The net effect of co-occurring biostabilising and destabilising benthos, and how this balance may shift on different temporal and spatial scales, has thus far only been investigated in small, location-specific studies and should be investigated at the ecosystem-level.

Once buried, particles may be stored and consolidated or recycled (Graf and Rosenberg, 1997). Within the benthic matrix, the complex materials which are not permanently buried are broken down chemically *via* oxidation and biologically by benthos and bacteria, allowing them to re-enter the cycling of elements. In permeable sediments, even living microphytes may be advectively flushed into deeper sediment layers and trapped there, leaving them to be mineralised more swiftly than they would be at the sediment surface when they die, thereby fuelling the recycling of nutrients and C (Ehrenhauss *et al.*, 2004). Advective flushing of particulate OM throughout permeable sediment alleviates concentrated hot spots by spreading the OM to a larger microbial community (Franke *et al.*, 2006). Diagenetic reactions vary in speed and consequently, affect the environment on different scales: very slow reactions occur mostly at depth and are of importance at geological time scales, while rapid ones define the biogeochemical conditions of the benthic boundary layer without having interfered in the sediment matrix at any significant depth (Aller, 2014). The major roles biological processes play in mineralisation do not only extend to the direct impacts of microbes which catalyse and drive the process itself but also the effects of larger organisms which modify OM burial rates and contribute to its break-down through grazing (Tait *et al.*, 2015; Queirós *et al.*, 2019). The translocation of particles and potential homogenisation of surface sediment layers as well as the introduction of fresh O_2 and OM to deeper layers by bioturbators, bioirrigators and even benthivores is a crucial determinant of diagenetic processes (Lindqvist, 2014).

Direct anthropogenic causes of particle resuspension include dredging, trawling, mining, anchoring and many others. Repeated dredging can lead to long-term modification of local sediment properties and particle and solute transport rates at the dredged site (Moon *et al.*, 1994; Pilskaln *et al.*, 1998; Mikkelsen and Pejrup,

2000) and the use of trawls and similar types of mobile fishing gear can have comparable effects (*e.g.* Palanques *et al*., 2001; Jennings and Kaiser, 2006). The removal of fine-grained particles from continental shelves through anthropogenic resuspension on a global scale is estimated to be up to six times as large as it would be through purely natural causes of resuspension, closely matching the input of fine-grained material from riverine sources (Oberle *et al*., 2016). On a local level however, this may not be the case (*e.g.* Schoellhamer, 2002; Ferré *et al.*, 2008). Mobile fishing gear can furthermore lead to the removal or disruption of micro and macro-phytic communities that would otherwise inhibit resuspension, as well as modification of the benthic macrofauna community composition (Hiddink *et al.*, 2006; Hiddink *et al.*, 2006), and burial of sediment surface chlorophyll a content (Tiano *et al.*, 2019). Biogeochemical impacts of trawling are more pronounced in naturally muddy than in sandy environments (Sciberras *et al.*, 2016), although some sandy sediments are likely to occur due to long-term granulometry changes resulting from chronic bottom trawling pressure (Hiddink *et al.*, 2006). Long-term biogeochemical changes of seafloor habitats associated with anthropogenic interactions, and associated shifts in B/P exchange processes remain, thus far, largely unknown. This is, amongst other reasons, due to a lack of data on baseline conditions collected prior to anthropogenic intervention.

1.1.3 Interactions and inter-dependencies

Most of the B/P coupling processes described in this review are difficult to consider individually, as they either interact very closely with others or have a wide range of effects and dependencies, making them hard to assign to any one section. Each is part of a feedback mechanism and interacting with others, thereby producing the overall effect on sediment and water column structures which results in the total rates of sediment and solute transport (Borsje *et al.*, 2008). The combination of interacting processes and the scales at which they affect exchanges between the benthic and pelagic zones varies in accordance with the respective physical and biological environmental conditions, the “ecological context” (Queirós *et al.*, 2011).

Most biologically important processes are dependent on both solute and particle B/P exchanges and interactions. One example of this is the cycling of OM, which is mediated by benthic heterotrophs. Most OM in the marine environment originates from primary producers such as phytoplankton, seaweeds and other macrophytes, which require light and nutrients in solution to grow, the latter being especially important during times and in locations of nutrient depletion (*e.g.* Davis *et al.*, 2019). During phytoplankton growth cycles, both Dissolved OM (DOM) and Particulate OM (POM) is produced and introduced to the environment surrounding the plankton (Biddanda and Benner, 1997). Each of these OM compounds may be utilised differently, as detailed in the previous sections of this review. While POM may be consumed by secondary producers and then exported towards the benthos, either passively through incorporation in faecal pellets and marine snow floccules, or actively through the vertical migration of the consumers, DOM may stay in suspension. Depending on the hydrological circumstances, the DOM may be fully utilised and degraded by the microbial community within the water column (Mari *et al.*, 2007). Throughout this process, DOM and POM are in constant interaction through a variety of pathways which are complex enough to warrant entire review papers by themselves (*e.g*. Mecozzi *et al.*, 2008; He *et al.*, 2016). Once the OM reaches the sea floor, however, it is utilised by macro and micro-fauna, and/or mineralised by the benthic microbial community (Gooday *et al.*, 1990). Both pathways are linked and require an oxidising environment to function, which is where B/P exchange of dissolved O_2 plays an important role (Snelgrove *et al.*, 2018). This brief excursion details only a part of the OM cycling process, and highlights how inextricably interlinked solute and particle B/P exchange pathways of C, O_2, nutrients and many more elements are. Due to the complexity of the marine system and associated observation or experimentation, there are still many questions in want of an answer, offering a guiding direction for future research.

1.1.4 Future direction

Historically, the exchange of particles and solutes, which were seen as two separate pools of resources, was studied one-dimensionally and often in isolation from other ecosystem processes. This review highlights the shortcomings of this treatment of solutes and particles as separate entities instead of inseparably interwoven parts of the same exchange pathways (see *e.g.* Kristensen *et al.*, 2012). It should be noted that in some fields, such as diagenetic research, the assumption of an integrated solute/particle framework has been the *status quo* for decades (Berner, 1980), but this has not been the case in many fields, and especially, in benthic ecology. These differences in approach could in many instances be attributable to a lack of interdisciplinary collaborations that require bridging in future work. A separate consideration of solutes and particles may be necessary in the exploration of specific transport mechanisms, but as B/P processes are typically affected by many types of exchanges simultaneously, such one-dimensional studies can only ever represent basic foundational elements on which a higher understanding is built. Rediscovering the ecological complexity and applying it in areas other than diagenetic research will thus lead to a better holistic understanding and predictive ability, regarding both drivers and consequences of

B/P exchanges. The insight that observations at the ecosystem level are too complex to be approached in the way most empirical ecological studies have done in the past, is nothing new (Lawton, 1999) and a change of perspective has already been suggested (Thrush *et al.*, 2009). Detailed guidelines have been suggested to aid scientists in their study design in order to allow the extrapolation of empirical study results to broader temporal and spatial scales (Hewitt *et al.*, 2007). This includes advice such as a) considering the contextual natural history to estimate expectable heterogeneity, b) integrating correlative and manipulative study elements, c) inclusion of iterative measurements between integrative studies, d) use of continuous explanatory variables during the analysis stage, and finally e) the integration of in-situ data and model outputs (Hewitt *et al.*, 2007). Time-series data have been assessed as one of the most useful tools to provide broad scale temporal context to ecosystem processes (Thrush *et al.*, 1996) such as B/P exchange. This review also highlights that although the awareness of a need for ecosystem-level approaches clearly exists, and individual B/P exchange processes are often well-studied, not all pathways have been explored equally well in the past and the multidimensional, transdisciplinary approach is still not used as the foundation of B/P exchange research, at large. Some gaps, such as the lack of objective rank-ability of the respective relative importance of drivers of solute and particle B/P exchanges require exactly the kind of temporal and spatial ecological context described in the previous paragraph. Information on individual driver processes cannot be balanced or compared with one another without coherent scale and contextual information. Furthermore, while some studies hint at parts of different exchange pathways across the sediment-water interface (*e.g.* Berner, 1980; Glud, 2008; Aller, 2014), there is generally a distinct lack of information regarding the exchanges themselves, and their importance in the greater ecosystem context, as noted in recent work (*e.g.* Middelburg, 2017). The consequence of this shift in perception is that when dissecting any B/P exchange pathway into its individual processes, it becomes apparent that often not all processes involved are well known well enough to allow for the accurate quantification of the entire pathway. Thus, even when consideration of the environmental spatial and temporal context permits a classification of drivers of exchange by relative importance, not all may be known in enough detail to be of use.

Examples of parameters into which more research should be invested are for example the effects of biological and anthropogenic actions of the diffusion of solutes other than O_2, in-situ observations of interactions of boundary layer dynamics with physical drivers of B/P exchange, potential seasonal dominance of biological drivers of B/P exchange over physical ones, lateral particulate matter transport, and residence times within the nepheloid layer.

Embracing the ecosystem as a whole, regardless of the discipline in which individual pieces of research were undertaken, is a vital step towards improved benthic-pelagic understanding (Widdo*ws et al*., 2000; Kristensen, 2001; Griffiths *et al*., 2017). This must be based on an in-depth understanding of individual drivers and processes, which drive important processes within the ecosystem. However, in order to integrate studies from various fields as is often necessary when investigating ecosystem level pathways, such as B/P exchanges, some caution must be exercised. Middelburg (2017) summarises the different approaches of various disciplines well on the example of organic Carbon cycling by pointing out areas of disagreement *versus* overlap, and accumulating elements from each discipline to form a complete picture of current knowledge on the topic. Collaborative research efforts must move past multidisciplinary approaches in which individuals or teams from different disciplines independently research the same environment, only to later collate their findings, to truly transdisciplinary working practices which take elements of the various disciplines into account from the start. The ideal next step in gaining a deeper understanding of B/P exchange in coastal marine ecosystems is to fully acknowledge the complexity and interdependencies of the processes involved in individual pathways. This will lead towards a more precise measure of real life ecosystem scaled processes, such as elemental cycling, gas exchange, quantification and subsequent mitigation of anthropogenic influences, and much more. Measuring this complexity in real systems will doubtlessly be a challenge, but it could also be the stepping stone to a deeper understanding of the marine environment at local and global scales, providing us with the means to better study, conserve and protect it. With ongoing environmental change, be it anthropogenic or natural, we will thus be able to make more accurate assessments of the state of the marine ecosystem functioning, and take appropriate actions to conserve it.

1.2 Aims and Objectives

The overarching aim of this thesis is to close some of the knowledge gaps identified in the literature review. Specifically, the unknown effects of temporal variability (see Sections 1.1.1.2, 1.1.1.3 and 1.1.2.2), the need for an ecological context in which observations should be placed (see Section 1.1.3) and the need for transdisciplinary approaches to obtain a holistic understanding of the ecosystem (see Section 1.1.4). To this end, the uncertainties about variations in influence of the various drivers of B/P exchange processes on different temporal scales are addressed, using multidisciplinary data sets. Time scales ranging from intra-annual, through inter-annual and multiannual, to long-term and future climate-driven trends are considered. This will provide a temporal ecological context that furthers our understanding of these ecosystem level processes and builds the foundation for future studies.

Chapter 2 investigates the effects of intra-annual variation of phenological and environmental parameters on the relative importance of the multiple drivers of B/P exchange and the dominant direction of exchange. Highly resolved experimental and in-situ measured data are combined with data collected as part of a long-term observatory, to provide information on the biological, physical, meteorological and biogeochemical environment at this location. In temperate environments, many of the drivers of B/P exchange follow seasonal cycles, which suggests that the impact they have on B/P exchange processes may also be intra-anually variable, affecting timing, relative magnitude and direction. Chapter 2 contains an original study which combines unique long-term data collections and highly resolved experimental data to characterise typical seasonal patterns in an average year.

In the natural environment, longer term multi-year trends and inter-annual variability resulting from extreme events often override typical patterns. “Average” years, such as the one characterised in Chapter 2, are in fact exceptionally rare under natural conditions. To examine this, in Chapter 3, a multi-annual, multidisciplinary data set from the same location was used to identify the main sources of deviation from the norm at the scale of a decade, thus providing some ecological context for medium-term temporal variation in B/P exchanges. Important multi-annual trends were identified and outlier values of extreme rates of B/P exchange were matched to co-occurring unusual biological, physical and meteorological events.

Although the decadal study provided an insight into inter-annual as well as multiannual patterns, a decade’s record is too short to detect any longer-term trends, such as for example climate-change driven shifts in B/P exchange processes. In Chapter 4, a system in which the potential effects of climate change can already be seen in today’s trends in the data, was surveyed. The Arctic environment was chosen as it exhibits some of the fastest rates of climate-induced environmental change. Chapter 4 contains the analysis of a set of multidisciplinary data of the various biological, physical and biogeochemical drivers of B/P exchange in areas north and south of the current Polar Front location in the Barents Sea, as well as in two years of different levels of sea ice cover. Using this data current conditions were characterised and potential climate-induced changes in the future were predicted.

Finally, in Chapter 5 the main findings are summarised and discussed in the context of prior related publications and knowledge gaps identified in this chapter. The implications of a co-occurrence of variability in B/P exchanges on different temporal scales are reviewed briefly. Furthermore, practical applications of the work carried out in Chapters 2 - 4 are discussed and advancements to the current views based on the findings of this thesis are laid out. Lastly, suggestions for future work are made.

Chapter 2

Seasonal patterns of benthic-pelagic exchange of solutes and particles

Note: This chapter contains an original study, which has been accepted for publication in Frontiers in Marine Science (Rühl, S., Thompson, C., Queirós, A., Widdicombe, S. (2020), Intra-annual patterns in the benthic-pelagic fluxes of dissolved and particulate matter, *Frontiers in Marine Science*). Author contributions: SR carried out field sampling and laboratory-based data collections, analysed the data and wrote the manuscript; CT and AQ helped in practical aspects of the experimental set-ups, as well as providing feedback and improvements to the manuscript throughout the writing process and while it was under review for publication; SW provided support in the conceptualising of the study as well as giving feedback and improvements to the manuscript throughout the writing process and while it was under review for publication.

2.1 Introduction

The marine ecosystem can perhaps be considered the most inter-connected ecosystem on Earth. As outlined in Chapter 1, there is a constant movement and flux of materials through the exchange of living organisms as well as the complex production, transformation and transport of particulate and dissolved matter throughout the system. Many of these connections are vital to the overall functioning of the marine ecosystem. For example, the influx of organic matter from the pelagic to the benthos provides a vital source of food for many benthic organisms (Middelburg, 2018), while nutrient depleted pelagic environments can be replenished from sedimentary sources (*e.g.* MacIntyre, 1998). As the exchange of dissolved and particulate matter between the benthos and the pelagic cannot be summarised in a single process, but rather comprises of a series of exchange pathways which are the product of physical, chemical and biological factors interacting in the environment, their joint consideration is required to gain a holistic understanding of the ecosystem in question (Rühl *et al.*, 2020). In the present study, I explore how the complex network of benthic-pelagic exchange pathways may be affected by phenological and other environmental patterns over the course of a year. Phenology, the cyclical and often intra-annual occurrence of important biological events, is known to shape environmental interactions in marine habitats around the globe, and especially the temperate coastal ocean (*e.g*. Rudnick *et al.*, 1985; Schafer *et al.*, 2002; Tonkin *et al.*, 2017).

Many of the pathways and processes involved in the exchange of DM differ from those involved in the transport of PM. While there is a distinct group of direct drivers in the case of DM B/P exchange, the exchange of PM can be influenced by a broader set of direct drivers which are best grouped into two categories to avoid unnecessary complication. As elaborated in Chapter 1, the primary drivers of DM exchange are a) the biological pumping of water by macroinfauna known as bioirrigation (Volkenborn *et al.*, 2007, 2012), b) the physical resuspension of sediments and pore waters by currents or waves (Morris and Howarth, 1998; Tengberg *et al.*, 2003; Durrieu De Madron *et al.*, 2017), c) the biological mixing of sediments and resulting release of pore waters by macroinfauna and bio-suspension (Berg *et al.*, 2001; van Hoey *et al.*, 2008; Bouma *et al.*, 2009; Montserrat *et al.*, 2009), d) advective flushing from tides, currents and waves (Ehrenhauss *et al.*, 2004), and e) diffusive flux (Berner, 1976; Revsbech and Jorgensen, 1980; Boudreau, 2001). The five direct drivers of DM B/P exchange are all weighted equally in this study, though depending on the environment their relative influences may vary (*e.g.* advection *vs* diffusion depending on sediment type; Glud, 2008). As there is a large number of drivers of PM exchange, these were grouped in this study, as detailed in Chapter 1, as: a) those that affect resuspension and upward transport of benthic material into the water column (bioturbation, physical resuspension, meroplanktonic larvae release, *etc*.), and b) those that affect downward flux and deposition of formerly pelagic particulate matter (zooplanktonic ingestion and vertical migration, hydrodynamic and thermodynamic water column properties, *etc*.). Secondary drivers of PM exchange within both groups are the specific processes which affect the likelihood and severity of particle flux as well as the nature of the PM in question.

However, PM and DM B/P exchange do not occur completely in isolation, and there are overlaps between their drivers of exchange (*e.g*. biological and physical forms of resuspension). Due to the complexity of drivers involved, for simplicity, in this paper, the B/P exchange of DM and PM will therefore initially be considered separately before being integrated to form a holistic framework.

Many drivers of B/P exchange of DM and PM exhibit periodic intra-annual variation. For example: nitrification and microbe community (Hansen *et al.,* 1981); vertical migration (Atkinson and Sinclair, 2000; Kane *et al.*, 2018); pelagic POM supply and flux (Wakeham and Lee, 1993); primary production (Barnes *et al.*, 2015) and weather (Keim *et al.,* 2004). The interactions of all drivers result in net fluxes of DM and PM that vary throughout the year.

Previous studies that described phenological drivers of B/P exchange focused on intra-annual variation (*e.g*. Graf, 1992), and organic matter cycling (*e.g.* Meyer-Reil, 1983), but yet ignored hydrographic processes such as tidal currents and storm events which can drive physical resuspension and advective fluxes. Annual phytoplankton bloom events are known to be a major source of short-term (intra-annual) temporal variation (Barnes *et al.*, 2015), but only over the summer months. In autumn, winter and pre-bloom periods it should thus not necessarily be assumed that biological drivers are key determinants of B/P exchange. In this study, a complete intra-annual cycle is covered, combining biological, biogeochemical, oceanographic and hydrological data to provide a holistic picture of all intra-annual periods at this study site. To this end, existing time-series data that were collected in other contexts, were supplemented with highly resolved and targeted in-situ sampling and experimental work. Thus, a uniquely holistic approach was facilitated, including both biological and non-biological drivers of B/P exchange and closing the gaps left by previous studies that focused on either of the two instead of integrating both (*e.g*. Graf, 1992; Tonkin *et al.*, 2017).

Through the integration of a comprehensive time series data set and targeted *in situ* and experimental measurements, temporal patterns of B/P exchange at a widely representative temperate coastal site are being investigated throughout the year, in a more integrated way than previously done. Because not all types of PM and DM exchange could practically be assessed, and given the differences between B/P exchange pathways of DM and PM, the focus lies first on a specific type of DM, dissolved inorganic nitrite (DIN), and then on a specific type of PM, particulate organic Carbon (POC), as examples individually. Then, they are considered together. This work plan was chosen to produce as complete as possible an assessment of examples of PM and DM exchange pathways, identifying their drivers (and of their variability) throughout the year, to improve our understanding how B/P exchanges occur in the temperate coastal ocean. These two fundamentally important types of DM and PM were chosen as they are deeply involved in key nutrient cycles in the global ocean and the biosphere, as well as being related to ecosystem services delivered by the global ocean, such as Carbon sequestration, which are paramount to regulation of global planetary systems such as the climate system.

Initially, periodic intra-annual variability in the environmental variables considered to be driving DM or PM B/P exchange will be assessed. Patterns in B/P exchange drivers and processes following the phenological periods will then be identified. Finally, utilising both sets of information, potential intra-annual changes in the relative influence of different driver groups will be evaluated and cause-effect relationships between drivers and processes will be identified.

2.2 Methods

A number of existing data sets from an established long-term monitoring station collected between 2009 and 2019 were averaged by month. This created a record of monthly conditions during an “average year”, smoothing over the influences of extreme events which are known to occur sporadically in some years but not others (*e.g*. Zhang *et al.*, 2015; Masselink *et al.*, 2016). The time-series data were then combined with targeted experimental and *in-situ* data collected from the same station across an annual cycle (see Appendix A, 2a and 2b, for a full list of variables included). To ensure the measurements made over a single intra-annual cycle were representative of “typical” conditions rather than outliers in a year shaped by extreme events, conditions of the year in question were investigated in context of the time-series data prior to the analysis. No extreme outliers could be identified in any of the variables in question, so they were found to be an acceptable representation of typical conditions at the study site.

2.2.1 The Western Channel Observatory

The majority of the data were collected at Station L4 of the Western Channel Observatory (WCO), situated in the English Channel 11 miles off the coast of Plymouth, UK (50.25°N; 4.22°W, see Figure 3). Water depth at this site is roughly 50 metres, and the site is characterised as having dynamic water flow with semi-diurnal tidal flow and riverine influences, experiencing depth-averaged current speeds of roughly 0.35 m/s (Smyth *et al.*, 2015; Uncles *et al*., 2015), as well as wave propagation impacts during high wave events (Joseph, 2019). The seabed comprises of sandy mud hosting an abundance of bioturbating and bioirrigating organisms (Queirós *et al.*, 2015). An organic-rich layer can be found immediately above the seabed, that is re-suspended during the tidal cycle (Queirós *et al.*, 2019), the nepheloid layer. This station is considered to be strongly representative of other coastal, temperate systems that experience seasonal thermal stratification. It is for instance being used as a reference biodiversity site by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR, 2020).

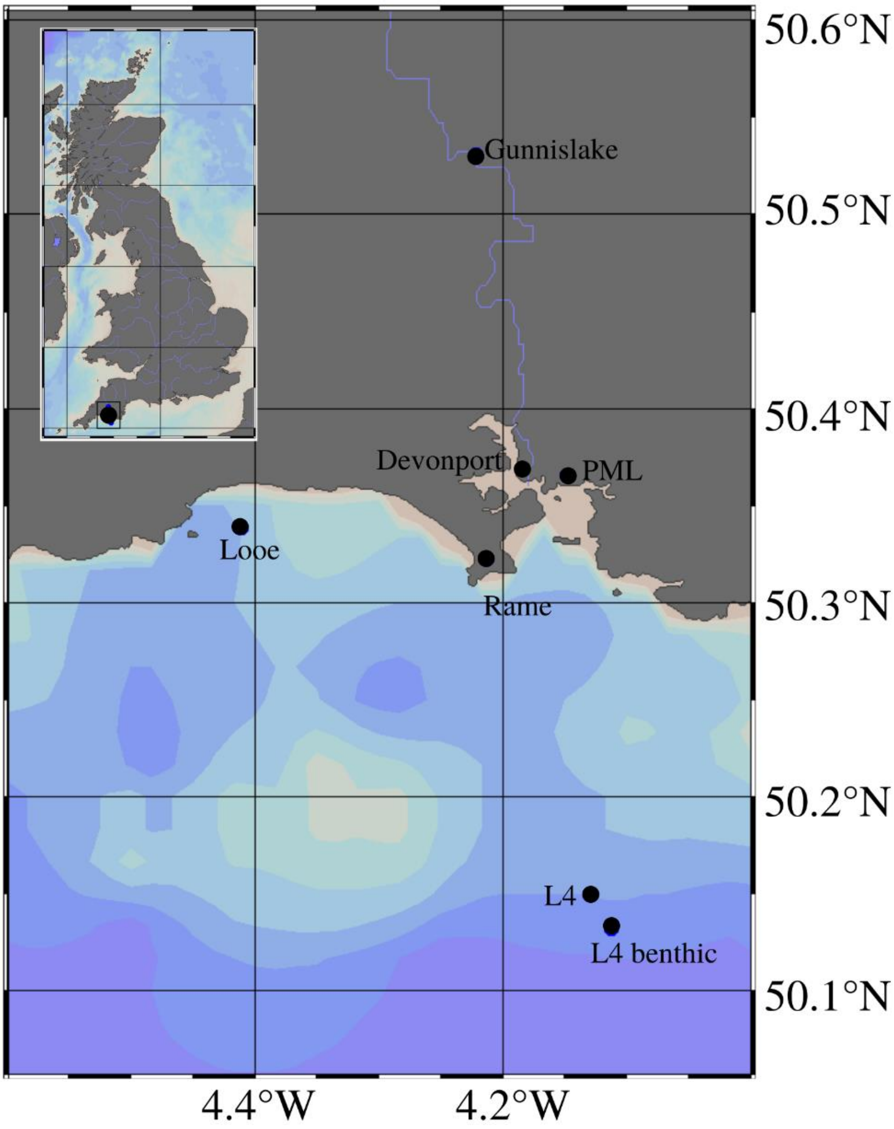

Figure 3: Location of sampling stations including the pelagic and benthic L4 sites, Rame Head MET station, Looe wave buoy, PML MET station, Devonport tidal gauge and Gunnislake river flow gauge, and their location relative to the UK in a broader geographical context in the top left corner box; map generated using Ocean Data Viewer (Alfred Wegener Institut, 2019)

Station L4 was first sampled in 1903 by the Marine Biological Association (MBA). It was subsequently aggregated into the WCO, run by Plymouth Marine Laboratory (PML), as part of the UK's Natural Environmental Research Council National Capability (Harris, 2010) in partnership with the MBA. Regular benthic sampling of L4 started in 2008, though sporadic benthic sampling in the Plymouth area has been documented since 1899 (Allen, 1899). Comparative benthic studies have been carried out since the 1930s, including investigations of changes in the benthic faunal community over time (Holme, 1953; Capasso *et al.*, 2010). The benthic L4 station is located roughly 4 nm from the pelagic L4 site (50.13°N 4.11°W, see Figure 3) and as connectivity between the two sites is well documented (Smyth *et al.*, 2015; Tait *et al.*, 2015; Zhang *et al.*, 2015; Navarro-Barranco *et al.*, 2017; Queirós *et al.*, 2019), both are hereafter collectively referred to as Station L4.

Station L4 annually experiences seasonal thermal stratification and nutrient depletion in surface waters (Smyth *et al.*, 2015). Organic matter inputs to L4 come from a variety of seasonally variable sources (Queirós *et al.*, 2019). Based on Conductivity/Temperature/Density water column profiles recorded between 2009 and 2018, thermal stratification at this site starts on average on the 24-25th of May and ends on the 03rd-4th of September, though it exhibits high inter-annual variation in both duration and timing (see also Smyth *et al.*, 2010). Data collected through the WCO time series utilised in this study include measurements of total and organic particulate Carbon and Nitrogen (TPC, TPN, POC, PON), coloured dissolved organic matter (CDOM; Groom *et al.*, 2009), SPM, dissolved O_2, phytoplankton abundance and biomass (Widdicombe *et al.*, 2010) as well as zooplankton and meroplankton abundance (Eloire *et al.*, 2010; Highfield *et al.*, 2010), benthic macrofauna abundance and biomass (see *e.g*. Zhang *et al.*, 2015), fluorescence and chlorophyll a (see *e.g*. Aiken *et al.*, 2004), water temperature, photosynthetically active radiation (PAR), and mean sediment grain size (d_{50}). More detail on the data sets listed above can be found in Appendix A, 2a.

2.2.2 *In situ* and experimental data collection specific to this study

Sediment erosion thresholds and critical shear stresses were measured at four time points throughout the 2017-2018 period, using the PML annular laboratory flumes (Figure 4, Widdows *et al*., 1998; see Appendix A, 2b). Further attempts at more frequent measurements throughout the year were made, but could not be completed due to weather constraints on the ship-based sampling opportunities.

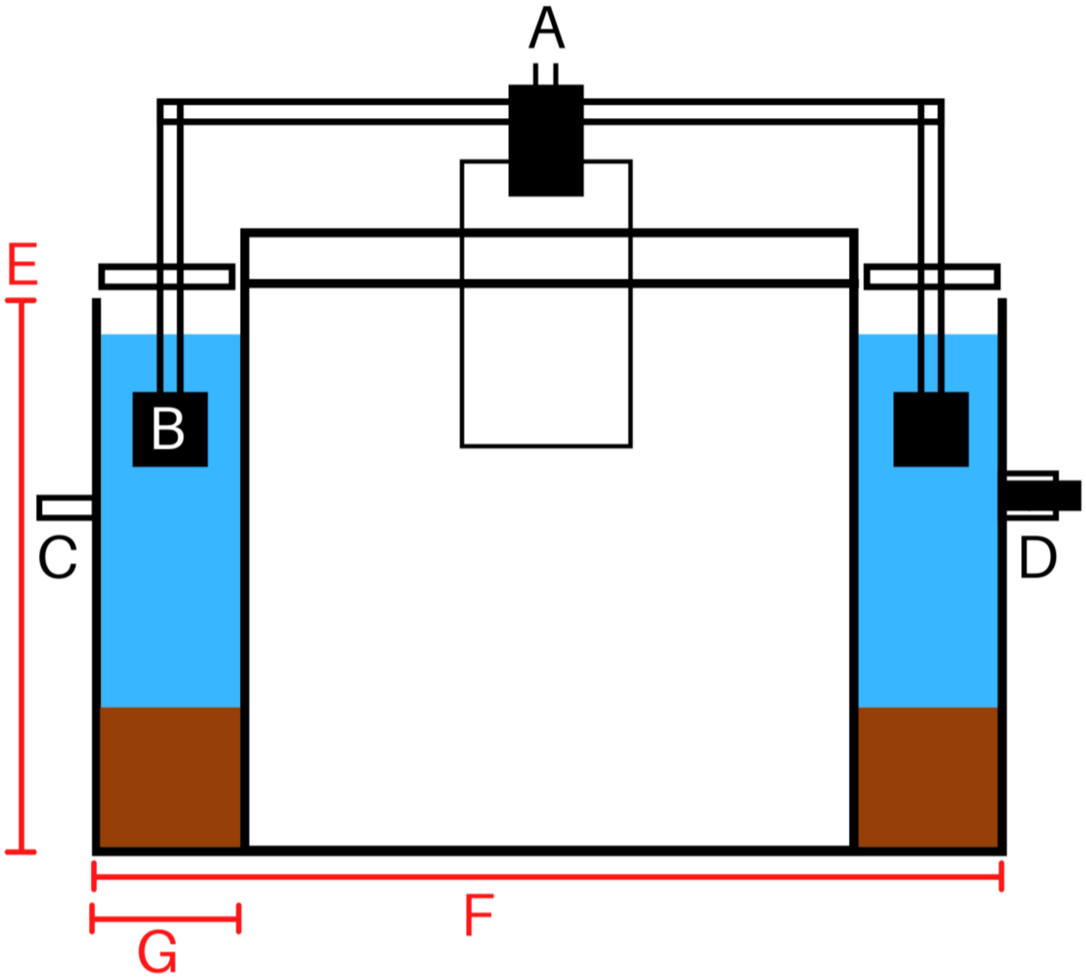

Figure 4: Flume schematic of PML flume: A) Motor unit; B) Paddles x4; C) sampling port; D) Optical Backscatter sensor; C) sampling ports at 25 cm height above the bottom of the flume; D) Optical

Backscatter sensors at 25 cm height above the bottom of the flume; E) height of the flume body, 40 cm; F) diameter of the flume, 64 cm; G) width of the flume channel, 12 cm

Sediment was collected using deployments of a 0.1 m^2 box core, ensuring the overlying water layer and sediment surface would be disturbed as little as possible throughout the coring process. The boxes were then subsampled using eighth-annulus custom corers (hereafter “sub-corers”) which were pushed into each sediment core and had their bases sealed on deck using neoprene seal fitted plastic lids. Overlaying bottom water retained in the box corer was preserved when sub-cores were sampled in this way, and was gently aerated for the duration of the transport back to the laboratory (<2 hours). During transport, all sub-corers were kept in shaded tubs, cooled by a seawater bath to help maintain temperature. Jostling and other disturbances during transport were avoided as far as possible as disruptions in the sediment fabric which alter sedimentary properties have previously been shown to be caused by transport procedures (Blomqvist, 1991). Upon arrival at the Plymouth Marine Laboratory mesocosm facility, the sub-cores were inserted into the annular flumes by gentle removal of sub-scorers, and water level topped using preserved bottom water from the collection site, as described. Water level was achieved by pouring the bottom water over a layer of bubble wrap to reduce disturbance to the sediment surface (as introduced in Widdows *et al*., 1998). The flumes were then left to settle for seven days in darkened and aerated conditions at L4 bottom water temperatures. The mescocosm laboratory is an environment controlled room where, in addition to other controls, air temperature is regulated on a monthly basis to follow the seasonal cycle of bottom water temperature at L4 (Queirós *et al.*, 2015).

The flumes were run using the appended program (see Appendix A, 2c) and sediment erodibility and cohesion were measured in terms of optical backscatter using Optical Backscatter Sensors (OBS) as well as SPM samples at each velocity step. SPM samples were taken from the upper third of the water column (see sampling port in Figure 4) during the run of the flume exactly one minute before the end of each velocity step using a Swinnex syringe filter system with pre–ashed (450 °C for 24 hours) pre-weighed 25 mm GFF (Whatmann). They were then placed in labelled containers and stored in a fridge at 2 °C; if further analysis was not possible within the next 24 hours, samples were transferred to a -20 °C freezer immediately after sampling. To determine the quantity of SPM and POC in each sample, filters were dried in an oven in pre-weighed petri dishes over night at 60 °C and weighed again. They were then placed in a furnace and ashed for 24 hours at 450 °C, after which they were weighed a final time.

In addition, 50 ml of in-flume water were extracted to assess Nitrite, Ammonium, Silicate and Phosphate concentrations, as well as the Nitrite/Nitrate ratio. Samples were collected at regular time points; immediately before the run, five minutes into each velocity step, and at the end of the flume run. The water was filtered through acrodisk® supor® membrane filters 0.8/0.2 µm (VWR) and stored at -20 °C immediately after sampling. A 5 channel Bran & Luebbe AAIII segmented flow auto analyser was used to estimate concentrations.

Background SPM at the time of *in-situ* core collection was measured by filtering, drying and ashing 10 litres of water collected *via* a Rosette sampler from 0 m, 10 m, 20 m, 30 m, 40m, 50 m depth, and water from 54 m (bottom water) was collected from multicorer deployments (four perspex tubes of 80 cm length and 10 cm diameter which capture the nepheloid layer immediately above the sediment surface). These water samples were processed in the same way as the flume water. Sediment properties were assessed during the field campaign, including bulk density, porosity, water content, permeability and POC content. Samples were collected using 50 ml syringe corers inserted vertically into the surface of three of the box cores at each time point. Syringe corers were sealed and transported from the field site to the laboratory upright to prevent water loss, in darkened, cool conditions. Each syringe core was used to extract sediment down to a depth of 5-6 cm, which was then split into four sections to create a depth profile: 0-1 cm, 1-2 cm, 2-3 cm and 3-5 cm. Each section was placed in a pre-weighed petri dish, weighed, dried over night at 60 °C, re-weighed, ashed for 24 hours at 450 °C and weighed again. The same types of sample were also collected from inside the flumes immediately after the end of the experiment. Sediment grain size was determined through sub-sampling the initial box cores using the same kind of 50 ml syringe corers. Samples were collected at 0-1 cm, 1-2 cm, 2-3 cm and 3-5 cm depth by dividing each syringe core *in-situ*, and several cores worth of segments were combined to gain samples of approximately 100 g of each depth. After transport in cold and dark conditions, samples were frozen at -20 °C until the time of their analysis, for which a Coulter LS Variable Speed Fluid Module plus particle size analyser was used. For the analysis, the sediment was mixed and subsampled into a glass beaker, diluted with freshwater and stirred thoroughly, before being inserted directly into the particle size analyser's sample chamber using a pipette dripper to reach an obscuration of between 8 and 12 %. Each sample was measured three times to ensure that all size fractions present in the sediment were represented in the output.

Mean grain size (d_{50}) values of each of the stations were used to calculate critical erosion velocities and shear stresses, following the methods outlined in Thompson *et al.* (2013), using power laws described in Soulsby (1997; see Equations (A) and (B) below).

$$u_{*crit} = 0.121({}^{5_{50}}/_{z})^{1/7}U_z \qquad \textbf{Equation (A)}$$

$$\tau_{0crit} = \rho u_{*crit}{}^{2} \qquad \textbf{Equation (B)}$$

In this, u_{*crit} = the critical erosion velocity (m s^{-1}), z = the height above the seabed (m), U_z = the velocity (m s^{-1}) at height z, τ_{0crit} = critical shear stress (Pa), and ρ = the fluid density (kg m^{-3}).

To measure bioturbation, four clear perspex corers (12 x 12 x 40 cm) were pushed directly into box cores also sampled during field campaigns, sealed with plastic, rubber and neoprene seals at each time point, and transported to the laboratory for incubation under the same conditions as the flume cores. Imaging and image analysis methods for the time-lapse images collected during the bioturbation experiments was carried out as described in Queirós *et al.* (2015). In short, particle tracing methods were used to measure bioturbation activity and depth of natural communities by use of 2D imaging under UV light of luminophore tracer distributions with images collected at hourly intervals over the course 7 days. Bioturbation activity was defined as the probability of particle displacement and bioturbation depth, or rather distance, describes the average distance single particles are moved within a single time step. Both were determined by fitting a random-walk bioturbation model (Schiffers *et al.*, 2011) to manually cropped automatically processed time-series using scripts and techniques described in Queirós *et al*. (2015).

In addition, community bioturbation potentials (BPc) were calculated from WCO macrofauna abundance and biomass data using mobility and sediment reworking indices from Queirós *et al.* (2013) and methods outlined in Solan *et al.* (2004).

Community bioirrigation potentials (BIPc) were calculated from the same data based on methods described in Rudnick *et al.* (2018) and indices derived from Queirós *et al.* (2013) as well as from the Marine Ecosystems Research Project Trait Explorer (Bruggeman, 2019).

2.2.3 Additional data acquisition

Further supplementary data were gathered from the Meteorological Office, the National River Flow Archive, the Permanent Service for Mean Sea Level and Looe Wave buoy services. The insights gained through additions from these sources provide relevant information on the weather conditions, potential riverine input and tidal state, all of which are factors that have previously been shown to affect L4 and the general Plymouth Sound area (Eloire *et al.*, 2010; Leynaert *et al.*, 2011; Milliman and Farnsworth, 2013; Barnes *et al.*, 2015; Smyth *et al.*, 2015). Sampling frequency and respective time series data collection lengths vary between the different variables incorporated in this study. A complete list of the supplemental data sets used and their respective sources can be found in Appendix A, 2a.

2.2.4 Data analyses

For the purpose of this study, the year was divided into phenological rather than meteorological periods (hereafter simply referred to as periods, Table I). Periodic groupings were chosen over monthly ones, as the resuspension experiments could only be carried out during four time points in the year. Further sampling events were attempted but were unsuccessful due to adverse weather conditions and a prolonged period of time during which the RV Quest, from which in-situ sampling was being carried out, was being refitted. The chosen five phenological periods were based around a) the occurrence of the spring plankton bloom, as this has been shown to be a highly influential factor driving local intra-annual variability in a number of variables (Graf, 1992; Widdicombe *et al.*, 2010), and b) the historically more hydrologically active part of the year around winter time. From the WCO phytoplankton abundance and biomass data collection, the average phytoplankton bloom dates at L4 were determined to be between the 12th April and the 28th June, lasting on average 78 days. There can, however, be large variations in bloom timing, magnitude and duration between years, with standard deviations of the start date of 23 days and standard deviations of the bloom ending of 60 days. These data were used to establish the unfolding of phenological seasons at the site across the time-series. Based on this, the bloom period was assigned the months of May and June (Table I), omitting April into the pre-bloom period as there typically is a delay between initial organic matter production and its interaction with the benthos. The winter period was defined as December to February (Table I), as this is the time of year during which more than half the storm events that cause significant wave heights above the storm threshold occur, based on the long-term records (NNRCMP, 2019). The pre-bloom season includes March and April (Table I) as a period during which the conditions needed for the phytoplankton bloom to occur are established. July to September are defined as the post-bloom season (Table I), during which thermal water column stratification and nutrient depletion prevail, as described above in Section 2.1. Autumn was assigned to the months of October and November as the period following this, a transition period between post-bloom and winter conditions.

Table I: Splitting of the year into five phenological periods

Period	**Months included**
Winter	December, January, February
Pre-bloom	March, April
Bloom	May, June

Post-bloom	July, August, September
Autumn	October, November

There are prior ecological studies in which dataset divisions into phenological periods were used in a similar fashion to determine inter-seasonal (*e.g.* Louis *et al*., 2009; Zhao *et al.,* 2012) or intra-seasonal (*e.g.* Kielland *et al.,* 1998) variability, though none of them studied the marine environment.

Variables were combined into a variety of data sub-sets for different parts of the analysis. To gain an understanding of the intra-annual variability of the L4 site as a whole, the complete data set with all variables was used (see Table II). To investigate individual B/P exchange drivers or processes, variables were selected for analysis based on relationships identified in Chapter 1 (Rühl *et al.* 2020; see Table II for a list of which variables were included in the determination of which drivers/processes). For example, variables which are known to affect bioirrigation-driven DM B/P exchange processes, were grouped together to assess that particular driver. Many of the variables were of significance in multiple driver groups (*e.g.* sediment porosity and grain size have an effect on both bioirrigation- and diffusion-driven DM B/P exchanges). Where this was the case, duplication was eliminated in the data sub set compiled for the investigation of the overall process to avoid an overestimation of any single variable’s relative impact (*e.g*. grain size was only included once in the assessment of overall DM B/P exchange processes, despite having an impact on several of the drivers).

Table II: Selection of variables into data sub sets corresponding to DM and PM B/P exchange drivers and processes; asterisks indicate variables in which DM and PM exchange processes affect one another (see analysis in Section 3.2.3)

Process → ------------------- **Variables** ↓	PM Resuspension	PM Deposition	Absolute PM flux	Diffusion-driven	Physical Resuspension	Advection	Biological mixing	Bioirrigation	Absolute DM flux
Particulate Organic Carbon (POC)	✓*	✓*	✓*						
Total Particulate Carbon (TPC)		✓*	✓*						
Total Particulate Nitrogen (TPN)		✓*	✓*						
Particulate Organic Nitrogen (PON)		✓*	✓*						
Coloured dissolved organic matter (CDOM)		✓*	✓*						
Suspended particulate matter (SPM)		✓	✓						
Oxygen (O_2)				✓	✓	✓	✓	✓	✓
Phytoplankton abundance and biomass		✓*	✓*						
Zooplankton abundance		✓	✓						
Meroplankton abundance	✓		✓						
Copepod abundance		(✓)	(✓)						

Benthic macrofauna abundance and biomass	✓*		✓*				(✓)*	(✓)*	(✓)*
Benthic fluorescence		✓*	✓*				✓*	✓*	✓*
Chlorophyll a		(✓*)	(✓*)				✓*	✓*	✓*
Rainfall		(✓)	(✓)						
Max wave height, T_{peak} and T_z	✓		✓		✓	✓			✓
Water temperature	✓		✓				✓	✓	✓
Salinity		✓*	✓*						
Sediment grain size	(✓)		(✓)	✓*	(✓*)	✓*			(✓*)
τ_{crit}	✓		✓		✓				✓
River flow		✓	✓						
Tidal flow	✓	✓	✓		✓	✓			✓
Nitrate				✓*	✓*	✓*	✓*	✓*	✓*
Nitrate/Nitrite ratio				✓*	✓*	✓*	✓*	✓*	✓*
Ammonia				✓*	✓*	✓*	✓*	✓*	✓*
Silicate				✓*	✓*	✓*	✓*	✓*	✓*
Phosphate				✓*	✓*	✓*	✓*	✓*	✓*

Data sets were normalised to account for differences in scale and units between variables. To avoid an over-estimation of the impact of variables that are derived from one another (*e.g.* BPc and BPIc are both dependent on macrofauna biomass), factors considered to be affected by this were selectively excluded. For example, in data sub-sets used as response variables in Analysis Of SIMilarity tests (ANOSIM; vegan package, Oksanen *et al.*, 2019) and Orthogonal Partial Least Squares discriminant analyses (OPLS, ropls package; Thévenot *et al.*, 2015), where both BPc and benthic macrofauna biomass were considered of importance, the latter was excluded, as it was already considered through the inclusion of BPc. Factors which were excluded through these considerations are indicated by brackets around their ticks in Table II. Rain fall and copepod abundance data, which through this were not considered directly in any of the data analyses, was used to aid in the interpretation of the results.

To address the first aim of the study and assess periodic intra-annual variability in environmental variables considered to be driving DM or PM B/P exchange, datasets were tested using ANOSIM. For all ANOSIM tests, the five periods (see Table I) were applied as the predictors and the respective groups of variables grouped into drivers and processes (see Table II) were used as responses (see Appendix A, 2d, for a table detailing the specific predictor and response groups for each ANOSIM test). Initially the complete set of variables was tested, to assess intra-annual variability at this location in general. To determine cause-effect relationships, and identify which factors are most important for inter-periodic variability, OPLS were then applied. OPLS were chosen due to their suitability for in between-class discrimination when large within-class variation may be present, and to allow incorporation of the various data sets to equal degrees (Bylesjö *et al.*, 2006). Within the OPLS, the month groups into which the data had been averaged (see data sets in Appendix A, 2b) or during which the data had been collected (see data sets in Appendix A, 2a) was applied as the class by which differences between dataset sub-groups were identified (for listing of predictors and responses of each model see Appendix A, 2e). Factors that contributed significantly to the model fit were identified by Variable Influence on Projection (VIP) values > 1. VIP values reflect loading weights of each model component as well as quantifying the variability of the response explained by the components (Mehmood *et al.*, 2012).

POC and DIN were chosen as model examples for PM and DM exchanges respectively, based on data availability and quality. The inter-periodic variability of POC and DIN was investigated using ANOSIM testing, to gain an understanding of the specific periodic fluctuations of the solute and particulate example specimens chosen for this study. Where periodic intra-annual patterns in DIN or POC were expected to be linked to other environmental parameters, based on causal relationships identified in the literature, this was tested using Pearson's correlation coefficient (Pearson, 1895).

Addressing the second study aim, net patterns in B/P exchange drivers and processes following the phenological periods were identified through directed OPLS modelling of the various data sub-sets (see Table II). The third study aim, evaluating temporal variation in the relative influence of different driver groups, was achieved through the alignment of the temporal variation of the drivers within a year, with that of the overall processes. Recognition of particularly influential drivers and factors was accomplished through the identification of factors which contribute significantly to the intra-annual variation (VIP > 1). Identification of intra-annual temporal patterns and drivers through the OPLS modelling then facilitated the further testing of individual drivers of specific interest for inter-periodic variability in B/P exchanges using ANOSIM. As the ways in which DM and PM exchange processes overlap and influence one another, individual pairs of drivers of DM and PM (and associated secondary driving factors) that have been identified as such (one-way or both ways; see Chapter 1 and Rühl *et al.*, 2020) were analysed jointly using crossed two-way ANOSIM (see response variables marked with asterisks in Table II).

To correct for potential Familywise Errors created through the repeated inclusion and analysis of the same variables in the various data sub-sets and tests, the Bonferroni correction was applied to p-values of ANOSIM tests, to adjust the alpha levels (Cabin and Mitchell, 2000). To avoid the introduction of Type II errors, alpha levels were adjusted separately for analyses specific to DIN or POC (to p = 0.01, see tests in Section 3.1), and analyses of either the complete data set or the sub-sets specified in Table II (p = 0.002, see first test in Section 3.1 and tests in Section 3.2), based on suggestions in Armstrong (2014). Statistical analyses were carried out using cran R (R Core Team, 2019) and PRIMER (PRIMERe version 7, Quest Research Limited).

2.3 Results

2.3.1 Periodic intra-annual variation in individual environmental variables

When all variables collected were considered, significant differences between the five periods were clear (ANOSIM, R = 0.906, p = 0.0001; for response and predictor variable details see Appendix A, 2d, test 1). Variation in the data throughout the year could be attributed to the inter-periodic differences (OPLS, R2X = 0.683, R2Y = 0.989, Q2Y = 0.945, pR2Y = 0.05, pQ2Y = 0.05). Variables which contributed significantly to the OPLS model fit are numerous, indicating that many of the variables considered in this study vary between the temporal periods defined in this study (VIP >1, see Appendix A, 2e).

This includes (in order of decreasing significance from top to bottom and left column before right):

- Wave height
- Silicate concentration in the water column
- River flow rates
- Wave duration
- Phytoplankton abundance
- Water column Phosphate concentration
- Water column Nitrate: Nitrite ratio
- Water column Ammonia concentration
- Surface SPM
- Near-bottom Ammonia concentration
- Near-bottom Nitrate: Nitrite ratio
- Phytoplankton biomass and
- Wave peak period
- Near-bottom Phosphate concentration
- Tidal flow
- Near-bottom fluorescence
- Critical shear stress
- Sediment OC content at 2-3 and 1-2 cm depth
- SPM at 10m depth
- Benthic macrofauna biomass,
- Near-bottom salinity and PAR

DIN concentration at L4 follows periodic patterns of depletion through the annual phytoplankton bloom (bloom and post-bloom periods) and subsequent replenishment through water column destratification (autumn; see Figure 5 top) during which the distribution of DIN throughout the water column varies significantly (ANOSIM, R = 0.446, p = 0.013; see Appendix A, 2d, test 2). The potential of shear-stress driven DIN flux measured in the flume experiment shows that this is also intra-annually variable (ANOSIM, R = 0.608, p = 0.005; see Appendix A, 2d, test 3), as was already indicated by OPLS model 1 (see Appendix A, 2e). Shear-stress driven fluxes switch from a release of DIN from the sediment during the pre-bloom period, to an influx from the water into the sediment during the bloom (see Figure 5 bottom). It must be noted that while the results of these experiments show that the potential for shear stress-driven DIN fluxes is temporally variable, it is unlikely that the required near-bed velocities are reached during all periods (Uncles, Stephens and Harris, 2015).

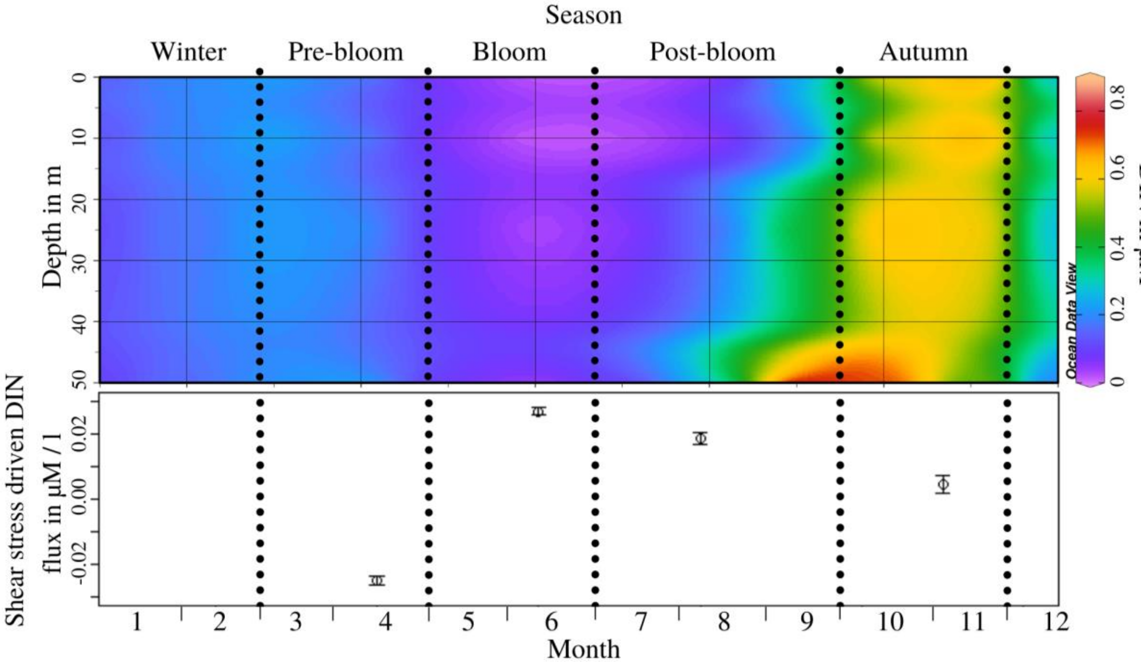

Figure 5: Top panel: Nitrite concentration throughout the water column at 0m, 10m, 25m and 50m depth by month, during an "average year's" cycle. Periods as indicated through the dotted lines are labelled at the top of the figure; Monthly resolution (x-axis) shown to illustrate concentration at 0, 10, 25, 30 and 50 m depth (y-axis); Bottom panel: Resuspension-driven B/P flux potential of Nitrite throughout the year, at critical erosion velocity; Negative values indicate influx from the water to the sediment and *vice versa*

The distribution of POC throughout the water column also varies throughout the periods (ANOSIM, R = 0.501, p = 0.004; see Appendix A, 2d, test 4). The generally low levels of POC in the water column are interrupted by surface maximums throughout winter. This is linked to riverine influx, which is particularly strong during this period (Pearson's, t = 2.9558, p = 0.01439; see also Uncles *et al.*, 2015). Concentrations in the nepheloid layer near the seabed, though generally higher than water-column levels throughout the year, are elevated in post-bloom and autumn periods (Figure 6, top) following the deposition of organic matter after the end of the phytoplankton bloom (Pearson's, t = -2.361, p = 0.03989). Within the sediment, the concentration of POC also changes with the periods (ANOSIM, R = 0.45, p = 0.004; see Appendix A, 2d, test 5), exhibiting high levels of POC in winter and autumn as well as a brief sediment surface maximum during the bloom and high levels of POC below 2 cm towards the end of winter

(Figure 6, middle). The surface maximum in the bloom period is connected to the deposition of organic matter from the phytoplankton bloom. Peaks in POC concentration within the sediment in November and, especially intensely, February, are less clear, but are likely to be connected to riverine sources of POC, based on a previously published study of riverine influences in this area (Uncles *et al.*, 2015). Sedimentary POC at 3-5 cm depth was positively correlated to benthic macrofauna biomass (Pearson's, t = 2.2949, p = 0.04739) but not to bioturbation potential, activity, or depth. It may also be connected to bacterial activity (Tait *et al.*, 2015), though as no microbial data was available for inclusion in this study, this hypothesis could not be tested. Shear-stress induced flux potential of POC across the sediment-water boundary does not exhibit periodic changes in direction, but rather in magnitude (Figure 6, bottom; ANOSIM, R = 0.635, p = 0.004; see Appendix A, 2d, test 6). Similarly to the shear-stress driven DIN flux in figure 2, the POC fluxes in Figure 6 represent not necessarily fluxes that are present in the natural environment throughout the entire year, but rather the potential magnitude and direction of shear-stress-driven fluxes, given a high enough near-bed water velocity.

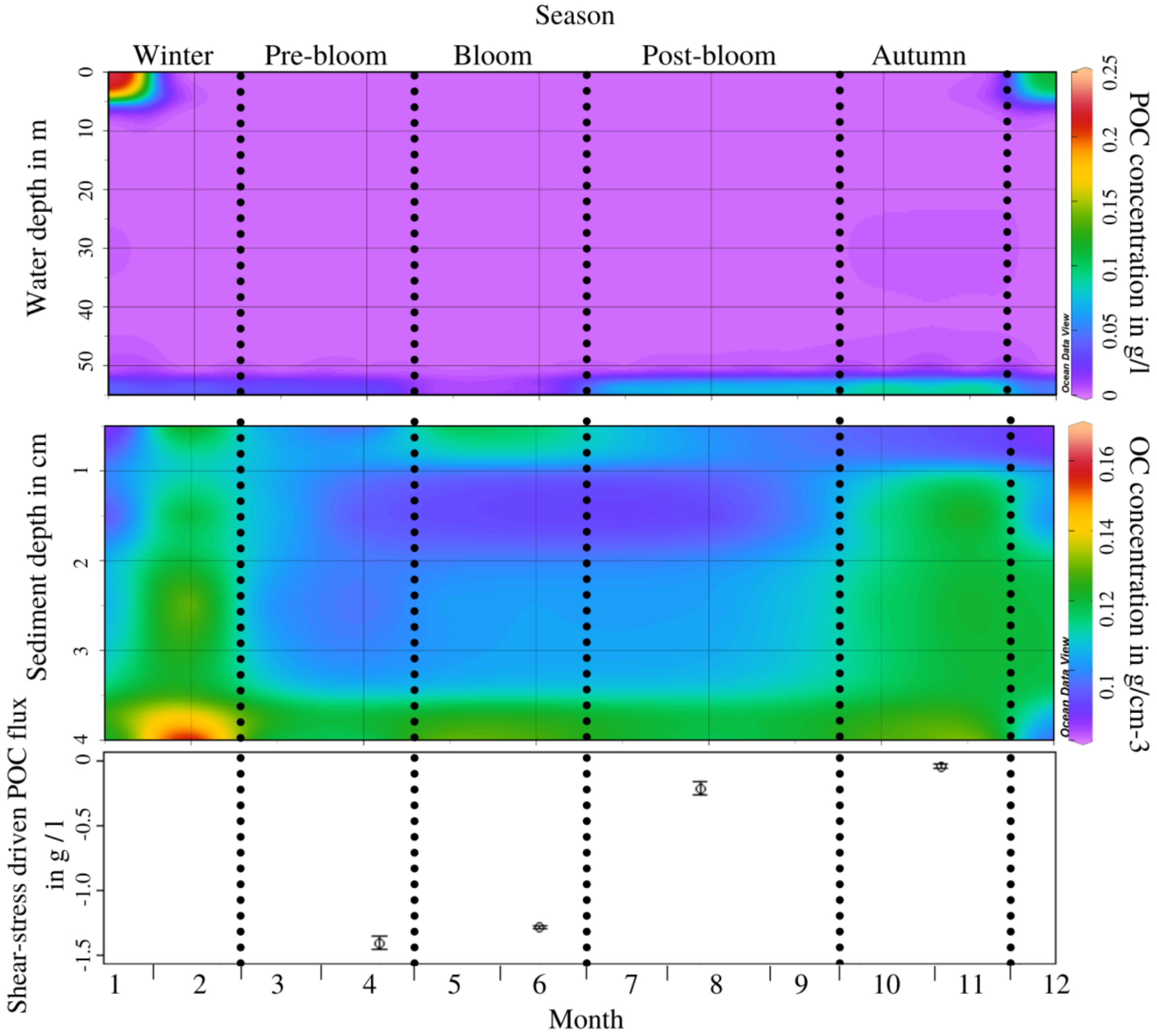

Figure 6: Top panel: POC concentration throughout the water column (depth scale from the surface on the Y-axis) by month, recorded during 2017/2018, including the nepheloid layer which is displayed at 54 m depth. Periods as indicated through the dotted lines are labelled at the top of the figure; Middle panel: POC concentration in the sediment (depth scale from the sediment surface (0) downwards on the Y-axis) by month; Bottom panel: Resuspension-driven B/P flux potential of POC from the water to the sediment throughout the year measured during flume experiments at critical erosion velocity; the consistently negative values indicate that the overall flux direction does not change, only its magnitude

2.3.2 Intra-annual periodic variation in drivers of B/P exchange

2.3.2.1 DM flux (of DIN)

Intra-annual patterns of DM B/P exchanges and the variables driving it (as identified in Chapter 1 and Rühl *et al.* 2020, see Table II) were investigated by focusing on DIN flux as an example.

2.3.2.1.1 Biological-mixing driven DM B/P exchange

There were no significant differences between the different periods (ANOSIM, R = 0.602, p = 0.003; see Appendix A, 2d, test 7; OPLS, R2X = 0.694, R2Y = 0.971, Q2Y = 0.623, pR2Y = 0.15, pQ2Y = 0.2; Appendix A, 2e, model 2). The OPLS model did however highlight a distinction between two groupings, winter and pre-bloom *versus* bloom to autumn periods, due to the rates of biological mixing being significantly larger in the second group than in the first. Variables of influence on the intra-annual variability of biological mixing were not only bioturbation activity and BPc, but also the water temperature at depth (as warmer temperatures lead to higher levels of faunal activity (Kinne, 1970) and mean sediment grain size in the top 0-1 and 1-2 cm. The latter parameter may be related to biological mixing conversely to what the model suggests as it is known that biogenic sediment mixing can alter grain size distribution (Ginsburg and Lowenstam, 1958).

2.3.2.1.2 Advective flushing driven DM B/P exchange

Significant differences in advective flushing could be found between periods (ANOSIM, R = 0.891, p = 0.0001; see Appendix A, 2d, test 8; OPLS, R2X = 0.657, R2Y = 0.775, Q2Y = 0.655, pR2Y = 0.05, pQ2Y = 0.05; Appendix A, 2e, model 3). The potential for advective flushing was higher in the colder half of the year (autumn and winter) when sediment density below the surface is lower and waves are higher and have longer peak periods and durations. This is a simple physical effect, wherein stronger shear stresses caused by increased wave action, in a less densely packed sediment, are more likely to lead to advective flushing.

2.3.2.1.3 Bioirrigation driven DM B/P exchange

A significant intra-annual difference in bioirrigation, and factors affecting bioirrigation levels, could be found between periods (ANOSIM, R = -0.446, p = 0.0013; see Appendix A, 2d, test 9; OPLS, R2X = 0.476, R2Y = 0.76, Q2Y = 0.417, pR2Y = 0.15, pQ2Y = 0.05). The OPLS indicated that the periodic variability of bioirrigation may be a product of the benthic animals' rates of activity, which is higher when more or larger animals live at elevated temperatures (water temperature VIP > 1, see Appendix A, 2e), such as the conditions from bloom time to autumn provide.

2.3.2.1.4 Diffusive flux driven DM B/P exchange

There were significant differences in diffusive flux and factors affecting diffusive flux between periods (ANOSIM, R = 0.875, p = 0.0002; see Appendix A, 2d, test 10). The OPLS model also showed a clear separation between the periods with only minor overlap between winter and pre-bloom (OPLS, R2X = 0.954, R2Y = 0.975, Q2Y = 0.87, pR2Y = 0.05, pQ2Y = 0.05; Appendix A, 2e, model 5). The OPLS highlights a grouping of winter to pre-bloom periods as well as post-bloom and autumn periods and a slight overlap of the bloom period into July, which was classed as post-bloom period. Factors shaping the model were O_2 and Nitrite concentration at depth and the density of the top 0-1 and 1-2 cm layers of sediment. Nutrient concentrations in the water column are known to fluctuate, driven by a depletion-replenishment cycle coupled to the pelagic phytoplankton bloom (Aiken *et al.*, 2004; Smyth *et al.*, 2010). The resulting concentration gradient between pelagic and benthic environments is what seems to be driving the intra-annually variable diffusion of solutes across the sediment-water boundary.

2.3.2.1.5 Physical resuspension driven DM B/P exchange

Overall, no significant difference in physical resuspension between the periods could be detected (ANOSIM, R=0.899, p=0.0001; see Appendix A, 2d, test 11), but the OPLS model showed some grouping and separation of the different periods (OPLS, R2X = 0.901, R2Y = 0.982, Q2Y = 0.959, pR2Y = 0.05, pQ2Y = 0.05; Appendix A, 2e, model 6). There was however an observable difference between winter, pre-bloom and autumn periods *versus* bloom and post-bloom, with a higher potential for physical resuspension in the former group. As the model was shaped by hydrodynamic factors (wave period and duration; tidal flow) this may be attributable to the higher amounts of dynamic energy and shear stress the seabed is exposed to in winter, pre-bloom and autumn. The hydrological environment at L4 is known to be more dynamic in winter, when the water column isn't stratified and storm events are more frequent and stronger (Smyth *et al.*, 2010; NNRCMP, 2019).

2.3.2.1.6 Net DM B/P exchange

Based on the results detailed above, the relative importance of the five drivers of benthic-pelagic solute exchange varies throughout the year. Physical resuspension and advective flushing are dominating the exchange in winter, diffusion is most influential during pre-bloom, and biological mixing and bioirrigation dominate starting during the bloom but most importantly in the post-bloom period. The dominance switches from physical to biological drivers early on in the bloom, and back again mid-way through autumn (see Figure 7). B/P exchanges are more difficult to characterize during the resulting inflection periods, as multiple drivers interact with similar intensity and need to be considered in interaction with one another.

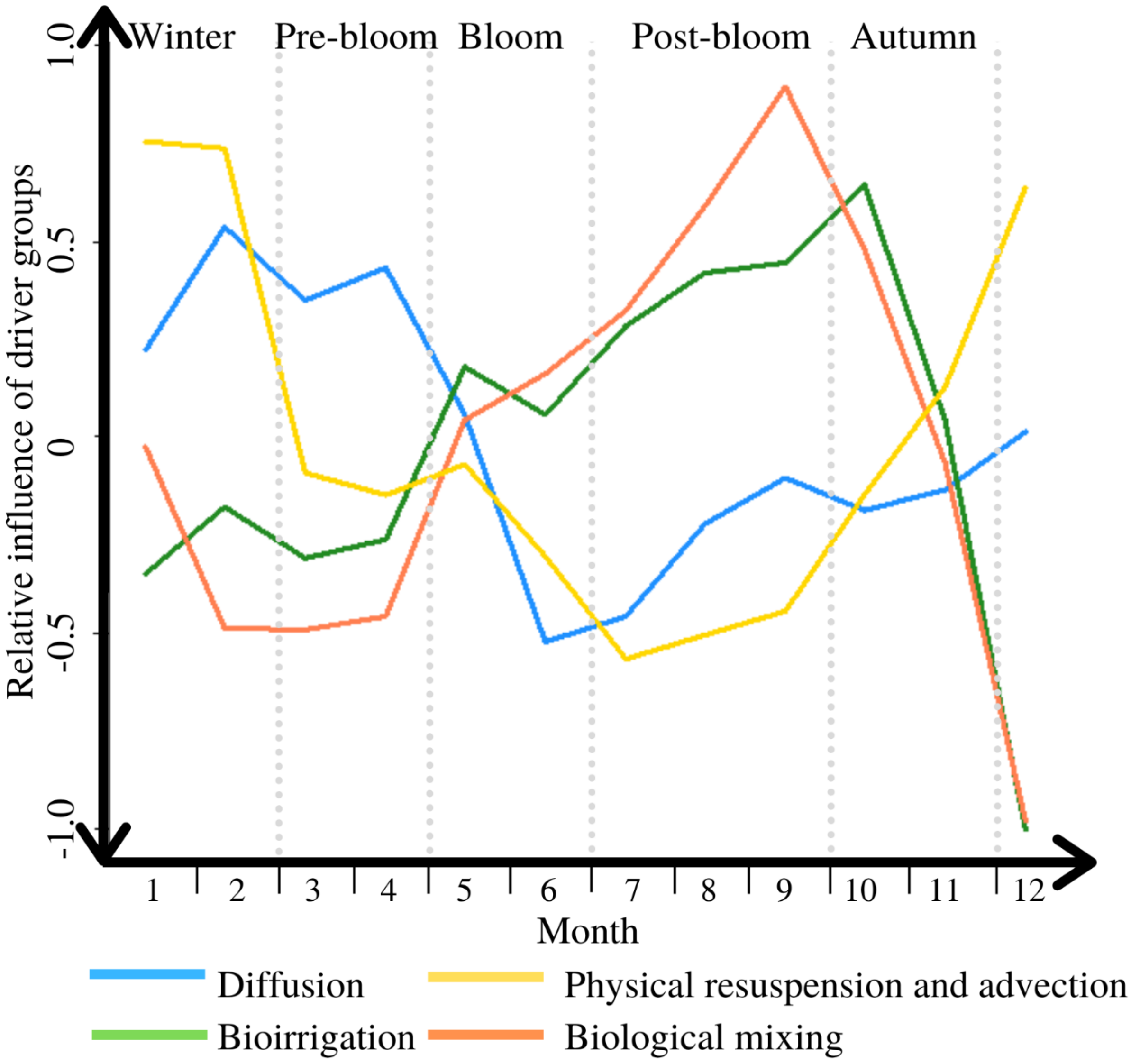

Figure 7: The variable influence of the DM exchange drivers throughout a typical year, between 1 = completely dominant, and -1 = irrelevant; periods are marked through light grey vertical dotted lines

As advectively driven and physical resuspension-driven B/P DM flux were both dominated by hydrodynamic elements, these two drivers shared the same pattern of intra-annually variable impact relative to the other drivers.

The inter-play of physical and biological drivers of DM B/P exchange throughout the periods leads to a distinct cycle of directional changes between upward and downward DM fluxes (see Figure 8).

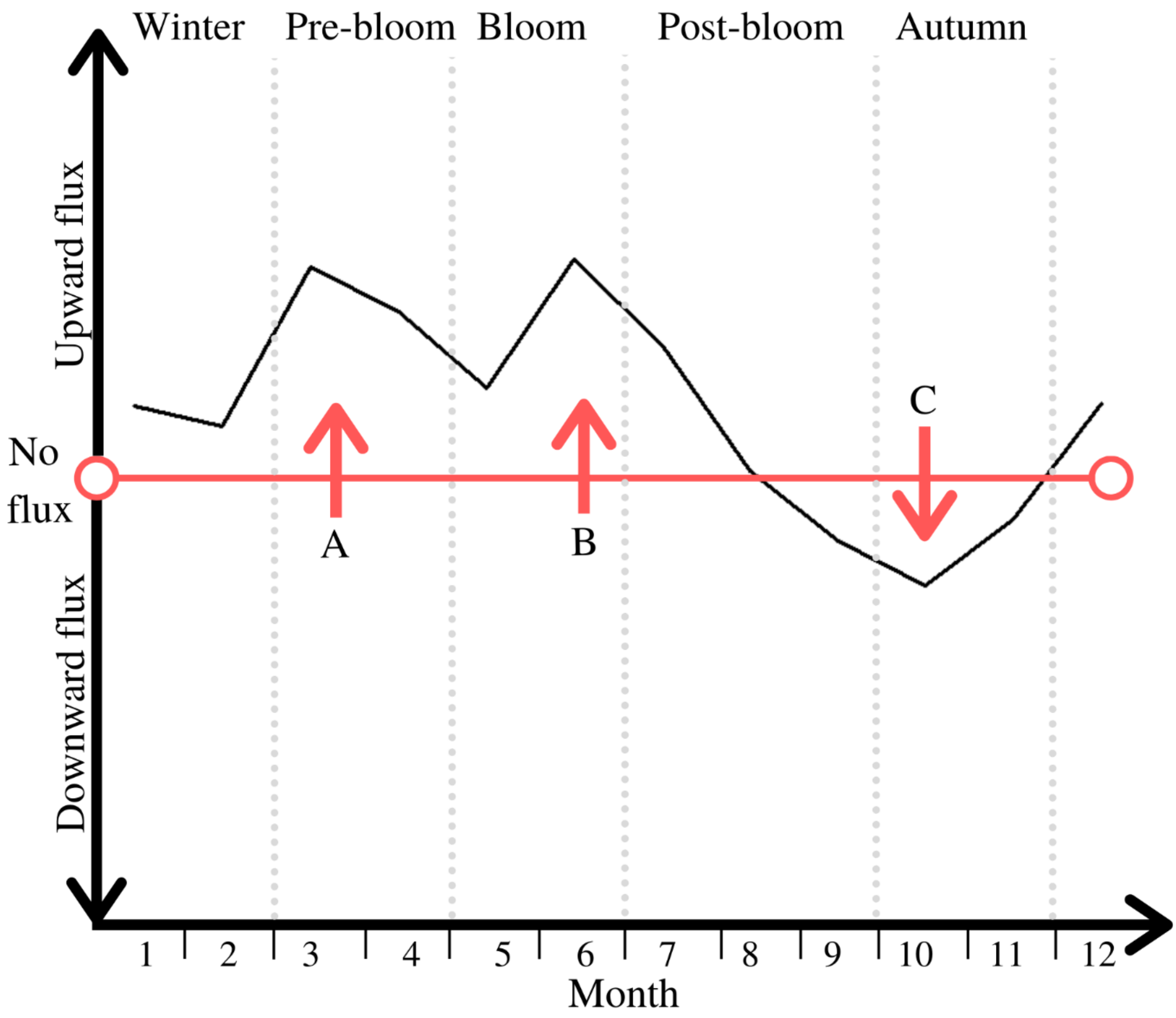

Figure 8: Direction of net DM B/P exchange throughout the five periods; periods are marked through light grey vertical dotted lines; notable peaks are labelled A, B and C

The first peak in this cycle (see peak A in Figure 8) is an upward flux of DM, likely shaped by diffusion driven fluxes (see Figure 7). Advective and physical resuspension drivers may also play a role in this overall upward flux, through for example the physical flushing out of buried DIN, though less so than diffusion (see Figure 7). Nutrients from the organic matter that had been deposited on the seafloor in the previous bloom period have been mostly remineralised at this time of year (Hansen *et al.*, 1981). Low concentrations of dissolved O_2 in late summer and autumn can inhibit nitrification processes but throughout the winter, well mixed conditions facilitate optimal conditions for DIN replenishment (Boynton *et al.*, 2017). The resulting nutrient concentration gradient between seafloor and water column prompts this upward flux, and coupled with the high levels of hydrodynamic energy and river flow in winter and pre-bloom periods, this leads to the replenishment of nutrients in the water column (Justic *et al.*, 1995; Barnes *et al.*, 2015).

The upward directed flux starting during the bloom period and lasting half-way into post-bloom (see peak B in Figure 8) is associated with the phytoplankton bloom in the water column as this is known to deplete pelagic nutrients, thus facilitating a replenishment from benthic sources and therefore upward flux (*e.g.* Howarth, 1988; Cullen *et al*., 1992). Lastly, the direction of DM B/P exchanges changes in post-bloom and a peak period of downward directed DIN transport occurs in autumn (see peak C in Figure 8). This corresponds to the biogenic uptake of DM through biological mixing and bioirrigation, and subsequent incorporation of DM in the benthos. Biological activity is at its peak during this time (see Figure 7), and has thus the greatest impact on the direction and magnitude of overall DM B/P exchange processes.

2.3.2.2 POC flux

Intra-annual patterns of PM B/P exchange and the variables driving it (as identified in Chapter 1; see Table II) were investigated for the example of POC flux.

2.3.2.2.1 Upward transport and resuspension of particulates

There are significant periodic intra-annual differences in the factors that directly and indirectly influence resuspension (ANOSIM, R = 0.708, p = 0.0001; see Appendix A, 2d, test 12; OPLS, R2X = 0.449, R2Y = 0.775, Q2Y = -0.241, pR2Y = 0.15, pQ2Y = 0.5). The OPLS model fit was shaped most distinctly by wave height, period and duration, closely followed by critical shear stress and sediment density.

However, sedimentary POC content, bottom water POC concentration, and bioturbation depth also played a role (see Model 7 VIP scores in Appendix A, 2e). This indicates that variations in the resuspension and upward transport of PM are affected by both hydrodynamic and biological parameters. Considering that the L4 environment has been shown to be more biologically active in the warmer half of the year (Smyth *et al.*, 2015) and that wave heights, peak periods and durations are typically higher in the winter months (NNRCMP, 2019), it can be assumed that the hydrodynamics are driving PM upward fluxes in winter and biological drivers take over in summer.

2.3.2.2.2 Downward transport and deposition of particulates

There were strong periodic intra-annual differences in PM deposition (ANOSIM, R = 0.934, p = 0.0001; see Appendix A, 2d, test 13), however the OPLS model did not show a clear Periodic separation (OPLS, R2X = 0.604, R2Y = 0.57, Q2Y = -0.222, pR2Y = 0.7, pQ2Y = 0.345). The model fit was most strongly driven by tidal flow, followed by suspended matter and POC concentrations throughout the water column at all depths except the one closest to the seafloor. Water temperature and river flow also played a role (see Model 8 VIP scores in Appendix A, 2e). When all factors that directly or indirectly drive PM deposition are considered, bloom and post-bloom periods are distinct from the others as times of higher deposition rates. In the model, pre-bloom and bloom times were separated from the others. The main reason for this divide is that during these two periods, a larger amount of suspended particulate matter and less dynamic hydrographic forces are present in the water column than at other times in the year. Overall this suggests that depositional flux at this site is proportional to the amount of suspended material: the more suspended matter there is the more can be deposited. There are large inputs of suspended matter into the water column through pelagic primary production in summer and riverine and resuspension input in winter (Dobrynin *et al.*, 2010; Widdicombe *et al.*, 2010). This is likely the reason, why no significant periodic intra-annual variation in downward B/P flux could be identified: although the flux is unlikely to be constant, it is largely independent of the periods as there is always some material in suspension. To focus more specifically on POC, SPM concentrations (which include both organic and inorganic particulates) were excluded and the model run was repeated. The resulting OPLS showed a clear separation between pre-bloom, bloom and post-bloom periods while autumn and winter periods were separate from the rest but grouped together (OPLS, R2X = 0.749, R2Y = 0.865, Q2Y = 0.048, pR2Y = 0.15, pQ2Y = 0.3). This model was still influenced by POC concentrations at 0, 20, 30 and 40m depth, but also by tidal and river flow, wave height, chlorophyll a concentration and zooplankton abundance (see Appendix A, 2e, Model 8a for VIP scores). This indicates that diel vertical migration, based on the additional copepod data most likely of copepods, in relation to the phytoplankton bloom reflected in the chlorophyll data plays a role in POC deposition, in addition to the factors previously mentioned to be impacting POC concentration in the water column and thereby the potential for downward transport and deposition.

2.3.2.2.3 Net PM B/P exchange

Overall these results indicate that inter-periodic differences in benthic-pelagic POC exchange at L4 are reflected in both deposition and resuspension. Comparing the intra-annual temporal variation in the net upward and downward fluxes, shows that the two alternate in terms of relative importance throughout the year (see Figure 9).

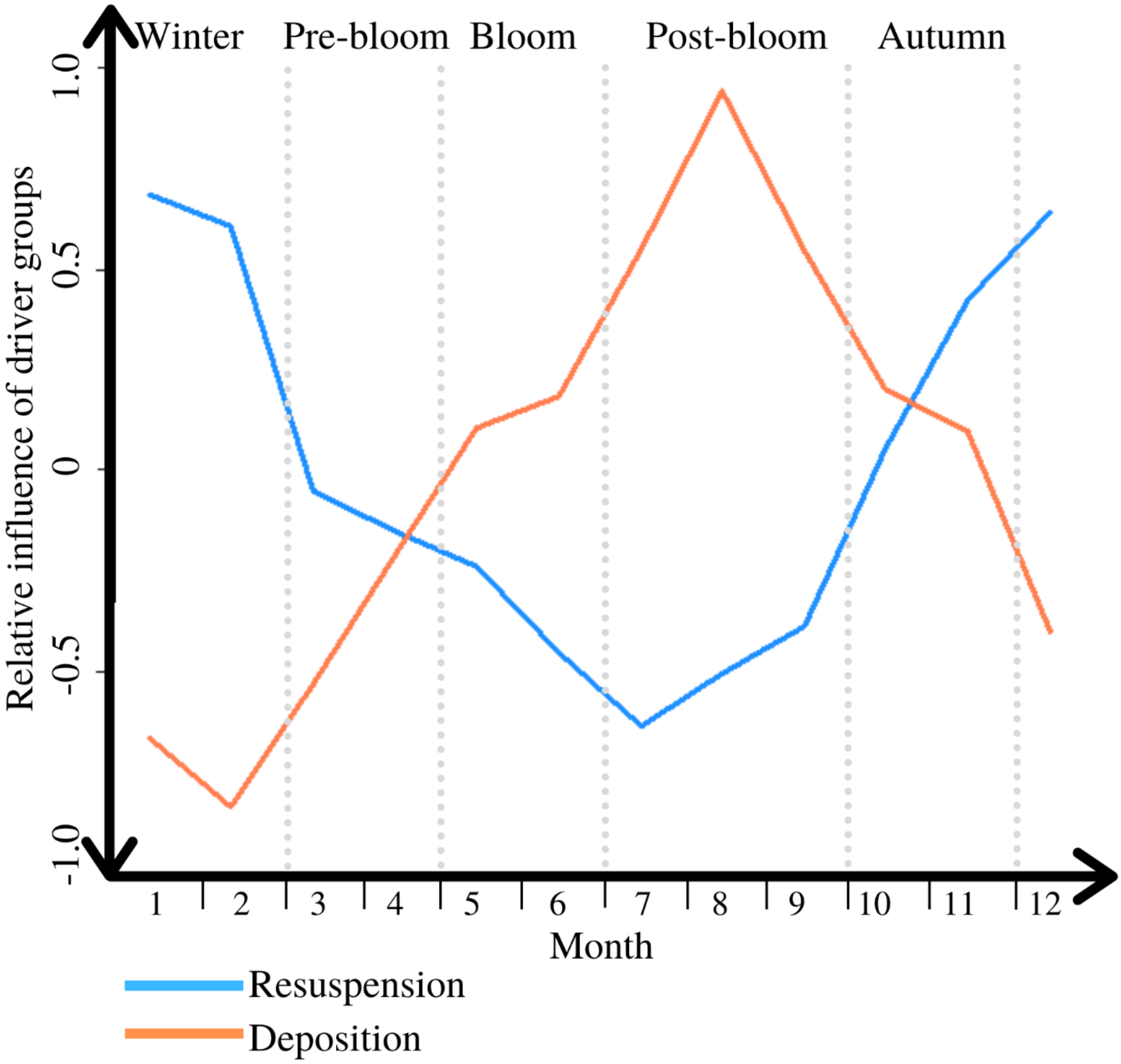

Figure 9: The variable influence of the dominant direction of PM exchange through the interactions of its two driver groups throughout a typical year, ranging from 1 = completely dominant, to -1 = irrelevant; periods are marked through light grey vertical dotted lines

As with DIN exchange, there is a divide in PM B/P exchange drivers between the colder and the warmer halves of the year. The switch between net upward and downward transport through the alternation in relative importance of deposition and resuspension throughout the year lead to a different cyclical pattern in the overall direction of exchange than that of DM exchange (see Figure 10).

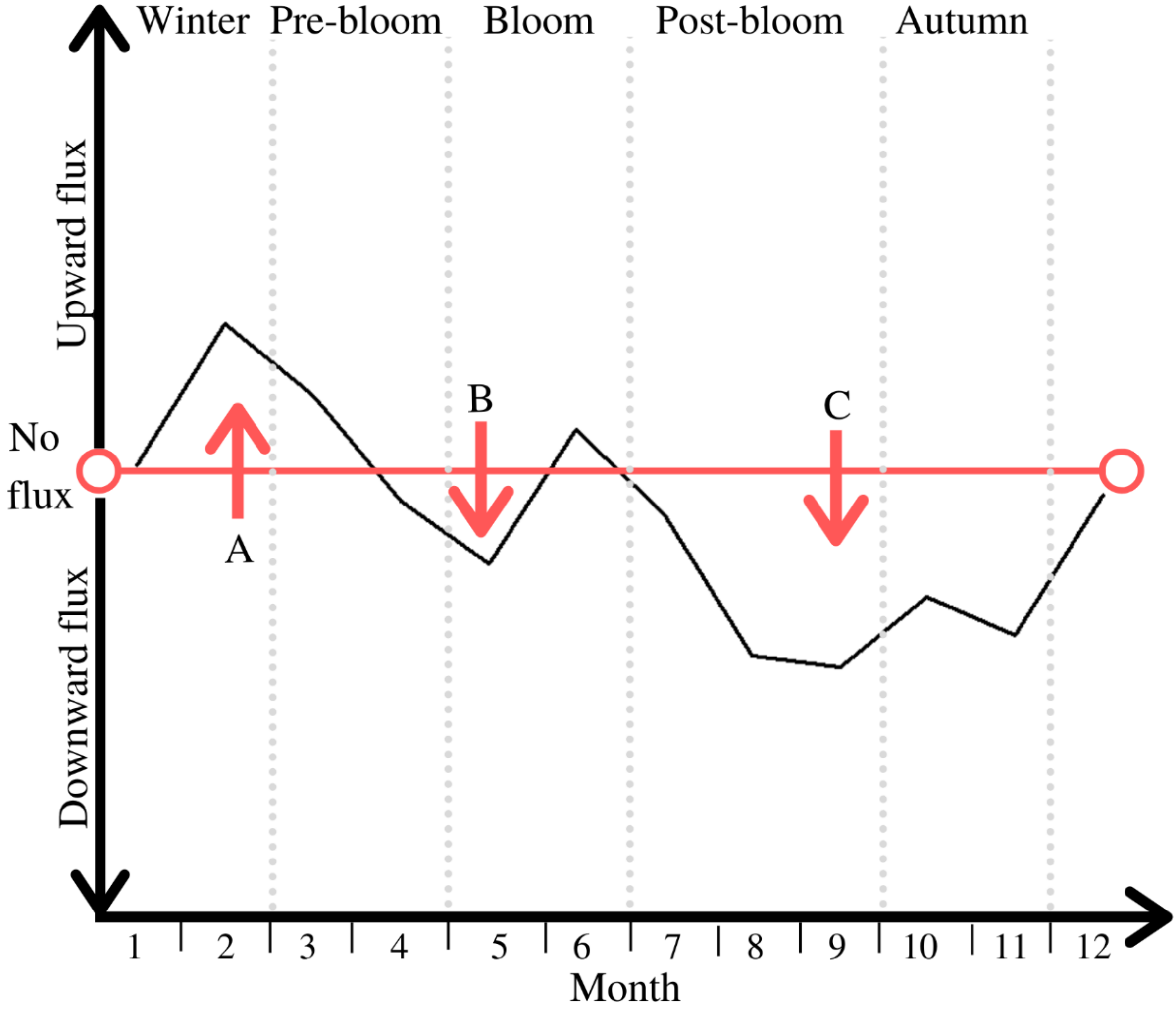

Figure 10: Direction of net PM B/P exchange throughout the five periods; periods are marked through light grey vertical dotted lines; notable peaks are labelled A, B and C

Unsurprisingly, there is a general upward flux of PM during winter and into the pre-bloom period (see peak A in Figure 10). As this lessens throughout pre-bloom, the particulates placed in suspension in winter sink downward again, leading to an overall downward flux prior to the bloom (see peak B in Figure 10), Another peak of deposition follows during the post-bloom period and into autumn, reflecting the organic matter generated in the bloom being deposited on the seafloor (see peak C in Figure 10). This downward-directed PM flux also represents POC burial during this time, as reflected in the POC distribution patterns within the sediment during that time (Figure 6).

2.3.2.3 Interactions between DM and PM exchange

The only DM driver whose inter-periodic variability was enhanced through the focus on those factors which were also affected by PM exchange (see Table II) was biological mixing (ANOSIM, R = 0.571, p = 0.0002; see Appendix A, 2d, test 14). Intra-annual variability of the variables driving physical resuspension- (ANOSIM, R = 0.805, p = 0.0003; see Appendix A, 2d, test 15) and bioirrigation-driven DM exchange (ANOSIM, R = 0.4, p = 0.014; see Appendix A, 2d, test 16), which were overlapped with variables driving PM B/P exchange, was reduced. Diffusion- (ANOSIM, R = 0.875, p = 0.0002; see Appendix A, 2d, test 17) and advection-driven exchanges were unaffected (ANOSIM, R = 0.739, p = 0.0001; see Appendix A, 2d, test 18). Drivers of DM exchange were expected to affect more aspects of PM deposition than PM resuspension. This is because they affect only the biological factors playing into each of them, and while particle deposition is driven almost equally by biological and physical factors, resuspension is more heavily driven by physical factors. Hence, the analysis of secondary intra-annual patterns in the form of only those drivers affected by solute exchange revealed that while both main drivers still displayed intra-annual temporal patterns, differences between individual periods were not significant in PM resuspension (ANOSIM, R = 0.4, p = 0.009; see Appendix A, 2d, test 19) but highly so in PM deposition (ANOSIM, R = 0.887, p = 0.0001; see Appendix A, 2d, test 20). This shows that while DM exchange plays a role in the intra-annual variation of PM deposition, it does not much affect that of resuspension.

2.4 Discussion

The results presented in this study represent the first time a diverse array of physical, chemical, meteorological and biological data have been combined to identify and quantify the various processes that drive intra-annual variation in B/P coupling in a coastal shelf sea. This allowed us to determine the interactions and trade-offs that underpin the net fluxes of PM and DM in temperate coastal ecosystems, throughout the period of a year.

The results of this study revealed clear intra-annual periodic patterns in both DM and PM B/P exchange drivers and processes, and identified the environmental variables which have the most influence on these patterns in each instance. In the case of DM B/P exchanges, three peak periods of exchange were identified. Firstly an upward flux in pre-bloom period, driven by high levels of diffusive flux due to a concentration gradient between benthos and pelagic following a period of thorough water column mixing in the previous period. The supply of nutrients from the benthos to the water column during this time of year fuels the formation of the phytoplankton bloom in the following period (Rees *et al*., 2009).

The second upward flux, during the bloom period, is driven by high rates of biological activity in response to increased temperatures and the beginning of the pelagic phytoplankton bloom. Gradual nutrient depletion of pelagic nutrient levels in this period creates a concentration gradient and perpetuates the continued domination of upward-directed DM B/P exchanges (Smyth *et al.*, 2010). Thirdly, a downward flux was detected in autumn. This was found to be influenced by a combination of biological and physical drivers, including high rates of biological mixing and bioirrigation, and an elevated potential for advective flushing due to low sediment densities in an increasingly hydrodynamic environment. This is likely connected to the bioirrigation and biological mixing-driven downward draft of DIN released from particulate organic matter deposited during the plankton bloom (Kristensen and Hansen, 1995). The high concentrations of DIN detected near the seafloor throughout the autumn are a sign that the turning point of this downward peak is reached, when the benthic remineralisation leads to the emergence of DIN from the sediment into the water column through advective flushing (Kristensen, 1988).

PM B/P exchanges on the other hand exhibited a clearly physically driven upward flux in winter, driven by the physical resuspension of material from the seafloor and prevention of SPM settling through the highly hydrodynamic conditions at this time of year (Jago *et al.*, 1993; Jones *et al.*, 1998; Dobrynin *et al.*, 2010). This was followed by a biologically driven downward flux in the bloom period, during which particulates produced in the pelagic phytoplankton bloom were starting to be deposited on the seafloor. Biogenic vertical transport through zooplankton feeding and migratory activity is likely to intensify the downward flux during this time (van Duyl *et al.*, 1992; Packard and Gómez, 2013). The small instance of upward PM flux during the bloom, between peaks B and C could be attributed to biogenic sources of resuspension, as physical drivers of B/P exchange were not of importance during this time of year. The source of this could for example be zooplankton activity (Eloire *et al.*, 2010) or the ejection of benthic particles, larvae or gametes from the benthos (*e.g.* Bass and Brafield, 1972). The third notable feature in the intra-annual PM B/P exchange cycle was another peak period of downward flux throughout post-bloom and autumn. Though initially driven purely biologically, by the continued deposition of pelagic organic matter and influenced by migratory zooplankton activity, some hydrological influences also played a role in this period of net deposition. Drastic increases in river and tidal flow, and hydrodynamic energy in this period, are likely to cause an influx of PM from fluvial and terrestrial sources, as well as the mobilisation of freshly deposited material, thereby increasing the potential for PM deposition (Lampitt *et al*., 1993; Milliman and Farnsworth, 2013). The downward flux of PM in the autumn period is likely not limited to exchange processes directed from pelagic to benthos, but also encapsulates exchanges within the sediment matrix. By autumn time, the POC deposited on the sediment surface after the pelagic phytoplankton bloom has been buried and while what was left at the surface has been depleted already, deeper layers are still saturated (Middelburg *et al.*, 1993). In addition to this, sediment density was recorded to be lowest in winter and autumn periods, while hydrodynamic energy was highest. This is due to the higher levels of physical resuspension and flushing, leading to the winnowing of small particles, resulting in increased pore spaces between grains. The lowered density is likely to cause some advective flushing of POC into the sedimentary pore spaces (see *e.g.* Ehrenhauss and Huettel, 2004).

The intra-annual patterns detected in this study, in the direction and magnitude of net DM and PM B/P exchange processes, and in the relative influences of the various drivers thereof, provide useful information to further our understanding of biogeochemical cycling and ecosystem functioning. For example, while seasonal nutrient depletion through pelagic bloom events and subsequent replenishment from benthic sources is a well-known phenomenon (*e.g*. Smyth *et al*., 2010), the insight provided in this study into the relative importance of the various potential drivers of the latter, aids our understanding of the overall process. Taking into account the periodic variability of drivers and processes in temperate environments provides a temporal context for *in-situ* measurements and sampling campaigns. The timing and duration of the periods may vary slightly between years, but the characteristics of each remain the same, and thus the overall patterns in B/P exchange drivers and processes hold up throughout any given year.

Previous studies of intra-annual patterns in B/P coupling have in many cases centered on the biological drivers of exchange such as phytoplankton bloom events (*e.g.* Graf, 1992; Tonkin *et al.*, 2017). This placed the focus on downward fluxes and the more biologically active half of the year. In turn, studies that did focus on intra-annual variability in hydrodynamically and physically driven B/P transport, often broadly neglect biological contributions, including only pelagic primary production (*e.g.* Jones *et al.*, 1998). There have been attempts to integrate biological and non-biological drivers of B/P coupling in estuaries (*e.g.* Ubertini *et al.*, 2012) or at very shallow sites (*e.g.* Chipman *et al*., 2012) and through modelling (*e.g.* Lee *et al.*, 2002). This however, is one of the first studies to take both aspects into account in a coastal environment, and to consider the interactions between biological and physical drivers of B/P exchanges throughout a full intra-annual cycle.

Single variable driver-process relationships, independently significant as each of them may be, need to be assessed in context of one another to recognise the true relative importance of each individual driver at the ecosystem scale. By investigating multiple drivers simultaneously and in relation to each other, the current study facilitates the identification of the most important driver-process relationships in the context of intra-annual variation in DM and PM B/P fluxes. Our current understanding of benthic-pelagic exchange processes is largely based on short-term investigations of specific B/P coupling pathways, often within a single period or focused on the more biologically active half of the year (although there are some exceptions such as Chipman *et al*., 2012). From this we know that in winter, wave action and current flow can lead to resuspension and advective flushing events (Lou *et al.*, 2000; Tengberg, *et al*., 2003; Kassem *et al.*, 2015), especially during storm events (Jago *et al.*, 1993; Madsen *et al.*, 1993; Corte *et al.*, 2017). It is also known that pelagic primary productivity and specifically the deposition of organic matter from phytoplankton blooms is a major driver of benthic biological activity (Gooday *et al.*, 1990; Zhang *et al.*, 2015). The current study investigates not only how each of these processes varies throughout a full intra-annual cycle, but also the interactions between them to evaluate their relative influence and find the short-term temporal patterns in the direction and magnitude of net B/P exchanges. From this, annual net B/P fluxes may also be derived.

In different environments, the relative importance of each of the drivers may vary but the core mechanics remain the same (*e.g.* animal activity is more heavily driven by temperature variations in temperate regions and more by food availability in Arctic regions; Brockington and Clarke, 2001). Phenological patterns differ between locations and must be identified in each case to allow the appropriate definition of two or more periods which may occur throughout the year. One good way to identify such patterns, if resources and local infrastructure allow it, is the establishment of time series data collections that include multiple long-term complementary data sets at the same site. Where such approaches are not feasible, existing time-series collections at approximately comparable locations may be used as reference by which to judge the validity of short-term intra-annual patterns found in one-off data collections. An example of this would be to use data from the Helgoland Roads time-series, to back up physical or biological measurements from other regions in the southern North Sea. By considering phenological and meteorological cycles and the state of the environment at the moment of investigation, field sampling and experimental designs of future studies can start off more well-informed and avoid miss-guided conclusions based on for instance differences in sampling period throughout a study. The result will be a higher level of comparability and cohesion between studies, and an ultimately better understanding of B/P exchange.

Indications of flux timing and directions as portrayed in this study are based on a typical year's conditions, but there are multiple drivers which may at any time sway the balance one way or another. Extreme events such as uncharacteristically long or plentiful phytoplankton blooms or particularly stormy years can be enough to swing the balance between upward and downward fluxes of DM and change the timing of peaks and times of overlap between DM and PM B/P exchanges (Madsen *et al.*, 1993; Zhang *et al.*, 2015; Masselink *et al.*, 2016). Interactions between dissolved and particulate matter exchange processes detected in this study are in accordance with existing literature which documents for example increased PM deposition through nutrient resuspension-fuelled peaks in primary production (Fanning *et al.*, 1982), triggering and exacerbation of DM exchange processes through PM resuspension (Tengberg *et al*., 2003) and enhanced rates of biological mixing and bioirrigation potentials driven by the deposition of particulate organic matter (*e.g*. Brockington and Clarke, 2001).

2.5 Conclusion

DM and PM B/P exchange processes vary on a short-term intra-annual temporal scale in both magnitude and dominant direction of exchange. Biological, physical and biogeochemical factors drive this temporal variation, and while biological variables were overall more dominant in the warmer months and physical drivers dominated in the colder months, there were significant periods of overlap during which several drivers affected the exchange processes interactively. These relationships between individual environmental variables and B/P exchange drivers and processes, identified in this study, further our understanding of B/P connectivity by providing a temporal ecological context. Future studies of biogeochemical cycles, or other ecosystem processes, will be able to utilise this contextualisation, to better understand short-term intra-annual ecosystem variability.

Chapter 3

Decadal patterns and trends in benthic-pelagic exchange processes

Chapter 3

Note: This chapter contains an original study, which is currently in review for publication in Progress in Oceanography (Rühl, S., Thompson, C., Queirós, A., Widdicombe, S. (in review), Decadal patterns and trends in benthic-pelagic exchange processes, *Progress in Oceanography*). Author contributions: SR analysed the data and wrote the manuscript; CT, AQ and SW feedback and improvements to the manuscript throughout the writing process and while it was under review for publication.

3.1 Introduction

Locally, B/P exchange of DM and PM are temporally variable, as the multitude of drivers they depend on are shaped by environmental change, on hourly to centennial time scales. On the shortest end of this time scale are tidal and diurnal cycles, which can, for example, affect suspended matter concentration in the water column (Widdows *et al.*, 2004) or benthic photosynthesis (Revsbech *et al.*, 1983). As demonstrated in Chapter 2, seasonal variability strongly influences B/P coupling processes, such as biologically driven exchanges, especially in temperate coastal environments (*e.g.* Graf, 1992). On an inter-annual basis, extreme meteorological or phenological events can be a source of environmental variation (*e.g*. Kendon, 2015; Zhang *et al.*, 2015). Factors such as an extreme positive or negative North Atlantic Oscillation (Hurrell *et al.*, 2003) or El Niño and La Niña phases (Philander, 1989), expressed on multi-annual and multi-decadal scales can, for example, have profound effects on storm magnitude and frequency (Keim *et al.,* 2004), and on other meteorological phenomena (Pozo-Vázquez *et al.*, 2005), all of which have the potential to affect B/P exchange processes. On even larger time scales, processes such as global climate change (Paek *et al.*, 2013; IPCC, 2019) may affect long-term patterns in B/P exchange drivers, and thus be detectable in B/P exchange trend analyses. Climate change affects temporal trends in primary production (Chavez *et al*., 2011), storm frequency and magnitude (Collins and Sutherland, 2019), eutrophication (Griffiths *et al.*, 2017) and benthic fauna and meroplankton community structure and condition (Kirby *et al.*, 2007), amongst others. This multitude of variability, occurring over various temporal scales, makes it difficult to determine what is specifically driving B/P exchange at any instant in time, as these different scale cycles and trends overlap and interact, and if one of them is exceptionally strong, it can overwhelm others.

Datasets including multiple B/P exchange drivers, capturing their variability, and at sufficient temporal resolution and coverage to assess B/P processes at the necessary range of scales are thus exceptionally rare. In this study, one such dataset was assessed. A ten year time series was collated, including data gathered as part of various programmes undertaken at the Western Channel Observatory (WCO), a benthic-pelagic long-term monitoring station offshore of Plymouth, UK (see Chapter 1; Smyth *et al.*, 2015). Data were analysed with two aims. 1) Assess connections between inter- and multi-annual trends of B/P exchange drivers, and patterns of B/P exchange processes, to identify causes of medium-term temporal variability. 2) Characterise the nature and drivers of multi-annual temporal patterns at the study site. The wider implications of these temporal patterns were then contextualised at a regional scale, as the nature of this unique data set, in both temporal longevity and breadth of available parameters, facilitates insights into the functioning of other temperate marine ecosystems.

3.2 Methods

3.2.1 Study site

The study uses data from L4, the main station of the WCO (Smyth *et al.*, 2015), as introduced in Chapter 2, Section 2.2.1 (50.25°N; 4.22°W, see Figure 3).

3.2.2 Datasets

In this study, pelagic and benthic data collated from L4 between 2009 and 2018 was analysed, covering the broadest range of available data for the area. The data were recorded at a variety of temporal resolutions, and reduced to monthly resolution for increased comparability. To this end, data which had been collected with higher resolution were aggregated using monthly averages (mean).

Additional data were sourced from the Met Office (Met Office, 2019; see PML and Rame Head markers in Figure 3); the National River Flow Archive (NRFA, 2019; see Gunnislake marker in Figure 3); the Permanent Service for Mean Sea Level (PSMSL, 2019; see Devonport marker in Figure 3); and the Looe Wave buoy (NNRCMP, 2019; see Looe marker in Figure 3). These sources provide important contextual information on the weather conditions, riverine input, wave conditions and tidal state, all of which have previously been shown to affect conditions at L4, and Plymouth Sound more widely (including influences on zooplankton community composition (Eloire *et al.*, 2010); benthic nutrient supply (Leynaert *et al.*, 2011); salinity, temperature and suspended matter influx (Siddorn *et al*., 2003; Milliman and Farnsworth, 2013); and phytoplankton abundance and biomass (Barnes *et al.*, 2015); *etc*.). Sea surface variables were included, as the connection between the benthos and pelagic are well established for L4 (Tait *et al.*, 2015; Zhang *et al.*, 2015;

Queirós *et al.*, 2019), despite seasonal stratification (Smyth *et al.*, 2010; Tim Smyth *et al.*, 2015). A complete list of the data sets used in this study are detailed in Table III.

Table III: List of Data sets included in this study and their respective temporal availabilities, sources as well as sampling locations and depths, as measured from the water surface down (maximum water depth at L4 = 54 m)

Variable	**Temporal availability**	**Data source**	**Sampling location**	**Water depth**
Particulate Organic Carbon (POC)	2009-2013	WCO	L4	10 m
Total Particulate Carbon (TPC)	2009-2013	WCO	L4	10 m
Total Particulate Nitrogen (TPN)	2009-2013	WCO	L4	10 m
Particulate Organic Nitrogen (PON)	2009-2013	WCO	L4	10 m
Coloured dissolved organic matter (CDOM)	2009-2013	WCO	L4	10 m
Suspended particulate matter (SPM)	2009-2013	WCO	L4	10 m
Oxygen (O_2)	2009-2017	WCO	L4	50 m
Phytoplankton abundance and biomass	2009-2015	WCO	L4	10 m
Zooplankton abundance	2009-2016	WCO	L4	10 m
Meroplankton abundance	2009-2018	WCO	L4	10 m
Copepod abundance	2009-2018	WCO	L4	10m
Benthic macrofauna abundance and biomass	2009-2018	WCO	L4	54+ m (sediment)
Fluorescence	2010-2016	WCO	L4	50 m
Chlorophyll a	2010-2016	WCO	L4	10 m
Rainfall	2011-2013	MET station	Rame Head / PML	N/A
Max wave height, T_{peak} and T_z	2009-2017	Looe buoy	Looe (50.203°N / 4.246°W)	Sea surface
Water temperature	2010-2016	WCO	L4	50 m
Salinity	2010-2018	WCO	L4	50 m

Sediment grain size	2009-2012	WCO	L4	54+ m (sediment)
River flow	2009-2016	NRFA	Gunnislake (50.531°N / 4.222W)	N/A
Tidal flow	2009-2017	PSMSL	Devonport (50.221°N / 4.111°W)	N/A
Nitrate	2012-2018	WCO	L4	50 m
Nitrate/Nitrite ratio	2012-2018	WCO	L4	50 m
Ammonia	2012-2018	WCO	L4	50 m
Silicate	2012-2018	WCO	L4	50 m
Phosphate	2012-2018	WCO	L4	50 m

Data on community bioturbation potential (BPc) were calculated from WCO macrofauna abundance and biomass inventories, using mobility and sediment reworking indices and methods from Queirós *et al.* (2013) and Solan *et al.* (2004). Data on community bioirrigation potentials (BIPc) were calculated from the same datasets, based on Renz *et al.* (2018) and trait indices derived from Queirós *et al.* (2013) and the Marine Ecosystems Research Project Trait Explorer (Bruggeman, 2019).

3.2.3 Data analyses

The complete data set including all variables is here-after referred to as the "overall data set". Different subsets of variables were also assessed, as contributors to individual drivers of B/P exchange and overall exchange processes (see Appendix B, 3a). The data were split into driver groups by separating and grouping factors identified as influencing the respective exchange processes in Chapter 1 (Rühl *et al.,* 2020). When individual variables were analysed, data were not normalised but when the overall data set, or variable subsets, were analysed in combination to determine patterns in B/P drivers and processes, the data were normalised to ensure equal representation of each of the factors. Each sub-set was analysed as follows.

To address the first aim of the study, temporal patterns in the data were decomposed (into trend, seasonality and random noise created by stochastic events) using Seasonal Decomposition of Time Series by Locally Estimated Scatterplot Smoothing (STL with LOESS; Cleveland *et al.*, 1990). This was applied to the individual variables, overall data set and PM and DM exchange driver and process sub-sets (see Appendix B, 3a, based on Chapter 1; Rühl *et al.*, 2020), as well as each of the driver groups, to more closely investigate temporal patterns in each of the processes. Within STL, seasonality is defined as a cyclically recurring pattern within a set time period (12 months in this case), trend represents a LOESS smoothed moving average of the data set after removal of the seasonal component, and the remainder variation is the result of subtraction of both seasonal and trend components from the original data set. The seasonality at L4 is of an additive nature as can be seen by the unchanging amplitude of the seasonal component (see Appendix B, 3c), so an additive decomposition model was chosen (Ellis and Sax, 2018). The STL model employs LOESS as a smoothing method. The smoother is also applied to infill data regions containing N/A observations, making it unsuitable for application to variables with large N/A occurrence. Because of this, the model was not applied to affected variables (*i.e.* Macrofauna abundance and biomass, BPc, BIPc, sediment cohesion and grain size). Through the STL, impact scores were assigned to each of the decomposed time-series components in the form of percentage ratios of the interquartile ranges of the data. As the allocated values are scalar, these are not comparable between models. They do however facilitate the assessment of the relative importance of seasonality, trend and remainder components across analyses. These analyses were carried out in CRAN R (R Core Team, 2017).

The data were further tested for correlations between temporal patterns in B/P exchange, and patterns in one or more of the drivers of exchange using Pearson's correlation coefficient (Pearson, 1895, carried out in CRAN R) using single variable and B/P exchange driver sub-sets of the data (see Appendix B, 3a), thereby also addressing the first aim of the study. Pearson's correlation coefficient was chosen due to its preferable facilitation of linear relationships over monotonic ones (Schober and Schwarte, 2018).

To address the second study aim, the general temporal structure of the L4 ecosystem was assessed by testing for potential ecosystem level differences across month and year groups within the overall data set using Analyses Of SIMilarity (ANOSIM; vegan package, Oksanen *et al.*, 2019), carried out in CRAN R (R Core Team, 2017). To further define the patterns of inter-annual variability within the overall data set, Orthogonal Partial Least Squares discriminant analysis models (OPLS, ropls package; Thévenot *et al.*, 2015) were carried out. Within the OPLS, the year in which data were collected was applied as the class by which differences between dataset sub-groups were identified. Factors which contributed significantly to the model fit were identified by Variable Influence on Projection (VIP) values > 1. VIP values reflect loading weights of each model components as well as quantifying the variability of the response explained by the components (Mehmood *et al.*, 2012), which enabled the characterisation of potential links between environmental variables and events, and B/P exchange processes and drivers. These analyses were appropriate to data rich in N/A, and were carried out in CRAN R.

Finally, addressing also the second study aim, the data were further split up and tested for inter-annual variation within five phenological and meteorological "periods", as defined in Chapter 2 (see Table I). ANOSIM, OPLS and STL decomposition methods were used as previously described, this time with the aim to assess intra-periodic changes across years. To this end, the overall data set as well as all B/P exchange driver and process sub-sets were analysed, within-period groups. This measure was chosen because it was suspected that the large influence of seasonality on many of the analysed variables may over-shadow other temporal signals.

3.3 Results

3.3.1 Connections between inter-annual variability and multi-annual trends of B/P exchange drivers, and patterns of B/P exchange processes

In order to identify temporal patterns in the overall dataset, each variable was decomposed individually using STL. Details of the relative influence of each of the three time series components on each variable that could be investigated using STL models can be found in Table IV. Many datasets exhibited strong seasonal patterns, with low impact scores for the trend and outlier components (Table IV). Where strong trend contributions were quantified, their pattern appeared to indicate inter-annual variability or multi-annual cycles, rather than long-term trends.

Table IV: Interquartile ranges (IQR) for each of the time series components; higher percentages indicate higher importance of that component, as marked in bold

Variable name	Data set IQR	Seasonal IQR	Trend IQR	Outlier IQR
Temperature	4.0979	**3.8315**	0.8190	0.5048
Wave height	0.4096	**0.4429**	0.1263	0.2900
T_{peak}	2.0239	**1.9381**	0.5265	0.8119
T_z	0.6852	**0.7805**	0.1804	0.3416
Rain fall	0.005471	0.002672	0.001880	**0.003820**
River flow	29.709	**31.140**	6.662	10.811
Salinity	0.13095	0.04904	**0.09250**	0.06756
Tidal flow	80.50	**93.38**	48.09	58.56
Phytoplankton abundance	1574.0	**1637.9**	237.5	921.0
Phytoplankton	35.75	**42.28**	13.00	19.85

biomass				
Zooplankton abundance	3746	**2598**	1711	1613
Fluorescence	0.5301	0.6981	**0.9098**	0.6472
Chlorophyll a	0.8691	**0.6879**	0.2285	0.3432
SPM	1.4431	**1.6179**	0.7664	1.0622
CDOM	2.775	1.877	1.086	**2.329**
Nitrite at 0 m	0.2445	**0.2077**	0.1255	0.1425
Nitrate/Nitrite ratio at 0 m	4.8758	**4.5056**	0.7191	1.0750
Ammonia at 0 m	0.6835	**0.6272**	0.2626	0.3232
Silicate at 0 m	1.6654	**1.3619**	0.3972	0.7358
Phosphate at 0 m	0.24991	**0.22807**	0.05435	0.08038
Nitrite at 50 m	0.27212	**0.20245**	0.06110	0.09803
Nitrate/Nitrite ratio at 50 m	4.9807	**4.2216**	0.8508	0.8539
Ammonia at 50 m	0.9363	**0.8386**	0.2689	0.3370
Silicate at 50 m	1.6508	**1.2915**	0.5932	0.5242
Phosphate at 50 m	0.23436	**0.19906**	0.04285	0.05764
TPC	288.2	**185.8**	175.7	145.9
TPN	48.32	13.53	**32.48**	27.74
POC	260.5	152.3	**320.4**	141.6
PON	22.26	25.48	**26.66**	13.12
O_2 at 0 m	28.196	13.647	8.309	**18.123**
O_2 at 50 m	39.72	17.48	13.85	**19.01**
Meroplankton abundance	701.5	**996.1**	236.9	440.8
Copepod abundance	2514	**1493**	1104	1318

The STL decomposition of PM and DM exchanges indicated that all drivers of PM and (non-diffusion driven) DM exchange were dominated by the seasonal component, whilst diffusion-driven DM exchanges was predominantly explained by stochastic events. Temporal patterns in overall DM exchange were mainly due to seasonality while patterns in overall PM exchange were attributable to the outlier component (see Table V and Figure 11).

Table V: Interquartile ranges (IQR) for each of the time series components; higher percentages indicate higher importance of that component; blue shading indicates DM drivers and processes, orange shading indicates PM drivers and processes

Variable name	Data set IQR	Seasonal IQR	Trend IQR	Outlier IQR
DM exchange overall	0.4984	**0.3896**	0.1736	0.2789
PM exchange overall	0.3646	0.1538	0.1382	**0.2586**
Diffusion-driven DM exchange	0.6072	0.2334	0.3667	**0.3940**
Bioirrigation-driven DM exchange	0.8832	**0.7702**	0.3303	0.4927
Biological mixing-driven DM exchange	0.9928	**0.7416**	0.3840	0.5347
Physically-driven DM exchange	0.5889	**0.6541**	0.1592	0.3761
PM deposition	0.5505	**0.3666**	0.1951	0.3470
PM resuspension	0.4154	**0.3586**	0.1618	0.3534

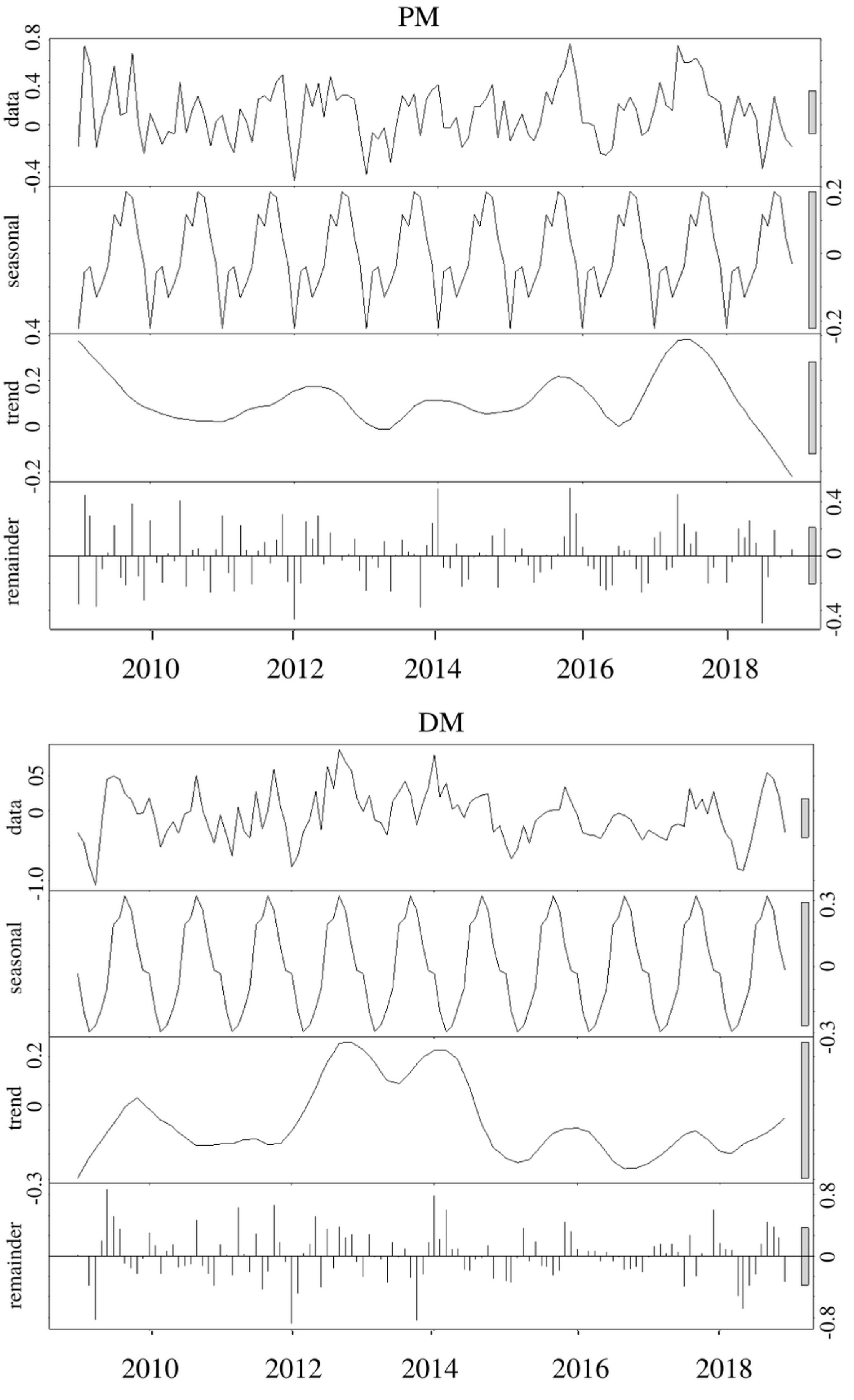

Figure 11: DM flux (top) and PM flux (bottom) time series between 2009 and 2018; Within each of the two plot groups, the original data is displayed on top (data) followed by the seasonal component

(seasonal), trend line (trend) and outliers from the norm (remainder); The grey bars on the right of each of the graphs illustrate their scaling relative to each other and the source data plot at the top.

The trend component of the PM exchange time series displayed a roughly bi-annual cycle (Figure 11, bottom). Similar patterns were found in parameters representative of pelagic primary production, such as phytoplankton abundance and biomass, and so it is possible that this cycle is biologically driven (Appendix B, 3b, Figure 1). The large peak in the overall PM trend between 2017 and 2018 (Figure 11, bottom) is present in the PM deposition data set as well, but not in the PM resuspension data (Appendix B, 3b, Figure 2). This indicates that this effect in the overall PM trend is likely driven by the processes of deposition. Likewise, the apparent bi-annual cycle in the trend component of DM exchange (Figure 11, top) is overshadowed by a double peak (2012-2014) which is also apparent in similar trends in diffusion, bioirrigation and biological mixing (Appendix B, 3b, Figures 3-4). This double peak is also present in the trend analysis of nutrient availability throughout the water column (Appendix B, 3b, Figures 5-6), river flow and rain fall (Appendix B, 3b, Figure 7), as well on that of wave height and T_z in the same period (Appendix B, 3b, Figure 8). This pattern in DM exchange could thus result from the effects of the extreme storm events observed in the 2013/2014 winter (Kendon, 2015).

Outliers shaping the remainder component of PM exchange (Figure 11) are also apparent in outlier events in either PM resuspension or deposition (see assignment of all outlier peaks >0.2 in Figure 12). The PM exchange outlier component was found to be correlated to both resuspension (Pearson’s correlation, $\rho = 0.85$, $p = 0.0001$) and deposition (Pearson’s correlation, $\rho = 0.71$, $p = 0.0001$). The only exceptions for which no clear equivalent outlier was present in either driver are the two peaks in 2014 indicated by the circles in Figure 12.

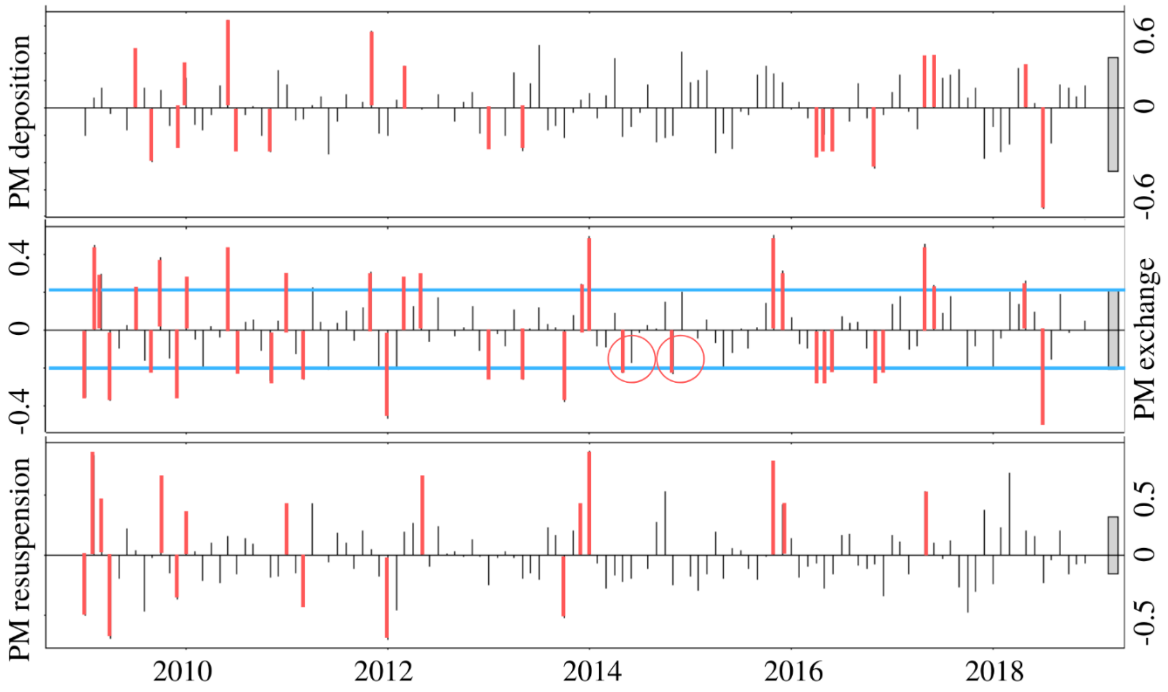

Figure 12: Outlier component of PM deposition (top), PM exchange (middle) and PM resuspension (bottom) time series data sets; outliers above 0.2 and below -0.2 in the overall PM exchange outliers which are likely to be linked also to peaks in deposition outliers or resuspension outliers are indicated by red lines; the blue lines in the middle graph indicate the 0.2 and -0.2 thresholds indicating the 30% of outliers which are most extreme threshold (determined from data context, as suggested in Mudelsee (2010)); instances where patterns in overall PM outliers have no equivalent in the PM deposition or PM resuspension outlier data sets are indicated by circles.

The first outlier without equivalent in the remainder component of either driver group occurred in June 2014 at the same time as an unusually high ammonia concentration and POC level temporal outlier (Appendix B, 3b, Figures 5 and 9). The phytoplankton bloom in 2014 was one of the shortest blooms recorded between 2009 and 2018, lasting for only 19 days between the 9th and 28th of April (median duration 46 days). This implies the potential for lag in recovery and rebound from extreme events such as the 2013/14 winter storms (Masselink *et al*., 2016), and is likely a contributing factor to these conditions. The second outlier is unique in magnitude in the main drivers' outlier components and occurred in November 2014, during a period of uncharacteristically low levels of tidal and river flow rates for that time of the year (as indicated by corresponding temporal patterns in the STL decompositions of river flow and tidal flow data, see Appendix B, 3b, Figures 7 and 9), which could affect particulate influx into and transport throughout the system.

Similarly to these results, the patterns in the outlier component of DM B/P exchange were in most cases also apparent in the remainder components of one or more of the direct drivers of DM exchange, with few exceptions (see Figure 13). Pearson's correlations suggested that the outlier component in the diffusion (ANOSIM, $R = 0.53$, $p = 0.0001$), bioirrigation (ANOSIM, $R = 0.69$, $p = 0.00001$) and biological mixing (ANOSIM, $R = 0.69$, $p = 0.0001$) datasets were correlated with the outliers in DM exchange (see Figure 13).

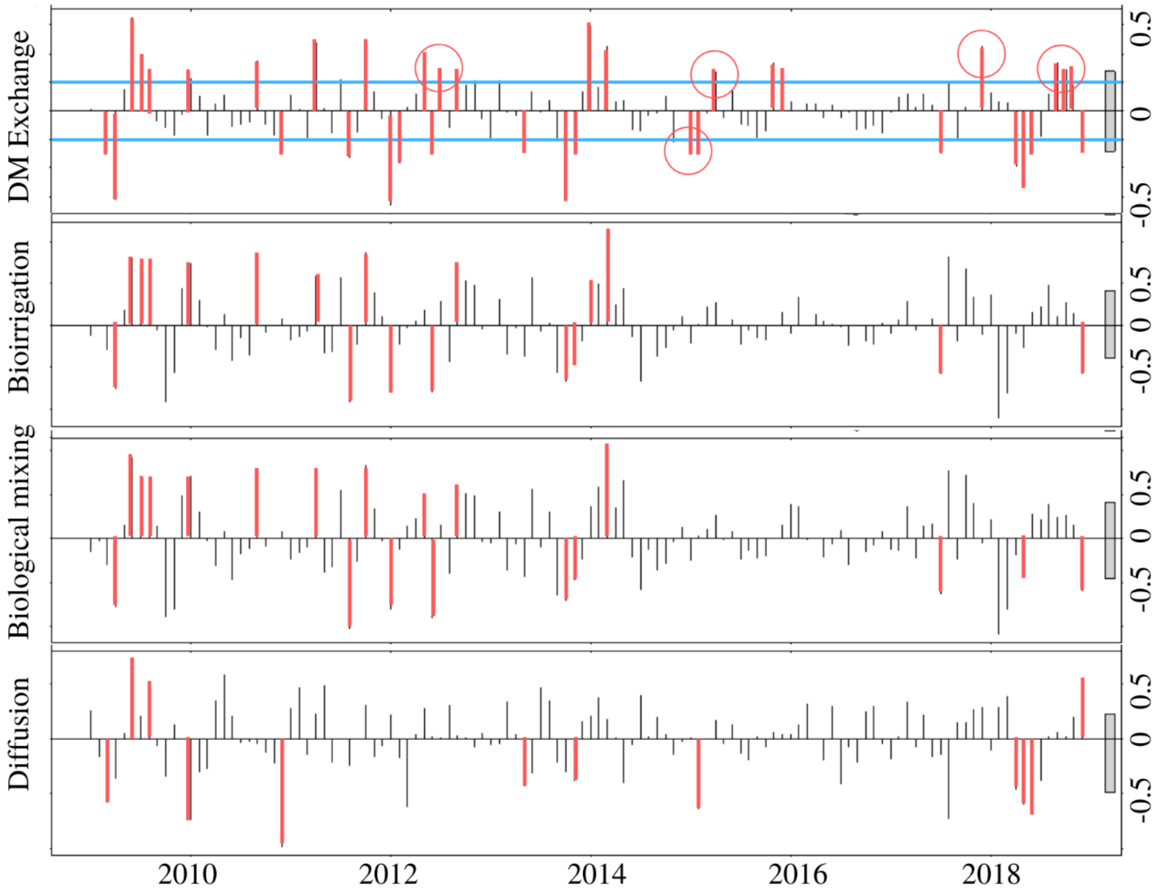

Figure 13: Outlier components of DM exchange, bioirrigation-driven DM exchange, biological mixing-driven DM exchange and diffusion-driven DM exchange time series data sets (top to bottom); outliers above 0.2 and below -0.2 (threshold indicative of most extreme 30% of outliers; Mudelsee, 2010) in the overall DM exchange which have equivalents in one or more of the drivers are indicated in red, cases in which the outlier in the DM-exchange data has no temporal equivalents in driver data outlier components are circled

There were ten instances of large DM exchange outliers, which were unparalleled by outlier events in bioirrigation, biological mixing or diffusion. Some of these outliers have equivalents in temporal patterns of the advection or physical resuspension. Specifically, the 1st, 5th, 6th and 7th outliers (December 2011, October and November 2015 and December 2017) coincided with periods of high storm occurrences that included wave heights above a storm threshold (return period 0.25 years, NNRCMP, 2019; see STL decompositions of wave height and duration in Appendix B, 3b, Figure 8) which can affect solute transport and exchange. In addition to that, the

2015-16 winter was under the influence of the co-occurrence of a large positive NAO and El Niño (NOAA, 2019), leading to unusually wet conditions and high river flow rates. This is likely to have increased the supply of DM from terrestrial and riverine sources to L4 (see STL decompositions of rain fall and river flow in Appendix B, 3b, Figure 7). Regarding other outliers, that in July 2012 is likely connected to the exceptionally large and long-lasting phytoplankton bloom event in 2012 (see STL decompositions of phytoplankton abundance and biomass in Appendix B, 3b, Figure 1, Zhang *et al.*, 2015), and the drivers of others were less clear. A number of significant storm events occurred leading up to and during December 2014 (return period 0.25 years, NNRCMP, 2019), but this does not seem to have caused extreme levels of advective or resuspension-driven DM transport. More likely, the synergy of positive NAO and El Niño during this time had a similar effect to the one mentioned previously. Corresponding outliers in the river flow and nutrient concentration data support this perspective (see STL decompositions of nutrients, rain fall and river flow in Appendix B, 3b, Figures 5-7). The 2018 period exhibited some of the same climatic synergy and although this period was unusually wet (Met Office, 2019), nutrient concentration data outlier components did not display unusual during this period (see STL decompositions in Appendix B, 3b, Figure 7). River flow data from the Tavy, one of the lesser tributaries of the Tamar, indicates no unusually high flow rates in November 2018 (Station 47015; NRFA, 2019).

3.3.2 Characterisation of the nature and drivers of multi-annual temporal patterns of B/P exchanges

High within year variability was found (ANOSIM, R = 0.031, p = 0.073). A weak trend over the course of the ten years could be detected, though there was considerable overlap between years (see OPLS Model 1, Appendix B, 3c, for numerical results). Factors contributing significantly to the model fit (VIP values > 1) were photosynthetically active radiation and fluorescence at 50m depth, wave height, duration and period, rainfall, community bioturbation and bioirrigation potentials, and overall POC and PON concentrations (for individual VIP values see Appendix B, 3d, Model 1). This indicates that weather and biological activity are the driving factors in the determination of inter-annual variability of the environment at L4.

3.3.3 Inter-annual patterns of B/P exchange, within phenological periods

Within-period testing using two-way crossed ANOSIM indicated that there were distinct inter-annual differences within the overall normalised dataset (ANOSIM, R = 0.301, p = 0.0001); the DM diffusion dataset (ANOSIM, R = 0.113, p = 0.013); and the PM deposition dataset (ANOSIM, R = 0.281, p = 0.0001); but not in other B/P exchanges. In the overall dataset, there were significant inter-annual differences within all periods except during the pre-bloom period, indicating that that period is overall the most stable and consistent and the least prone to inter-annual variation due to stochastic events (see Appendix B, 3c and 3d for results of OPLS models 2-6). Inter-annual differences in DM diffusion were largest in pre-bloom and mostly attributable to nutrient concentrations in the water column, while inter-annual PM deposition varied most in post-bloom, autumn and winter (see Appendix B, 3c and 3d, for results of OPLS models 7-11 of intra-annual DM diffusion and models 12-16 for intra-annual PM deposition). In the case of inter-annual differences in PM deposition, factors of significant contribution to the model fits (VIP >1) differed between periods. While primary production level seem to have been influential year-round, inter-annual variation in winter and pre-bloom periods was also influenced by river flow and temperature, bloom and post-bloom by tidal flow (and temperature in post-bloom) and in autumn, wave activity and rain fall were of importance (see VIP scores in Appendix B, 3d, Models 12-16). Overall, this supports the hypothesis that biological activity and weather are the most likely causes of inter-annual variability at this location. STL testing indicated that the trend component was dominant in both DM and PM exchange in all periods, except for PM exchange during post-bloom (see Table VI).

Table VI: Interquartile ranges (IQR) for each of the time series components; higher percentages indicate higher importance of that component

Variable name	Data set IQR	Seasonal IQR	Trend IQR	Outlier IQR
DM exchange winter	0.39735	0.08982	**0.27312**	0.18461
DM exchange pre-bloom	0.40610	0.03837	**0.40986**	0.21191
DM exchange bloom	0.314977	0.007038	**0.253913**	0.171590
DM exchange post-bloom	0.5128	0.1749	**0.3191**	0.2708
DM exchange autumn	0.505874	0.002606	**0.274000**	0.214328
PM exchange winter	0.3961	0.1366	**0.2616**	0.2038
PM exchange pre-bloom	0.21345	0.01592	**0.19841**	0.12324
PM exchange bloom	0.24129	0.03768	**0.26148**	0.13944
PM exchange post-bloom	0.26382	0.07948	0.17597	**0.25020**
PM exchange autumn	0.15204	0.04827	**0.14463**	0.12511

The first notable element of the trend component in DM B/P exchange was a peak from winter until the bloom period between 2012 and 2014, which is also apparent in the trend component of the wave height, wave duration and rainfall data sets (see Appendix B, 3b, Figures 7-8). This shows a potential connection to the unusually active storm periods in those years (Met Office and Centre for Ecology and Hydrology, 2014; Kendon, 2015). There were 34 storm events that caused significant wave heights above the storm threshold (NNRCMP, 2019), most of which coincided with strong positive North Atlantic Oscillation (NAO; National Oceanic and Atmospheric Administration, 2019). During post-bloom, a distinct peak in 2012 could be detected. As this is the period in which organic material produced through pelagic primary production is deposited on the seafloor and therefore available to benthic organisms, the aforementioned extremely long and abundant phytoplankton bloom that occurred in 2012 is likely connected to this trend (see Appendix B, 3b, Figure 1; Zhang *et al.*, 2015). DM exchange in autumn displayed a similar, though lower peak, which likely marks the on-going effects of the heightened levels of biological activity in 2012.

Intra-annual trends in PM B/P-exchange on the other hand include high peaks in 2013, 2015 and 2017 in winter, in 2016 and 2018 in pre-bloom and in 2017 during bloom and post-bloom. Periods of unusually low PM exchange were recorded in 2015 during the bloom and in 2013 in autumn. In winter, the peaks in the trend each occurred at times before which at least five significant storm events had taken place (NNRCMP, 2019), signifying that these trends were likely connected to the enhanced quantities of suspended particulate matter (see SPM and POC concentration data series decompositions in Appendix B, 3b, Figure 12). The 2016 and 2018 peaks during pre-bloom are also in parallel with the meteorological conditions, as these are some of the few occasions during which storms of significant magnitude occurred during that period (NNRCMP, 2019). High points in bloom and post-bloom period trends in 2017 are also apparent in the trend component of phytoplankton bloom parameters (see Appendix B, 3b, Figure 1), as well as similar trends detected in general zooplankton abundance, in particular that of copepods (see Appendix B, 3b, Figure 13). The 2017 bloom was dominated by diatoms, which are the preferred food source for copepods over other phytoplankton such as *phaeocystis* or dinoflagellates, which are also commonly found at L4 (Turner *et al.*, 2002; Gill and Harris, 2019). More abundant zooplankton with an aptitude for diel vertical migration as well as associated increased amounts of marine snow may have been connected to more intense PM B/P flux during and after the 2017 (phytoplankton) bloom period.

The outlier component which was identified as the dominant factor in PM B/P-exchange in post-bloom (see Table VI) shows extreme lows in August 2009, July 2010 and September 2015, as well as an extreme high in September 2009. In 2009, the (phytoplankton) bloom ended on the 11th of August, but the thermocline persisted until the 7th of September. This is the only instance within the time series data set analysed in this study during which the bloom ended while the thermocline was still in place. Thermoclines can affect phytoplankton species composition (Barnett *et al.*, 2019) and the co-occurrence of this event with the extreme in PM exchange may in this case indicate the delayed export of organic matter produced in the bloom to the benthic environment. In 2010, the copepod and meroplankton abundances were uncommonly high in May and June. This could have contributed to vertical PM transport through marine snow production and increased benthic faunal activity due to the abundantly available food sources in July (Graf *et al.*, 1982). The data from September 2015 however shows no patterns equivalent to that found in the PM outlier component, which gives indication that biological PM transport is unlikely to have played a role in these unusually high rates of intra-annual B/P PM exchange. However, the extremely low amount of rain fall which led to outliers in the form of high salinity and low river flow at that time, may be connected (see Appendix B, 3b, Figures 7 and 14). This could have resulted in an unusually low amount of terrestrial and riverine SPM influx, leading to an overall low in PM B/P exchange.

3.4 Discussion

Throughout the analyses undertaken in this study, there is a strong connectivity between inter-annual variation and multi-annual patterns of B/P exchanges and their drivers. Patterns seen in the temporal trend and outlier events in DM and PM exchange datasets were also apparent in the trend and outlier components of their respective driver data. Identifying the correct drivers to characterize an ecosystem process is vital, as these may be used as indicators of change, and proxy measurements when the process of interest is not itself directly measurable, or data are sparse (Link *et al.*, 2010). Following this, predictions can be made about future trends, based on the understanding of driver-process relationship dynamics exemplified in this study. These results suggest that meteorological and biological drivers are paramount in shaping the inter-annual variability of B/P exchange drivers and processes in this representative coastal environment. This is supported by previous studies that have recorded wide-reaching impacts of biological and meteorological extremes on environmental parameters known to affect B/P exchanges (such as the distribution of nutrients and microbes (*e.g.* Witzrau and Graf, 1992); biostabiliser presence and effectiveness (*e.g.* Ebeling *et* *al.*, 1985), benthic faunal activity (*e.g*. Graf *et al.*, 1982; Joseph, 2019), *etc*.). The results of this study also indicate that in locations with strong seasonal cycles, the search for long term temporal patterns of drivers in BP exchange requires consideration of within-season dynamics, as well as longer time-series records. As shown here, this applies to inter-annual and multi-annual scales, but also to longer term investigations.

More specifically, this study shows that biological extremes such as phytoplankton blooms of unusual magnitude, their duration or intra-annual timing can change the relative importance of biological drivers of B/P exchange compared to physical ones. Particularly large or long blooms provide more organic matter to the water column than usual, which are deposited on, and incorporated into, the seafloor, fueling the activity of benthic organisms (Gerino *et al.*, 1998; Tait *et al.*, 2015). This promotes an overall down-ward shift in the direction of B/P exchange processes for the duration of the effects of the bloom. Meteorological extremes, such as particularly strong and/or long storm events on the other hand, can have the opposite effect. Strong shear stresses such as those induced by wave action during a storm event may be of relatively short duration but can have lasting impacts (Pusceddu *et al*., 2005; Masselink *et al*., 2016). The extreme or prolonged erosion and resuspension of sediment and benthic organic matter can also have lasting effects on the benthic environment, and thereby shift the baseline balance between B/P exchange drivers (*e.g*. less spatial variation in benthic macrofauna assemblages (Corte *et al.*, 2017); changes in OM distribution and chemical composition (Pusceddu *et al.*, 2005); and export of fine sediment fractions off the continental shelf (Ferré *et al.*, 2008)). Synergetic, global climatic processes, such as co-occurrences of El Niño and positive North Atlantic Oscillations, are likely to also shift the balance and relative importance of the various drivers of exchange for the duration of the multi-year trends they have been shown to cause.

B/P exchanges within years can therefore vary across years (in timing and in response to inter-annual variations in the magnitude of their drivers), and thus that sampling done throughout any given year may not be representative of the precise timing of cyclically re-occurring intra-annual events of a site over longer periods of time. In this case, strong biannual cycles were evident, that were further complicated by multi-annual, global process cycles. The added value of time-series collections from long-term observatories, such as those analyzed here, is thus that they can also enable the identification of extreme events which affect ecosystem level functioning (see also Ducklow *et al.*, 2008). Very few such observatories exist. Some, such as the Hawaii Ocean Time Series (HOT; ALOHA, 2020) which was established in 1988 include benthic elements (added to HOT in 2011). Most, however, focus on oceanographic and/or pelagic processes and are therefore not sufficiently multidisciplinary for ecosystem level analyses (see list of time-series data collections accumulated in the Global time series resources data base; Alfred Wegener Institut, 2020). The WCO is thus, in many ways, a unique observatory from which coastal benthic-pelagic dynamics can be comprehensively scrutinised. Meta-analysis has shown, that studies based on long-term ecological time-series are more frequently published in highly regarded peer-reviewed journals, get cited more frequently than shorter-term studies, and play a disproportionately large role in informing environmental policy (Hughes *et al*., 2017).

In order to identify long-term trends in the B/P exchange process dynamics at L4, spanning multiple decades or centuries, such as the long-term effects of climate change, a longer time-series is needed still. However, indications of occurrence and magnitude of the effects of environmental extremes, such as the ones analysed in this study, allow us some insight. Known drivers of multi-decadal environmental change, such as global climate change, are known to affect, for example, the frequency and magnitude of storm events (Collins and Sutherland, 2019; IPCC, 2019), which, based on the results of this study, could indicate that periods of high B/P exchange become more frequent too. Models based on the increase of resuspension-driven SPM throughout the North Sea and English Channel in the past 100 years corroborate this perspective (Fettweis *et al.*, 2012; Capuzzo *et al.*, 2015; Wilson and Heath, 2019). Pelagic primary production, identified in this study as another influential environmental driver of temporal B/P exchange trends, may be affected by climate change. Changes in pH and the increased frequency and distribution of low-oxygen-zones could for example cause a shift in the global distribution of primary producers and overall rates of productivity (Chavez *et al.*, 2011).

Finely resolved single year studies are necessary, as they can provide insights into specific processes that are too costly, or resource intensive, to investigate at the scale of long-term observatories. However, a multi-year record of the background environment enables researchers to then contextualise such studies into a broader context of intra-annual and inter-annual change, providing added information about how the timings identified in annual studies may change with the phenology of their drivers. The combination of the two types of information can then be used to improve ecosystem modelling efforts of current environments, beyond local scales, as well as predictive modelling approaches that identify longer-term temporal trends, whilst finely resolving mechanistic links between ecosystem processes and components. The WCO time series is a unique resource for holistically exploring complex marine ecosystem processes and linkages, providing insights into other temperate coastal systems. The methods used in this study were effective in exploring drivers of inter-annual variability and highlighting potential future ecosystem states linked to future climate change (*e.g.* increased storm frequency effects). However, true long-term trend analysis requires multi-decadal datasets.

It is worth mentioning that this study required the assumption that all the data provide meaningful insights into the sampled processes. In some cases, datasets were sporadic (resulting from short term programs), and other data sets had not been collected throughout the whole decade analysed, such as benthic macrofauna abundance, biomass and activity. These datasets are less regular because generating benthic biodiversity datasets, or measuring animal behaviours related to B/P exchanges, are resource intensive measurements, requiring expensive, dedicated ship and staff time to generate the data. These types of datasets cannot easily be generated over long time periods, relative to other data analysed in the scope of this thesis, for which much better coverage exists. Temporal patterns extracted from those less resolved datasets may thus be less reliable, highlighting a difficulty in maintaining resources required to sustain long-term, coupled benthic-pelagic observations. It is the combination of both types (high frequency and low frequency) of datasets with overlapping temporal coverage that allows for greater insight. Datasets with high frequency (*e.g.* measurements of rain fall and river flow) may be used in combination with one another, and factors known to directly affect others can be implemented as proxies (*e.g.* primary production is known to be a driver of benthic biological community composition and activity; Graf *et al.*, 1982; Gooday *et al.,* 1990). Guided by the underlying temporal structure of the WCO sampling, this provides a sufficiently strong temporal frame onto which all datasets can be aligned and thus used to provide greater insights about the ecosystem analysed. Whilst not all variables that affect B/P exchange could be considered here (such as seafloor porosity or topography), it is the coordinated sampling program of this observatory, like in others, that allows for greater insight into the coupling of benthic and pelagic, the atmospheric processes expressed through meteorological events, and the greater, global multi-annual cycles.

3.5 Conclusions

At this particular temperate coastal location, the most influential causes of inter-annual variability were extreme outlier events of biological and meteorological nature. Although the seasonal signal in temperate locations is strong, it was possible to disentangle inter- and multiannual temporal patterns in B/P exchange drivers and processes from a decadal data set. The impact extreme outlier events had on B/P exchanges, was long-lasting enough to create multi-annual patterns, but the data set was not long enough to also assess multi-decadal trends. Within-period testing was found to be a useful tool for studies of temperate environments, to avoid over-shadowing of inter-annual patterns by the strong intra-annual signal.

In general this means that the potential for extreme inter-annual variability needs to be taken into account in the planning of sampling campaigns, especially if a specific phenological event or time period is to be captured. The fact that outlier events can have long-lasting effects, despite being of short duration, implies that a broad temporal context is required to correctly assess ecosystem processes. However, while the occurrence and magnitude of the effects of extreme events can indicate potential long-term trends, multi-decadal records are needed to quantitatively assess true long-term changes, such as those driven by climate change.

Chapter 4

Long-term climate driven changes to benthic-pelagic exchanges in the Arctic

4.1 Introduction

The most pressing long-term environmental challenge of our time is global climate change, which has been well documented in having wide-reaching impacts in marine ecosystems around the globe (IPCC, 2019). One of the locations at which the effects of climate change can already be observed today is the Barents Sea continental shelf in the Arctic, globally one of the most rapidly changing environments due to climate change related warming processes (Serreze and Barry, 2011). Of all Arctic regions, the Barents Sea displays the fastest rates of change (Onarheim *et al.*, 2018).

The Polar Front located on the Barents Sea shelf, where Arctic and Atlantic water masses meet (Johannessen and Foster, 2008), has been thought to be shifting northwards as the width and warmth of the North Cape Current increases (Ingvaldsen, 2005). The front is currently located approximately in the southern and central Barents Sea (Fossheim *et al.*, 2006; Oziel *et al.*, 2016), although its precise location is influenced not only by topographic features but also by seasonal and inter-annual variations in Atlantic water inflow, temperature and wind speed (Ingvaldsen, 2005; Ellingsen *et al.*, 2007). Barents Sea climate regularly shifts between a cold and a warm stable state in irregular inter- to multi-annual intervals. The variability causing switches between the two states is triggered through oceanic and atmospheric circulation variations (Ådlandsvik and Loeng, 1990; Ingvaldsen *et al*., 2004). The Atlantic water is relatively warmer (> 3 °C) and more homogenous than the Arctic water, which exhibits a strong halocline type stratification (Olli *et al.*, 2002; Reigstad *et al.*, 2002).

Sea ice formation generally only occurs in areas dominated by Arctic water, although there are large inter-annual variations in the extent of the sea ice due to climate cycles such as the Arctic Oscillation (Fyfe *et al*., 1999; Wang and Ikeda, 2000; Rigor e*t al*., 2002; Barton *et al.*, 2018) and variations in heat influx from Atlantic waters (Årthund *et al.*, 2012). The climate-driven reduction in seasonal sea ice cover levels in the Barents Sea is the fastest and most extreme of all Arctic regions (Onarheim *et al.*, 2018; IPCC, 2019). Some models predict the Barents Sea may be completely free of ice year-round by 2080 (Furevik *et al*., 2002). While some studies state that sea ice cover can have an effect on deep water tidal flow in this area and *vice versa* (Kowalik and Proshutinsky, 1994), others discount ice influence below surface waters (Gjevik *et al*., 1994). From a biological standpoint, a decline in sea ice is very likely to affect both pelagic and benthic environments, as the two have been shown to be tightly coupled (see previous chapters; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Olli *et al.*, 2002; Renaud *et al.*, 2007). Productivity of benthic fauna in Arctic shelf regions is highly dependent on energy and matter input through downward flux of OM from pelagic phytoplankton blooms and ice algae (Wassmann *et al.*, 1996; Aschan and Trannum, 2006; Tamelander *et al.*, 2006; Renaud *et al.*, 2008; Cochrane *et al.*, 2009). Nature and magnitude of pelagic OM vertical export potentials are shaped by water column stratification and zooplankton activity (Olli *et al.*, 2002).

Although warmer years have been linked to higher rates of productivity (Sakshaug, 1997), a loss of sea ice is likely to affect the quantity, quality and timing of OM input to the benthos (see *e.g*. Wassmann *et al.*, 1996). This could lead to an increase in benthic macrofauna biomass in the northern regions (Cochrane *et al.*, 2009). Another potential impact that climate-driven sea ice loss might have, is that non-indigenous species may invade or get introduced to the area (Alvsvåg *et al.*, 2009; Ware *et al.*, 2014). Furthermore, benthic areas which had previously been protected by the ice cover in winter may be disturbed year-round through anthropogenic actions such as trawling (Misund *et al.*, 2016). Shellfish fisheries are the most likely to have large impacts on benthic fauna due to the destructive nature of the fishing gear (Puig *et al.*, 2012).

Changes to sea ice coverage and water mass distribution have the potential to cause shifts in fundamental processes at the ecosystem level, such as the movement of DM and PM throughout the marine environment. A shift in source and/or sink of OM in an area could lead to changes in the nature and intensity of local B/P exchange pathways towards a more physically driven process, as described in Chapter 3. Changes to the benthic macrofauna community through lowered OM quantity and quality, alien species introduction and/or trawl disruptions are likely to perpetuate changes in biologically driven DM and PM flux pathways such as bioturbation and bioirrigation potentials (see *e.g*. Maiti *et al*., 2010). The lowering of biological Carbon processing rates due to a northward movement of the Polar Front and seasonal ice edge is predicted to entail an increase in Carbon burial and sedimentation (Stevenson and Abbott, 2019). Increased fishing pressure is furthermore likely to affect seafloor properties and topography (Palanques *et al.*, 2001; Puig *et al.*, 2012), thus leading to shifts in physically-driven DM and PM exchange processes such as resuspension and advective fluxes.

This study set out to test whether a shift in the Polar Front and reduction in the annual duration of sea ice cover will be likely to cause a change in benthic-pelagic fluxes. To capture the binary nature of these changes (ice *vs*. no ice; north of Polar Front *vs*. south of Polar Front), a North-South transect through the Barents Sea was investigated which included stations north and south of the current Polar Front. The average annual sea ice cover durations across the stations covered a wide range, providing a proxy for current and likely future conditions. To determine whether the switch to a more Atlantic-water dominated ice free Barents Sea will cause changes to B/P exchange processes, we first characterised the physical, biogeochemical and biological environment along the transect, then quantified PM and DM B/P exchange drivers and processes and finally determined what effects the above described climate-change-driven changes are likely to have on these processes.

4.2 Methods

4.2.1 Study site

The environmental gradient along a North-South transect (see Figure 14) was sampled in July 2018 (Solan, 2018) and 2019 (Barnes *et al.*, 2019) respectively. The stations (B13 – B17) cover varying water mass distributions and typical levels of seasonal sea ice cover from South to North. The mean pelagic Polar Front intersects the transect north of station B14 (Figure 14, green line; Fossheim *et al*., 2006; Stevenson and Abbott, 2019), while the benthic Polar Front, determined based on the divide between Arctic- and boreal-dominated benthic megafauna community composition, intersects nearer B13 (Figure 14, red line; Jørgensen *et al.*, 2015). All stations were selected to be in areas of comparable depth (see Table VII).

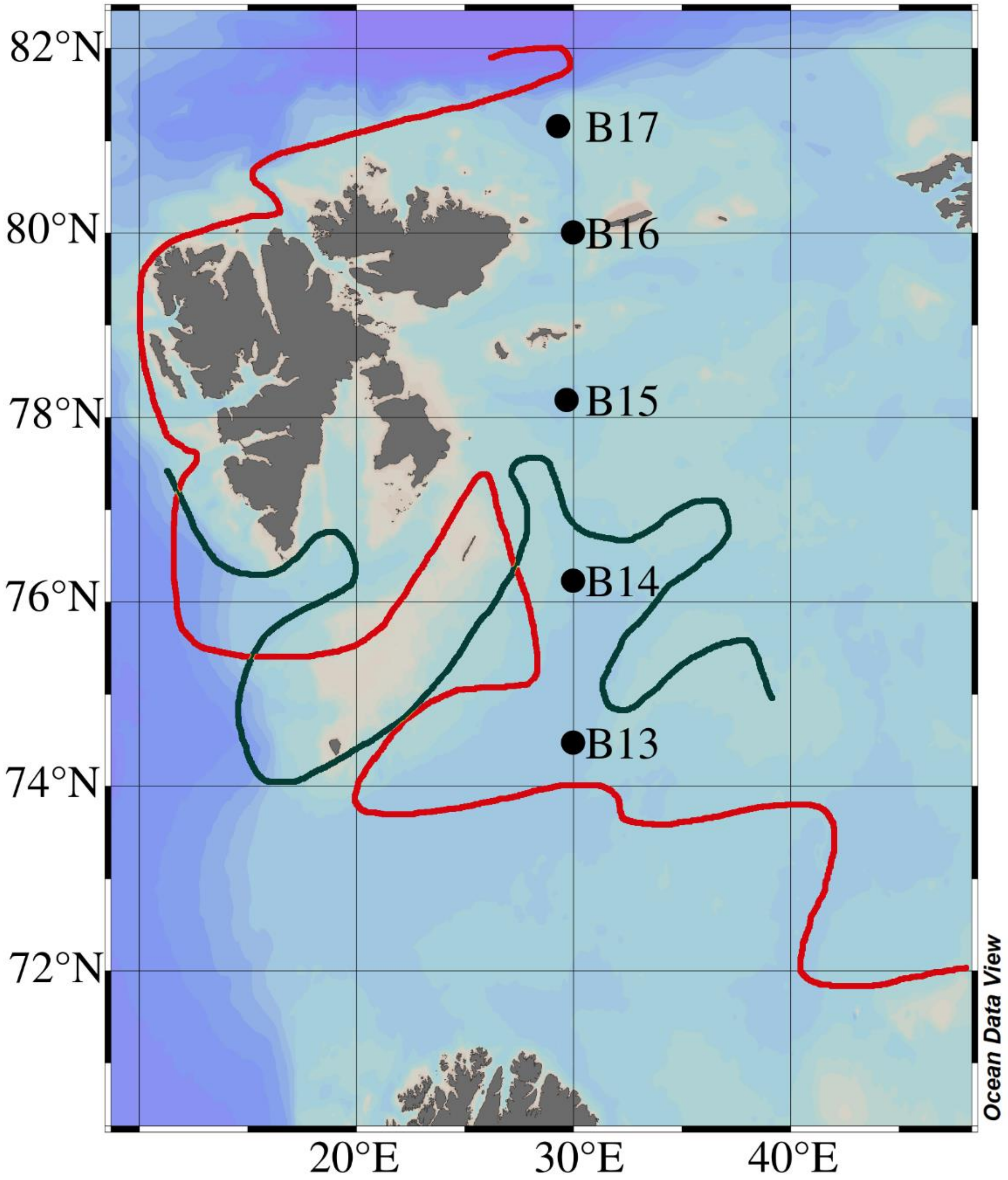

Figure 14: Map of benthic stations B13, B14, B15, B16 and B17 along the 30° longitudinal line east of the main Svalbård archipelago; green line indicates the typical location of the pelagic Polar Front after Fossheim *et al.* (2006) and Stevenson and Abbott (2019); red line indicates the typical location of the benthic Polar Front after Jørgensen *et al.* (2015)

Table VII: Sample station locations and approximate depths (+/- 2.9 m on average, see Appendix C, 4a); annual average sea ice coverage percentages based on 2009 to 2019, calculated from sea ice data provided by the Norwegian Meteorological Institute in grid boxes +/- 1 °N and +/- 1 °E of each station (Norwegian Meteorological Institute, 2020); annual sea ice coverage percentage based on 1981 to 2000 from latitudinal thresholds published in Maiti *et al*. (2010)

Station	**Latitude**	**Longitude**	**Depth in m**	**Decadal average % sea ice cover, based on 2009-2019**	**Annual % sea ice cover (based on Maiti *et al.,* 2010, from 1981-2000)**
B13	74.30 °N	30.00 °E	358	0%	0%
B14	76.30 °N	30.30 °E	292	6.18% (stdev 6.96)	20%
B15	78.15 °N	29.59 °E	313	53.68% (stdev 12.27)	50%
B16	80.07 °N	30.04 °E	280	63.75% (stdev 22.52)	70%
B17	81.16 °N	29.19 °E	334	62.52% (stdev 25.23)	70%

Annual sea ice coverage at the sample stations, determined from data of the most recent decade (2009 – 2019), was generally lower than previous estimates based on earlier data suggested (1981-2000; see Table VII; especially at station B14). Although the winter sea ice extent varies between years, the furthest south the ice edge typically comes is to 76 °N (Onarheim and Årthun, 2017). B17 has a lower decadal average percentage of sea ice cover than B16 (see Table VII), even though it is further north, because warm Atlantic water advances further north on the western side of Svalbård, thereby frequently creating an ice free area north of the archipelago that can reach as far east as station B17 (Loeng, 1991; Loeng, Ozhigin and Ådlandsvik, 1997).

Each of the stations was located in a glacial trough containing postglacial glacimarine / marine trough-fill (Vorren *et al.*, 1989), in the form of fine-grained cohesive sediments. Seafloor topography on the Barents Sea continental shelf, though dominated at large scales by the troughs themselves, also exhibits a range of trawling and iceberg plough marks (Thorsnes *et al.*, 2016), which can be distinguished by their shape and size. Anthropogenic impacts on the benthic environment have been recorded even in areas that are covered by sea ice for the majority of the year and are thought to account for much of the small-scale seafloor variability (Sswat *et al.*, 2015). Water mass transport and exchange throughout the shelf is guided by the bathymetric relief of troughs and banks (Pfirman *et al*., 1994) and has been shown to be variable on a seasonal as well as inter-annual basis (Loeng *et al*., 1997). Main current directions are an eastward flow in the southern Barents Sea and a westward flow in the North (Ellingsen *et al.*, 2007). Tidal flow is also an important hydrodynamic force, though it is spatially variable in direction and magnitude throughout the Barents Sea and can be locally enhanced through topographical features (Kowalik and Proshutinsky, 1995).

The seabed at the sampling stations is typically inhabited by a range of invertebrate epi-benthic and benthic macro and micro fauna (Cochrane *et al.*, 2012), the community composition of which has been shown to be impacted by natural as well as anthropogenic influences (Aschan and Trannum, 2006; Sswat *et al.*, 2015). Considering the depth of the water, fine-grained nature of the sediment and generally low current velocities, bioturbation has been estimated to be vastly more important for internal sediment mixing than abiotic drivers (Maiti *et al*., 2010). Although the majority of local benthic macrofauna are surface or subsurface deposit feeders, low intensity sediment mixing to shallow mixed depths does take place (Carroll *et al.*, 2008). Within the Barents Sea, areas of seafloor depression such as glacial troughs exhibit the lowest infaunal taxon richness and biomass, but the deepest biogenic sediment mixing depths of any habitat type (as determined through sediment profile imaging techniques by Cochrane *et al.*, 2012). Because the glacial troughs are specialised environments and spatial variation of the seafloor throughout the Barents Sea is substantial (Norges Geologiske Undersøkelse, 2020), the results of this study are only representative of this specific environment, not of the shelf as a whole.

During the current study, the location of the Polar Front was confirmed through CTD measurements to be roughly around the middle of the study transect at the time of sampling (between B14 and B15), so around the mean pelagic Polar Front location (see Figure 14; Fossheim *et al.*, 2006). Weather conditions during both cruises were calm with little wind, next to no waves and an abundance of fog. During the first cruise in July and August 2018, five stations along the 30° eastern latitude were sampled (B13 – B17; see Appendix C, 4a, and 4c) while during the 2019 cruise only four of the stations could be sampled (B13 – B16; see Appendix C, 4a and 4c), due to the density and thickness of the ice around B17. The extent of sea ice cover varied substantially between the two years (see Figure 15). Station B15, while enclosed in very close drift ice at the beginning of the 2019 cruise, was ice free at the time of sampling five days later (see Appendix C, 4b, for dates and times of sampling at each station).

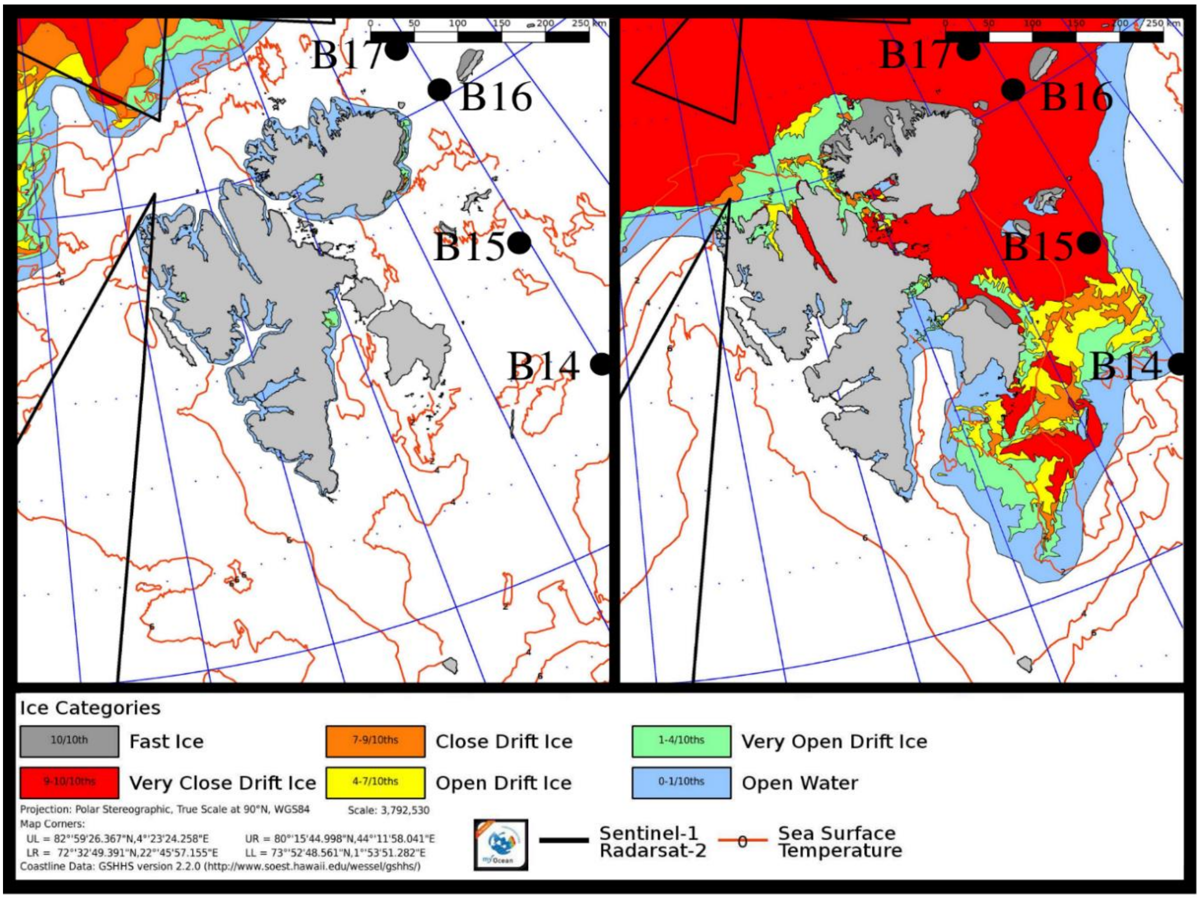

Figure 15: Left: Sea ice cover immediately before the beginning of JR17007 cruise on 11th July 2018; Right: Sea ice cover immediately before the beginning of the JR18006 cruise on the 5th July 2019; Sea ice maps generated through the Norwegian Meteorological Institute Ice Service, Cryo (2019); approximate positions of stations B14-B17 are indicated by black markers on sea ice maps

4.2.2 Sampling methods

Sediment samples were taken with a 0.25 m^2 box corer by randomly selecting a series of spots within a 200 m^2 box surrounding the station centre. Re-sampling of any single point was avoided through tracked drift within the box in a randomised direction, oriented on current and wind directions (see Appendix C, 4b, for average distances between replicate cores at each station in both years).

From each corer box, a 30 cm diameter round sub-corer was used to extract an intact sediment core and the overlying water. Sub-cores were transported into a temperature controlled laboratory (CT laboratory) immediately after extraction.

Disruption of the sediment matrix and accidental resuspension during core transport where avoided by using a carrying frame and rolling platform for core transport. The CT laboratory was kept at the current bottom temperature of each station as determined by the CTD drop preceding the sediment sampling where possible (see cruise reports in Solan 2018 and Barnes *et al*., 2019), and at 2 °C in cases when further cooling was not physically possible. Where the water level was insufficient upon taking the sub-cores, bottom water from CTD samples was used to top it up using bubble wrap and airline tubing to minimise surface disturbance, as described by Widdows *et al.* (1998; see Appendix C, 4b, for CTD bottom depths). Cores that surfaced without any water were rejected as the drainage of the overlying water may have swept the top-most sediment layer away with it. Cores in which the sediment displayed cracks upon box-coring or sub-coring were also rejected. Each core was given a 24 hour period between sampling and processing to settle, during which the water was aerated gently using diffusing air stones and cores were kept in the CT lab in the dark.

Granulometry samples were taken from three to five USNL box cores at each station using 50 ml syringe corers. From each box core, three depth-integrated (0 to 5 cm depth) syringe cores were extracted, combined and homogenised for subsequent sub-sampling during the analysis (see sampling details in Solan, 2018 and Barnes *et al.*, 2019).

During the 2019 cruise, a 75 kHz RD Ocean Surveyor Acoustic Doppler Current Profiler (ADCP) fitted to the ship’s hull provided profiles of horizontal current velocities, from approximately 20 m below the sea surface, to 20 m above the sea floor. ADCP data were only collected in 2019, instead of during both cruises, as the option to make such measurements only became apparent to the author after the first cruise had already finished. Raw data were collected in 8 m depth bins in a narrowband water tracking mode using RD VmDas software (Communication Technology, 2019). A 60.08 º miss-alignment rotation was applied within the software. Single ping, bin-mapped, earth-coordinate data within the proprietary binary files was read into MATLAB for further processing and quality control. The single ping ADCP time stamps and the position, attitude, time and heading information from the ships Seapath320+ were also inserted into MATLAB. Ensembles with no ADCP data or missing heading information were removed. The single ping ADCP velocities were rotated from the vessels centre line to a True North reference. Further screening was performed to remove data where: there was a low signal to noise ratio in any bin; a 4-beam solution was not possible; the maximum change in heading between pings was > 10 ° per ping; the maximum change in the ships velocity between pings was > 0.55 m s^{-1} per ping; and where the error velocity was more than twice the standard deviation of error velocities of a single ping profile. Velocities close to the bottom that were contaminated by strong reflections from the seafloor were also discarded. Lastly, 10 - minute averages were created and the absolute water velocities were determined using the ships GPS derived velocity. Depth mean velocities comprising the barotropic tidal velocity and any non-tidal contribution to the depth average flow (*e.g*. a density driven geostrophic current) were calculated. The ship worked at each site for 30 - 48 hours therefore between 2.5 and 4 semi-diurnal tidal excursions were resolved.

For both cruise periods in 2018 and 2019, tidal current predictions were generated at each site using the Oregon State University (OSU) Tidal Prediction Software and the 2018 regional 5 km Arctic Ocean Tidal Inverse Model, AOTIM-5 (Egbert and Erofeeva, 2002; Padman and Erofeeva, 2004). Predictions were based on twelve harmonic constituents (including M2, S2, N2 and K2). Maximum tidal flow in the month of July was extracted from the tidal model for both years.

Directly observed velocities measured via ADCP contain both the oscillatory tidal contribution and any other non-tidal components. Most short-term temporal variability in such measurements is typically associated with tidal flow, and the magnitude of tidal currents is comparable to other current components that may vary along longer time-scales which could not be captured in the present measurements. The tidal currents from the model are therefore a prediction of the contribution that the tides make to the total (observed) signal, providing an estimate of the maximum current speeds that each site might experience by including a spring tide.

4.2.3 Sample processing

Sediment resuspension experiments were based on the Core Mini Flume (CMF) methods described in Thompson *et al.* (2013), see Figure 16.

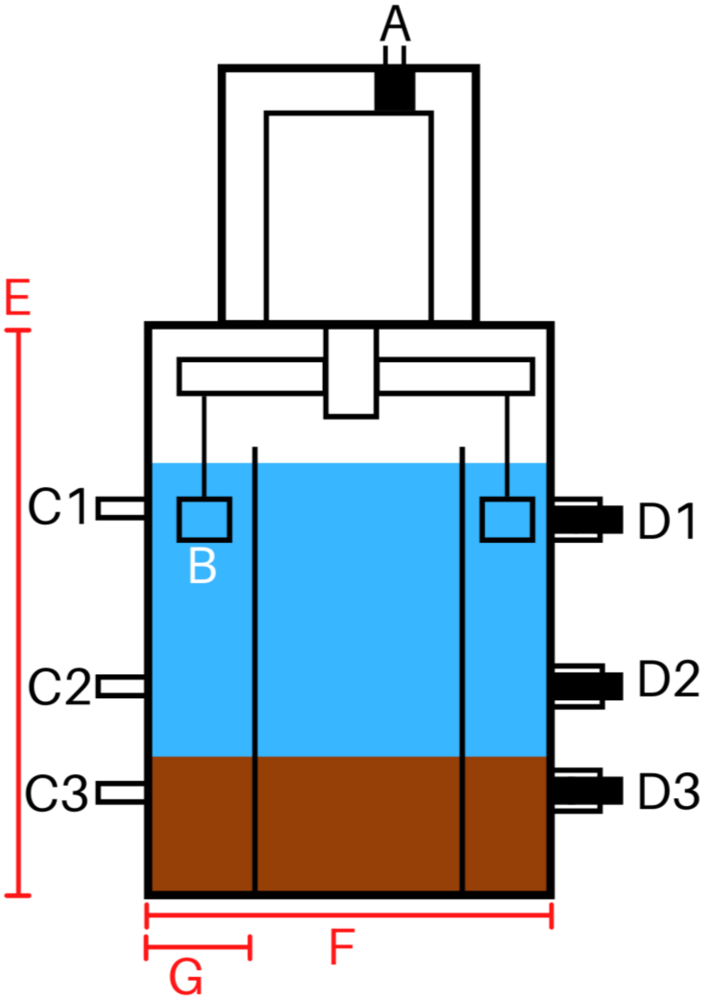

Figure 16: Flume schematics of Core Mini Flume: A) Motor unit; B) Paddles x2; C) sampling ports at 20 cm (1), 10 cm (2) and 4 cm (3) height above the bottom of the flume; D) Optical Backscatter sensors at 20 cm (1), 10 cm (2) and 4 cm (3) height above the bottom of the flume; E) height of the flume body, 34 cm; F) diameter of the flume, 19 cm; G) width of the flume channel, 4 cm

The flume was post-calibrated with a side-looking Nortek Vectrino Acoustic Doppler Velocimeter (ADV) as described in Thompson *et al.* (2013) using sediment from each station. In addition to the OBS recorded to monitor the erosion and resuspension process during the flume run, SPM was sampled using a 50 ml Swinnex syringe filter system with pre–ashed (450 °C for 24 hours) pre-weighed 25 mm Glass Fibre Filters (Whatmann) before and after the critical shear stress application experiments as well as immediately before the end of each velocity step. The exact quantity of filtered water was recorded and filters were frozen at -

20 °C for later analysis. Throughout the flume run, the overlying water was also sampled for nutrients (Nitrate, Nitrite, Ammonium, Phosphate and Silicate) by taking 30 ml at the same intervals as the SPM samples. Nutrient samples were filtered through acrodisk® supor® membrane filters (0.8/0.2 µm; VWR) and refrigerated until analysis, which was carried out within 24 hours of sampling using a Lachat Quikchem 8500 flow injection analyser (Hach US, 2020; see methods detailed in Solan, 2018).

In addition to the water samples detailed above, sediment property measurements were undertaken representative of conditions before and after critical shear stress application by syringe coring areas of the sediment from areas which remained untouched by the resuspension (pre-resuspension), and those within the flume channel (post-resuspension; see Figure 16 flume channel and middle section). The syringe cores were frozen and stored vertically, then sliced in sections of 0-1, 1-2, 2-3, and 3-5 cm depth from the sediment surface. Both SPM filters and sediment property samples were weighed wet, then dried in an oven in pre-weighed petri dishes over night at 60 °C and weighed again. To determine OC contents of both sediment and SPM, samples were then placed in a furnace and ashed for 24 hours at 450 °C, after which they were weighed a final time. Sediment porosity was calculated using the wet-dry method described in Maiti *et al.* (2010). Erosion depths were calculated based on the surface area of sediment within the flume, pre-resuspension sediment density measurements, SPM volume placed in suspension throughout the flume run and the volume of water in the flumes.

Granulometry samples were analysed using a Laser Coulter Sizer LS 130 micro volume model (Coulter International Corporation, 1996). Each replicate was sub-sampled five times and analysed, leading to a total of 15-25 measurements per station for each year. From this, the averages were used to determine in-situ depth-averaged grain size distributions. Mean grain size (d_{50}) values of each of the stations were used to calculate critical erosion velocities and shear stresses, following the methods outlined in Thompson *et al.* (2013), using power laws described in Soulsby (1997; see Equations (A) and (B) in Chapter 2).

Sediment erosion and deposition are largely controlled by currents and shear stresses near the seabed. Friction at the seafloor creates a benthic boundary layer, within which currents increase logarithmically with height above the seabed towards free-stream velocities (Soulsby, 1997). Although it is known that bottom-friction reduces flow speeds near the seabed, there may be more vertical shear through the resulting turbulence (Richards, 1990). The ship fitted ADCP was unable to make measurements of current speed near the seabed and the tidal predictions are for a barotropic current. Bottom-near current velocity estimates therefore had to be derived mathematically. The boundary roughness was determined to be between zero and 0.5 times the water depth. This is a conservative estimate as actual roughness elements are likely to be closer to the lower end of this scale than the upper end. Near bed velocities were then estimated using Equation (C) in which $\overline{U}$ = depth-averaged current speed (m s^{-1}) and h = water depth (m; Soulsby, 1997; see Equation (C) below).

$$U_{(z)} = (\frac{z}{0.32h})^{1/7}\overline{U} \qquad \textbf{Equation (C)}$$

Near-bottom velocities thus derived were then compared with critical shear stresses measured at each station to determine whether typical near-bed current speeds at each site could cause seafloor resuspension events.

Other parameters collected during the same cruises were used to supplement the data set (see below for a description of these and cruise reports for sampling methodologies: Solan, 2018; Barnes *et al.*, 2019). Bioturbation estimates based on mean and maximum mixed depths, surface boundary roughness and bioturbation coefficients, as well as bioirrigation measurements recorded by Solan *et al.* (in press) were included to gain an understanding of the biological activity at each of the sites. These bioturbation and bioirrigation data were collected at the same stations that are investigated in this study, but during the 2017 and 2018 cruises instead of 2018 and 2019. Sea ice and water mass distribution conditions in 2017 and 2019 were similar, which is why the 2017 data on benthic biological activity will be used as a proxy for ice-covered conditions here (Hopkins *et al.*, 2018; Solan, 2018). Information on potential bio-stabilisation of the sediment through microphytobenthos and benthic Extracellular Polymeric Substance (EPS) production was available through personal communications and insights into unpublished data sets on sedimentary pigment composition and degradation, and water column Transparent Exopolymer Particle (TEP) concentration data (Airs, 2020; Zänker, 2020). These data had been collected throughout the 2018 and 2019 cruises during which this study’s samples were taken (Solan, 2018; Barnes *et al.*, 2019), but as they are still in the process of being analysed and/or published, they could not be directly included in this study.

Localised sea ice cover duration data were provided by the Norwegian Meteorological Institute (Norwegian Meteorological Institute, 2020) and supplemental data on the sea ice extent between 2006 and 2017 were sourced from the Environmental monitoring of Svalbård and Jan Mayen platform (MOSJ, 2020).

As temporal or spatial patterns in grain size and particulate resuspendability between the two years may be connected to variations in fishing effort, due to processes such as trawl-driven winnowing (Ferré *et al.*, 2008), an estimation of fishing pressure was approximated using landings data exported from the ICES data set collections (ICES, 2020) as well as fishing effort data based on automatic identification systems (AIS; Global Fishing Watch, 2020). As trawling is the most likely fishing technique to impact the B/P interactions (Puig *et al.*, 2012), the trawling data were isolated out of the AIS data set and concentrated on for this study. As the algorithms currently used by Global Fishing Watch do not differentiate between different types of trawlers (bottom and mid-water), the trawling impact on seafloor environments based on this data may be over-estimated. AIS data was extracted from grid boxes surrounding each of the station's locations measuring an extra 0.01° latitude north and south, and an extra 1° longitude east and west (see Table VIII).

Table VIII: Station locations and AIS grid box latitude and longitude selections

Station	**Location**	**Latitude grid**	**Longitude grid**
B13	74.30 °N / 30.00 °E	74.29 °N – 74.31 °N	29.00 °E - 31.00 °E
B14	76.30 °N / 30.30 °E	76.29 °N – 76.31 °N	29.30 °E – 31.30 °E
B15	78.15 °N / 29.59 °E	78.14 °N - 78.16 °N	28.59 °E - 30.59 °E
B16	80.07 °N / 30.04 °E	80.06°N - 80.08 °N	29.04 °E – 31.04 °E
B17	81.16 °N / 29.19°E	81.15 °N – 81.17 °N	28.19 °E – 30.19 °E

The longitudinally elongated grid box shape was chosen due to this study's focus on the North-South gradient in water mass distribution and sea ice cover. Using this data, typical local annual fishing effort was estimated based on averages over the seven year period data was available for (2012 – 2018).

4.2.4 Data analysis

To test whether a reduction in sea ice cover duration and northward shift of the Polar Front could lead to changes in B/P exchange processes, seafloor and water flow properties had to be characterised, to provide context. Sedimentary conditions along the transect were characterised in both ice free and ice-covered conditions. In the contextual characterisation of the benthic environment, Analysis of Similarity tests (ANOSIM; vegan package, Oksanen *et al.*, 2019) were chosen to check for differences between the five stations as well as the two years due to their flexibility in within-group as well as between-group testing. Predictors for ANOSIM testing were the two years of sampling, the sampled stations, and a selection of sampled stations divided into those north of, and those south of the Polar Front, respectively. Response variables were the environmental variables investigated in each of the reported ANOSIM tests. To satisfy the conditions of ANOSIM testing, data were pre-screened for heteroscedasticity between groups *via* Breusch-Pagan testing (Breusch and Pagan, 1979) and found to be satisfactorily homoscedastic in all cases. Samples taken across a range of time points (*e.g*. throughout a resuspension cycle) or along sedimentary depth profiles were also tested for differences between time points and/or depths using

ANOSIM. Correlation analyses between sea ice extent and fishing effort between 2006 and 2017 and 2012 and 2016 were carried out, using landings and AIS data respectively as a proxy for trawling. Data that displayed normal distributions were tested using parametric correlation analysis (Pearson, 1895) and non-normally distributed data were tested using non-parametric correlation (Spearman, 1904). Critical erosion thresholds determined through experimental flow channel measurements were compared against predicted tidal current speeds and directly measured current velocities to reveal the effects of physically driven exchange processes through tidal and current flow along the seabed.

In order to quantify B/P exchange potentials of DM and PM within their individual driver groups as well as those of the exchange processes themselves at each station in both years, variables were combined into a variety of data sub-sets for different parts of the analysis. OM flux was used as an example of particulate B/P exchange and Phosphate and Silicate fluxes were used as examples for solute exchange. To investigate individual B/P exchange drivers or processes, variables were selectively included based on relationships identified in Chapter 1 (Rühl *et al.,* 2020; see Table IX for a list of which variable was included in the determination of which drivers/processes). Data sets were normalised using z-scoring, to account for differences in scale and units between variables.

Table IX: Selection of driving factors for each direct driver of DM and PM exchange, as well as the overall exchange processes; blue shading indicates DM drivers and processes, orange shading indicates PM drivers and processes; variables in brackets denote selective exclusion of these variables from some tests, to avoid over-weighting them as they are already represented within other variables (see in-text explanation)

Process	**Driving variables**												
	d_{50}	τ_0	Sediment density	Sediment TOC concentration	Sediment porosity	Phosphate and Silicate concentration	Phosphate and Silicate fluxes	SPM and suspended OC concentration	SPM and suspended OC flux	Bioturbation (depth and surface boundary roughness)	Bioirrigation (biodiffusion coefficient and Bromide tracer flux)	Max. current velocity	Trawling
PM Resuspension	(✓)	✓	✓	✓					✓	✓		✓	✓
PM Deposition								✓				✓	
Absolute PM flux	(✓)	✓	✓	✓				✓	✓	✓		✓	✓
Diffusion-driven DM exchange					✓	✓							
Phys.Resuspension driven DM exchange	(✓)	✓	✓			(✓)	✓			✓		✓	✓
Advection-driven DM exchange	(✓)	✓			✓	(✓)	✓					✓	
Biological mixing driven DM exchange						✓				✓			
Bioirrigation-driven DM exchange					✓	✓					✓		

Absolute DM flux	(✓)	✓	✓		✓	(✓)	✓			✓	✓	✓	✓

To avoid an over-estimation of the impact of variables that are interdependent or derived from one another (*e.g.* τ_0 is partially derived from d_{50}), factors considered to be affected by this were selectively excluded, based on where strong inter-variable dependencies were found in preliminary analyses. For example, where both τ_0 and d_{50} were considered of importance, d_{50} was excluded as a separate factor as it was already considered through the inclusion of τ_0. Factors which were excluded from models through these considerations are indicated by brackets around their ticks in Table IX.

To quantify B/P exchange driver and processes and determine cause-effect relationships between the two as well as to individual environmental variables, the sub-group defined in Table IX were analysed using OPLS analyses (as introduced in Chapter 2; Thévenot *et al.*, 2015). OPLS were chosen due to their suitability for between-class discrimination when large within-class variation may be present, and to allow incorporation of the various data sets to equal degrees (Bylesjö *et al.*, 2006). Within the OPLS, the individual stations and the North / South (ice / no ice) divide were applied as the classes by which to group the data. Factors which contributed significantly to the model fit were identified by Variable Influence on Projection (VIP) values > 1. VIP values reflect loading weights of each model components as well as quantifying the variability of the response explained by the components (Mehmood *et al.*, 2012).

The contextual information provided through the previous analyses paints a vivid picture of the conditions at the seafloor-water boundary in areas representing the current, ice covered, Arctic as well as future ice free conditions. Using this, a non-quantitative assessment of the effects of sea ice loss and Polar Front location shift on the direction and magnitude of B/P exchanges was made.

4.3 Results

4.3.1 In-situ B/P conditions

4.3.1.1 Shear-stress induced resuspension and its effects

Critical shear stresses were significantly lower in 2018 than in 2019 (ANOSIM, R = 0.38, p = 0.002; see Figure 17).

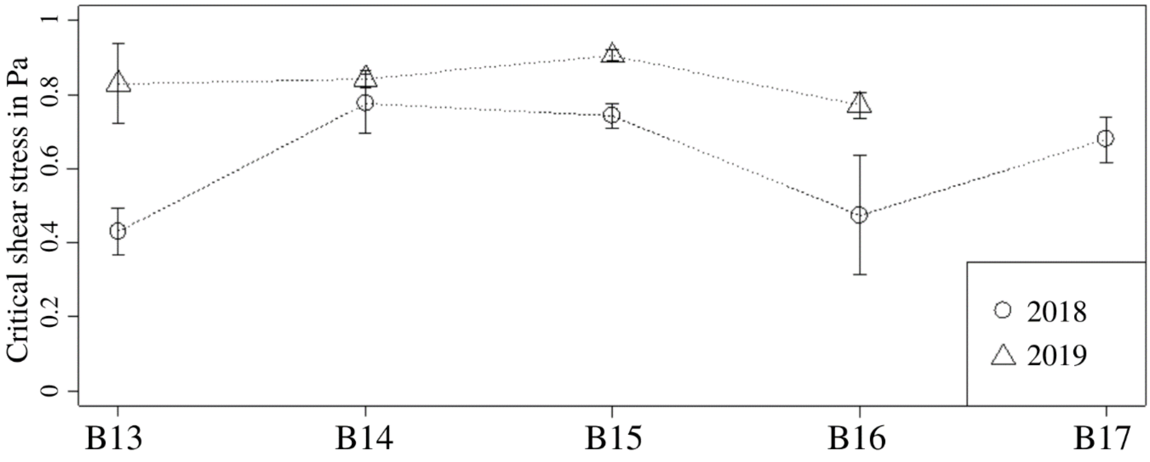

Figure 17: Critical shear stress at each station in 2018 and 2019

The differences between stations within each year were not as distinct but still significant, with higher values at B14 and B15 and lower values at B16 and, in 2018, at B13 which is due to the corresponding differences in mean grain size (ANOSIM, R = 0.198, p = 0.032).

4.3.1.2 Sediment properties

Mean sedimentary grain size was smaller at the two northernmost stations than in the south in both years (2018: ANOSIM, R = 0.221, p = 0.0001; 2019: ANOSIM, R = 0.21, p = 0.0003; see Figure 18), although grain sizes were very fine along the whole transect so this difference, despite its statistical significance, may not have an ecological impact.

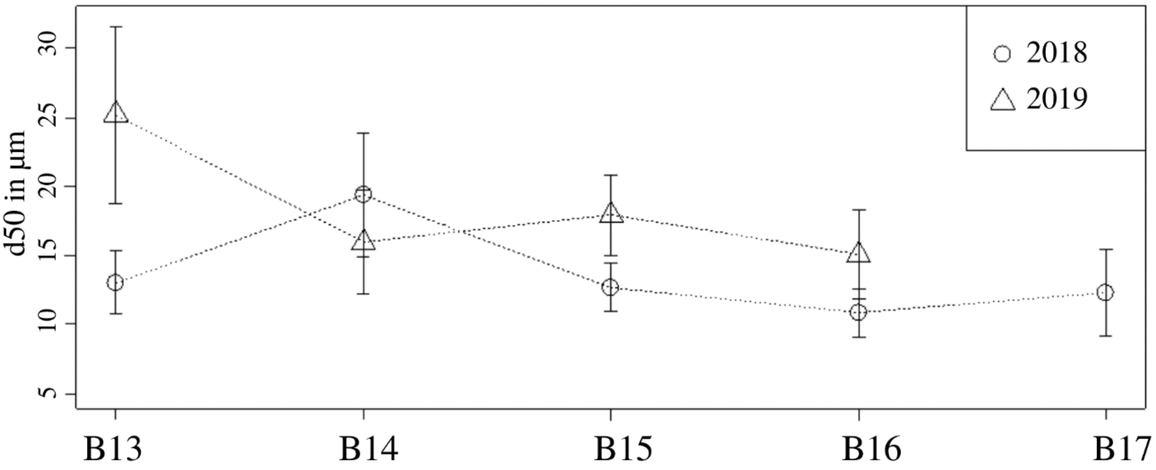

Figure 18: Mean sedimentary grain size (d_{50}) at each of the stations in 2018 and 2019

There were also variations in volumetric size class distribution along the transect in both years, exhibiting a higher clay content in the North and more silt in the South (2018: ANOSIM, R = 0.241, p = 0.001; 2019: ANOSIM, R = 0.216, p = 0.0007; see Figure 19).

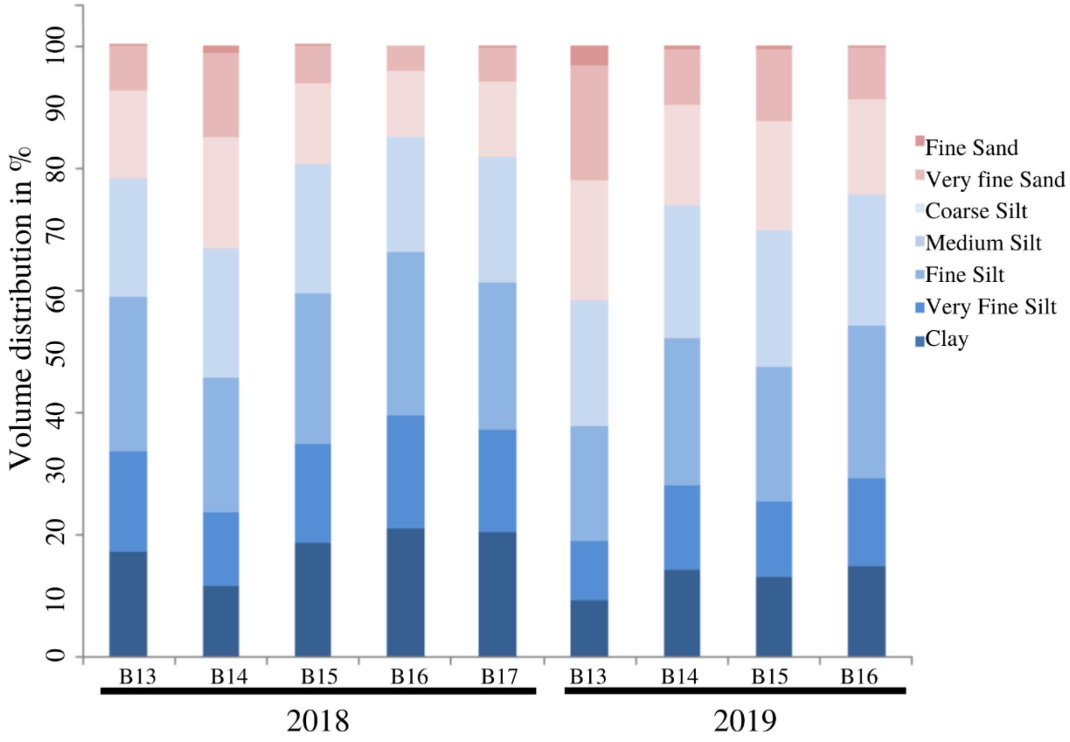

Figure 19: Sediment size fractions at each of the stations in 2018 and 2019

There was no significant difference in bulk sediment density between the different stations within year and depth groups (ANOSIM, R = -0.001, p = 0.57) and overall, sediment density was higher in 2019 than in 2018 (ANOSIM, R=0.544, p=0.0001; see Figures 20 and 21). The effects of critical shear stress-induced resuspension on measured sediment density were most notable in 2019, leading to lower densities in the top 1 cm (ANOSIM, R = 0.125, p = 0.036). Lower sedimentary layers were also affected by shear-stress application in 2019, showing an increase in average density at both B14 and B16 at 3-5 cm depth that was however not significant (ANOSIM, R = -0.029, p = 0.595; see Appendices 7 and 8). Sediment porosity was also overall higher and more variable in 2018 than in 2019 within station groups (R = 1, p = 0.008). Porosity varied with depth (ANOSIM, R = 0.134, p = 0.0001) and correlated to the variation of the sediment density (Pearson's, t = -10.332, df = 246, p < 0.000001; see Figures 20 and 21).

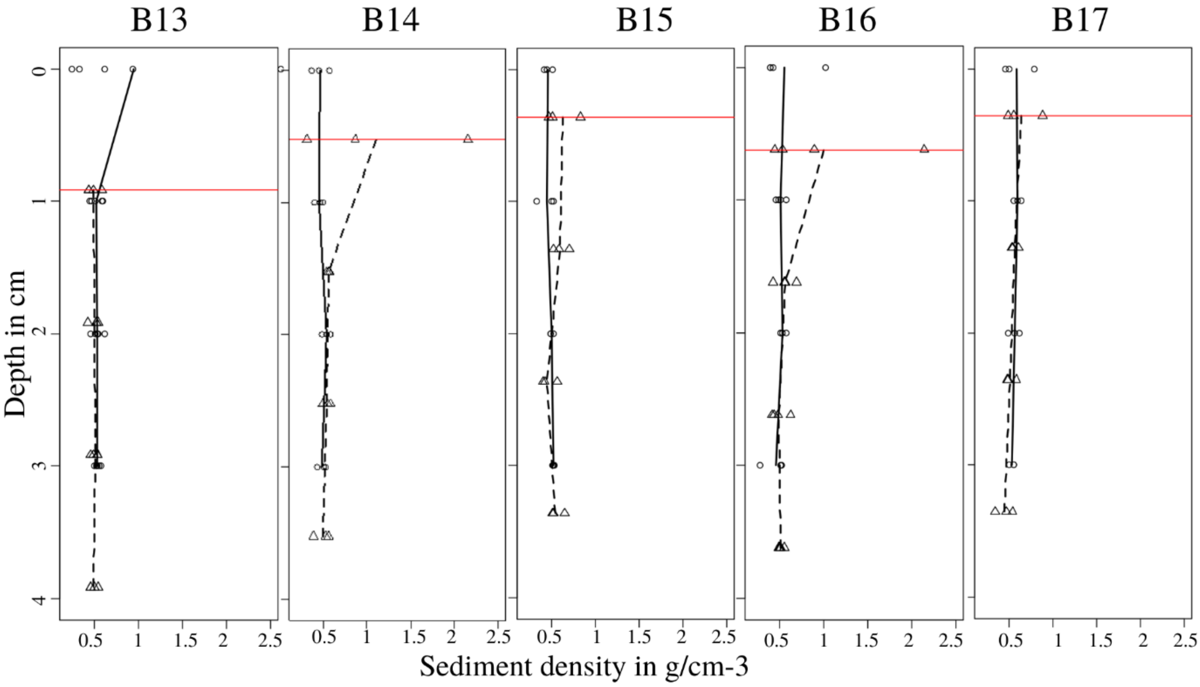

Figure 20: Average sediment density before (continuous line, variability shown through plotting of replicate samples as circles) and after resuspension (dotted line, variability shown through plotting of replicate samples as triangles) at each station in 2018; the red horizontal line shows the erosion depth, which is also the new sediment surface from which the sediment density depth profile was measured after resuspension has taken place

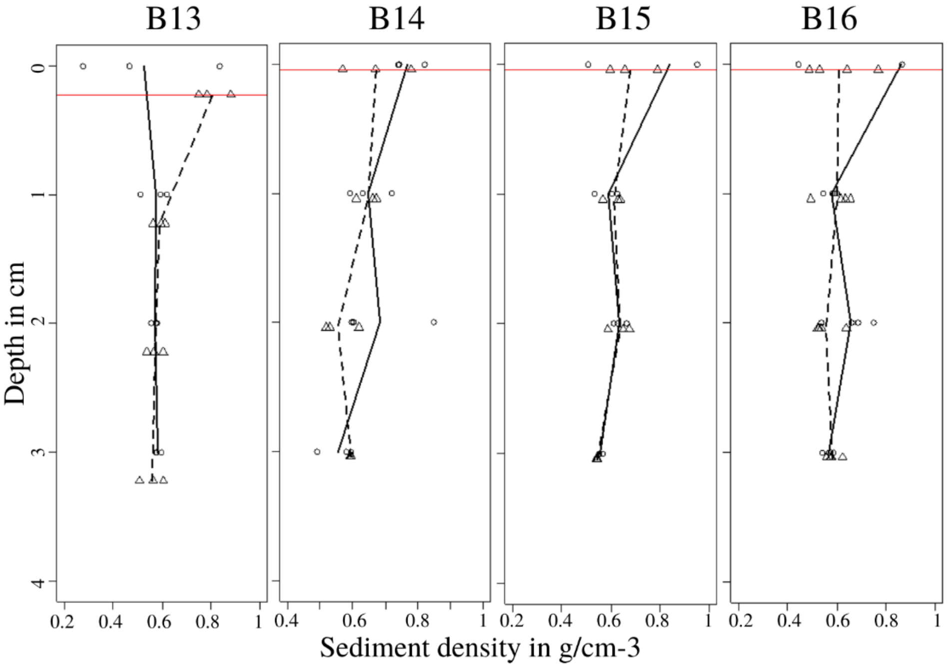

Figure 21: Average sediment density before (continuous line, variability shown through plotting of replicate samples as circles) and after resuspension (dotted line, variability shown through plotting of

replicate samples as triangles) at each station in 2019; the red horizontal line shows the erosion depth, which is also the new sediment surface from which the sediment density depth profile was measured after resuspension has taken place

In terms of the total organic Carbon (TOC) content within the sediment, overall TOC concentrations were higher in 2018 than in 2019 (ANOSIM, R=0.575, p=0.0001, see Figures 22 and 23). Most inter-station variation was found within the 3-5 cm depth layer in 2019. Variation in TOC content with depth was significant within each year and at each station (ANOSIM, R=0.464, p=0.0001; see Figures 22 and 23 for depth distributions). The differences in TOC content between samples collected from the same cores before and after resuspension experiments were not statistically significant (2018: ANOSIM, R = -0.077, p = 0.987; 2019: ANOSIM, R = -0.028 p = 0.65). Sediment density and TOC content across all stations were not correlated in either year (2018: Pearson’s, t = -0.9773, df = 142, p = 0.3301; 2019: Pearson’s, t = -0.36508, df = 102, p = 0.7158).

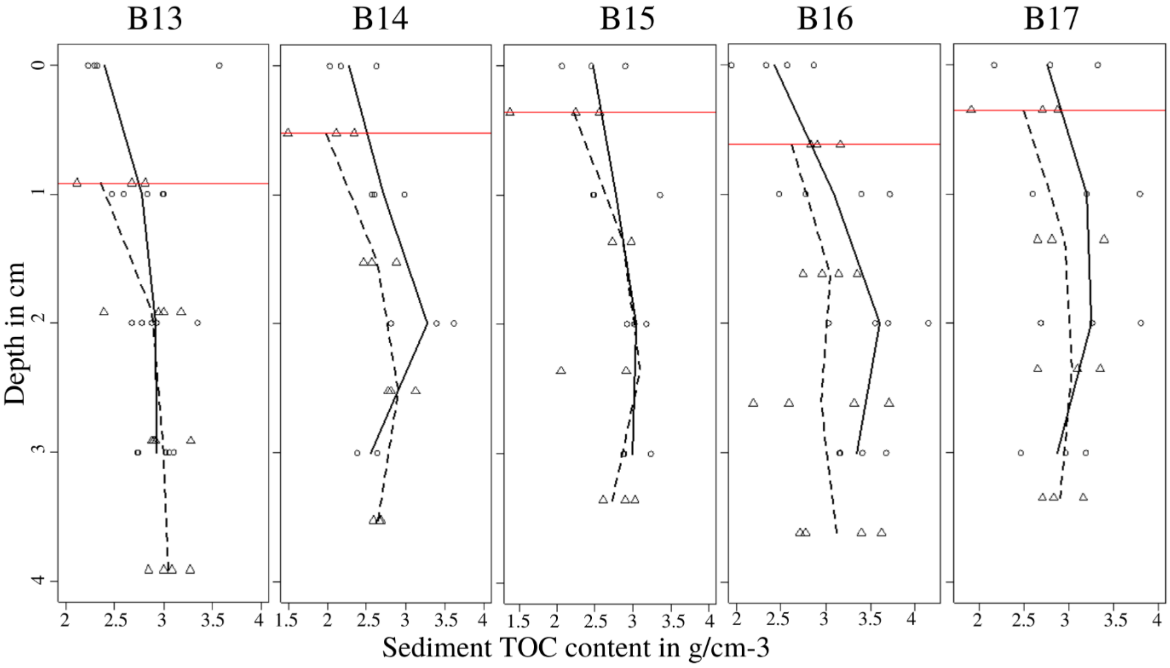

Figure 22: Average sediment TOC content before (continuous line, variability shown through plotting of replicate samples as circles) and after resuspension (dotted line, variability shown through plotting of replicate samples as triangles) at each station in 2018; the red horizontal line shows the erosion

depth, which is also the new sediment surface from which the sediment TOC content depth profile was measured after resuspension has taken place

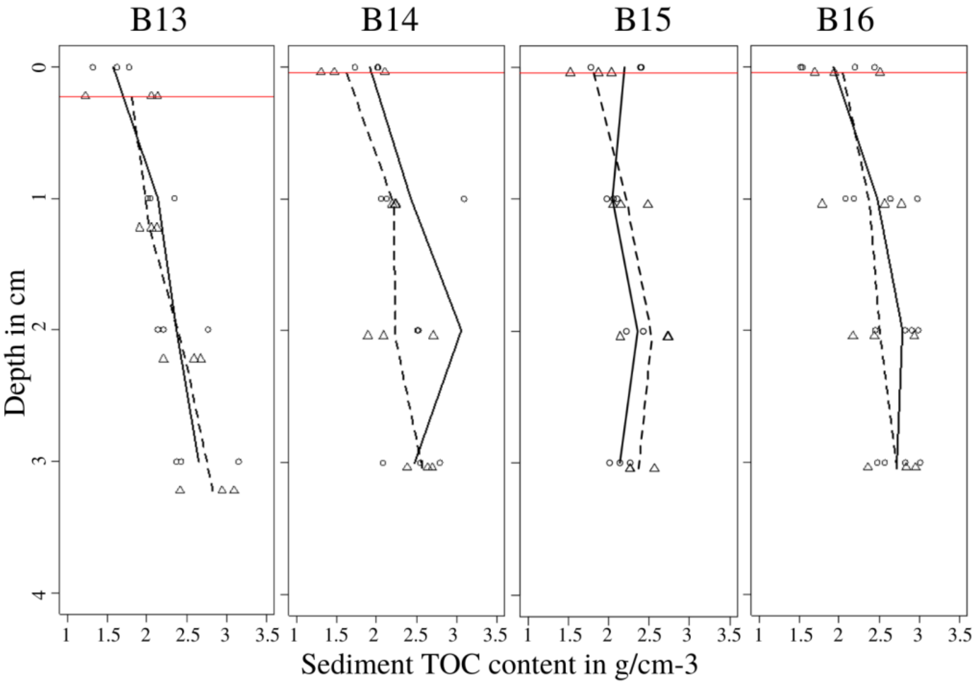

Figure 23: Average sediment TOC content before (continuous line, variability shown through plotting of replicate samples as circles) and after resuspension (dotted line, variability shown through plotting of replicate samples as triangles) at each station in 2019; the red horizontal line shows the erosion depth, which is also the new sediment surface from which the sediment TOC content depth profile was measured after resuspension has taken place

Erosion depths were overall deeper in 2018 than in 2019 (R = 0.152, p = 0.009, see horizontal lines in Appendices 7-10), but were found to be independent of sediment grain size (Pearson's, t = -1.5367, p = 0.1682), 0-1 cm depth in-situ sediment density (Pearson's, t = -0.2142, p = 0.8365) and 0-1 cm depth in-situ sedimentary TOC content (Pearson's, t = 1.5792, p = 0.1583).

4.3.1.3 SPM levels and shear-stress driven OC resuspension

Ambient levels of SPM and OC prior to resuspension were higher in 2018 than in 2019. Throughout the in-flume shear-stress application, the amount of SPM and OC increased over time at all stations during both years (SPM: ANOSIM, R = 0.851, p = 0.003; OC: ANOSIM, R = 0.812, p = 0.003; see Figure 24). Ambient OC concentration, as measured within flumes after the 24 hour settling period before the start of the resuspension experiments, in 2018 was highest at B13, followed by B15 and B17, and lowest at B16 and B14. While in 2018 ambient SPM levels were highest at B15, lower at B13 and B17 and lowest at B14 and B16, in 2018 the concentration of both SPM and OC was found to be highest at B13, decreasing continuously northwards along the transect. The concentration of suspended OC before and after resuspension showed no correlation with TOC levels at the sediment surface (2018: Pearson's, t = 0.40177, df = 32, p = 0.6905; 2019: Pearson's, t = 0.66749, df = 24, p = 0.5108).

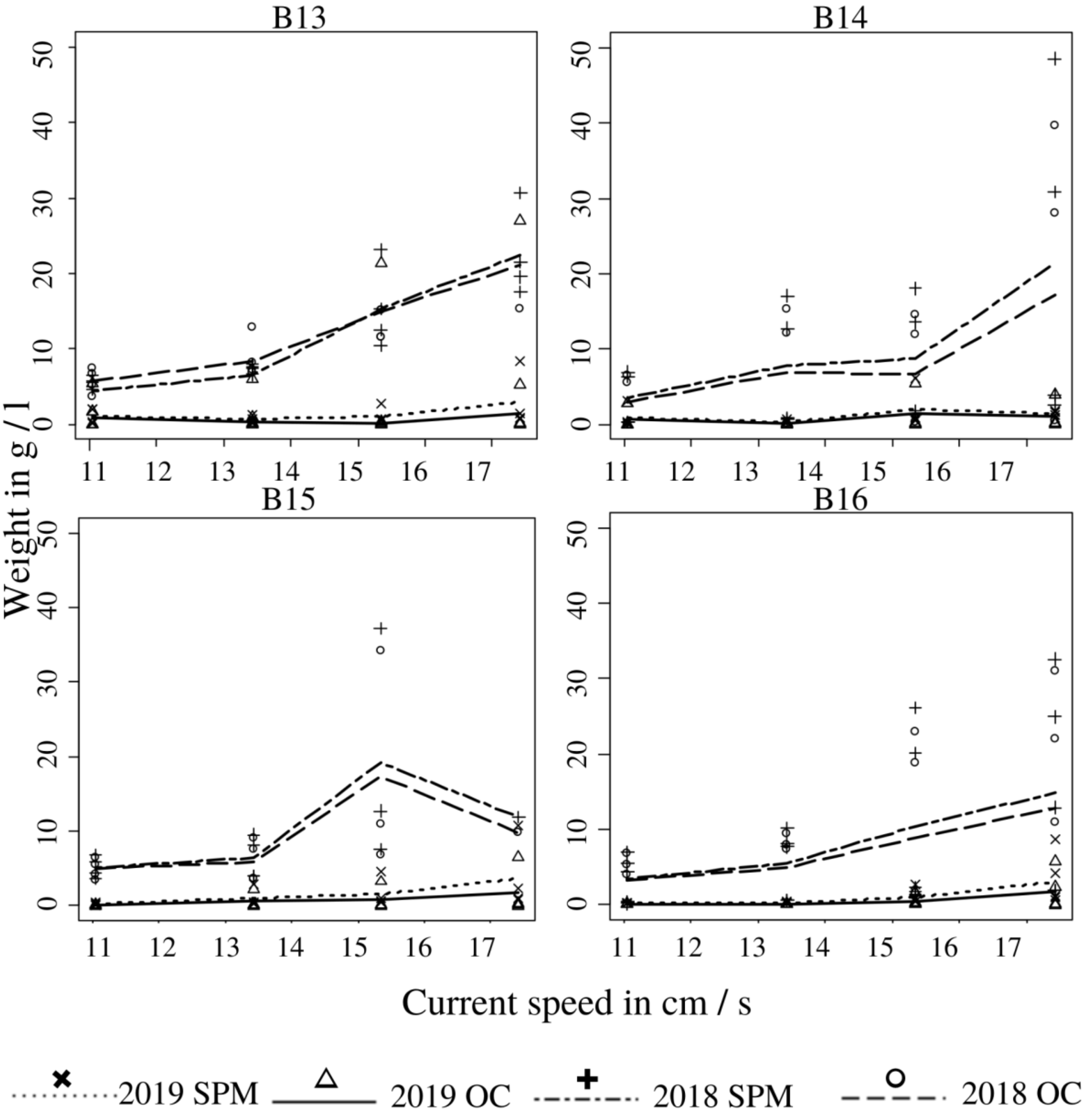

Figure 24: SPM concentration across stress-driven resuspension cycle, starting roughly at the point of resuspension and increasing with rising applied shear stress. The points of various shapes represent data points of replicate samples and the lines represent averages of the replicate

4.3.1.4 Shear-stress driven nutrient fluxes

Shear-stress-driven B/P flux rates of Ammonium, Phosphate, Silicate and Nitrite did not significantly differ between 2018 and 2019 (ANOSIM, R = 0.131, p = 0.19). Sediments in the area were a net source of Phosphate and Silicate but a net sink for

Nitrogen, which is why no distinct flux was detected here for any of the Nitrogen compounds. Silicate and Phosphate fluxes from the sediment into the water were initiated even at very low current speeds, below the respective critical erosion velocities (between 1.06 and 1.55 cm/s in 2018 and between 0.13 and 0.79 cm/s in 2019) had been reached (see Figure 25).

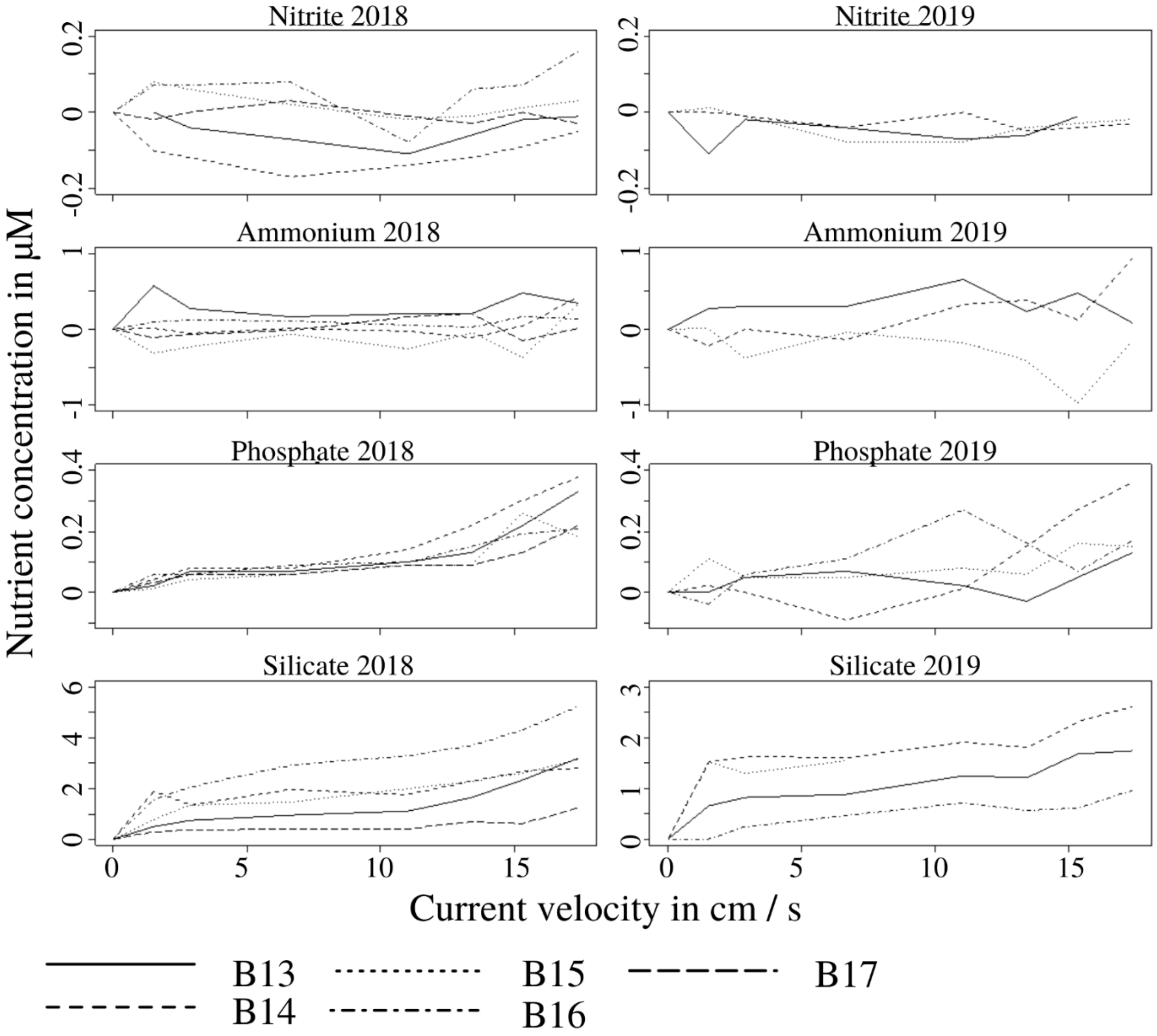

Figure 25: Nutrient fluxes driven by increasing current velocities during resuspension experiments

Shear-stress driven increase in Phosphate in the water column was highest in B14 and lowest at B15 in 2018, but highest at B15 and lowest at B16 in 2019, with significant inter-station differences in both years (ANOSIM, R = 0.491, p = 0.0001).

Net Silicate efflux was largest at B16 in 2018 and B14 in 2019 and smallest at B14 in 2018 and at B16 in 2019 (ANOSIM, R = 0.246, p = 0.017).

4.3.1.5 Benthic biology

Benthic macrofauna species assemblages varied along the transect, showing a clear separation between the southern (B13 and B14) and the northern stations (B16 and B17), with higher levels of biodiversity in the North (Solan *et al.*, in press). Bioturbation led to deeper mixing depths and rougher surface boundaries in ice free conditions than under ice cover (Figures 26 and 27), across the whole transect (ANOSIM, R = 0.488, p = 0.0002) but neither differed significantly between stations within each year (ANOSIM, R = 0.05, p = 0.23).

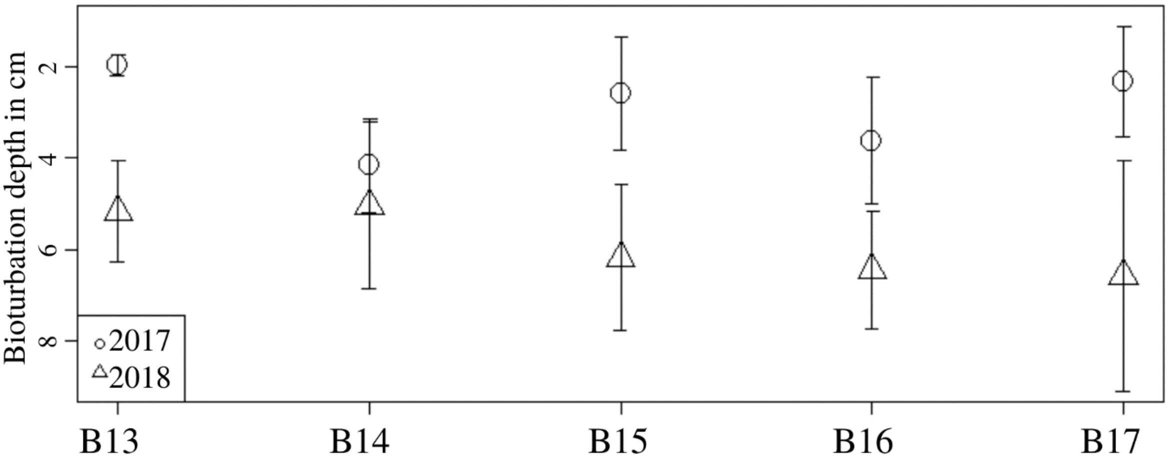

Figure 26: Bioturbation depth in cm at each of the stations in both 2017 (ice covered conditions roughly equivalent to 2019) and 2018 (ice free conditions)

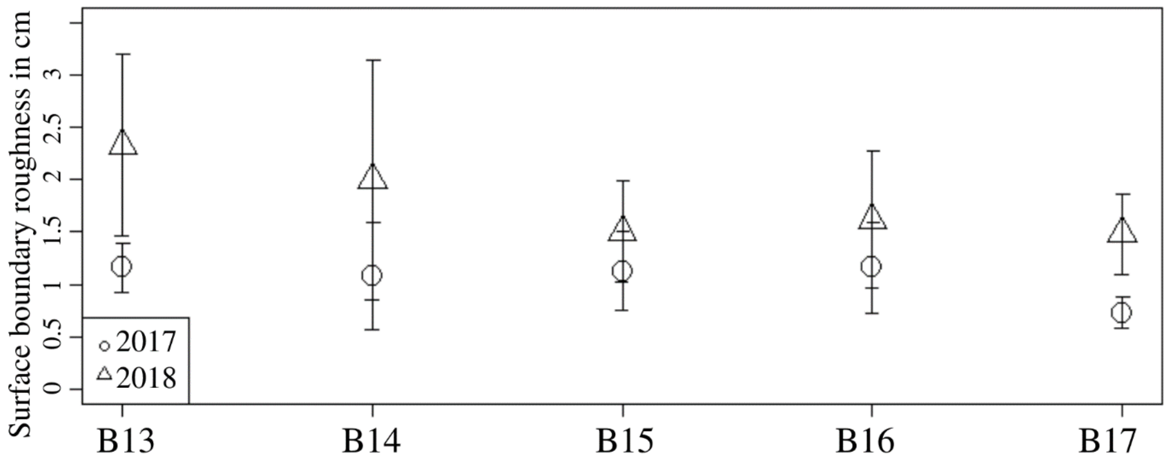

Figure 27: Surface boundary roughness in cm at each of the stations in both 2017 (ice covered conditions roughly equivalent to 2019) and 2018 (ice free conditions)

Bioirrigation did not vary significantly between stations in 2017 but in 2018 bioirrigation rates were higher at B13 than the rest of the stations (ANOSIM, R = 0.211, p = 0.014; see Figure 28).

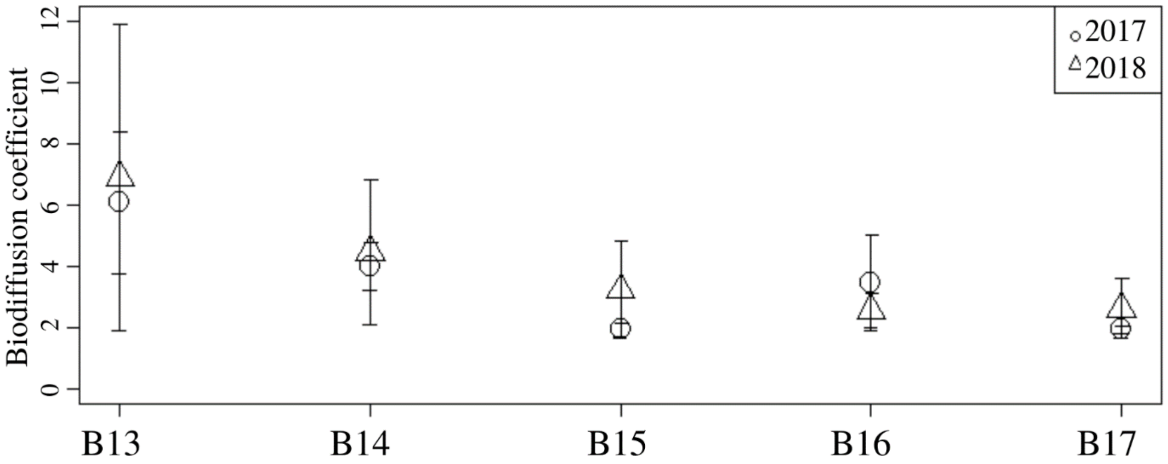

Figure 28: Biodiffusion coefficient at each of the stations in both 2017 (ice covered conditions roughly equivalent to 2019) and 2018 (ice free conditions)

Based on personal communications and unpublished data, sediment surface pigment concentrations varied along the transect (Ruth Airs, personal communication 2020). Overall pigment concentrations peaked near the Polar Front in both ice-covered and ice free conditions, while the percentage of unaltered chlorophyll a was highest at the station nearest the ice edge, so B17 and B14 in 2018 and 2019 respectively. Arctic ice algae, growing on the underside of sea ice and sinking towards the benthos when the ice melts, is known as an important seasonal food source in the arctic (Riebesell *et al*., 1991; McMahon *et al*., 2006). Ice algae was observed during both cruises in small quantities, but not sampled directly as no appropriate sampling gear had been prepared to collect the algae. Pigment samples taken at the sediment-water interface are however thought to include both plankton and ice algae material, particularly in locations where the recent sea ice retreat would have caused a down-flux of algal organic matter.

TEP area per volume in near-bottom water was lowest at B14 near the Polar Front (Birthe Zänker, personal communication 2020).

4.3.1.6 Current and tidal regimes within the benthic boundary layer

Tidally, East-West currents were dominant at B13 and B14 while North-South currents prevailed at the northern stations (see Figures 29 and 30). The strongest tidal currents were found at B16.

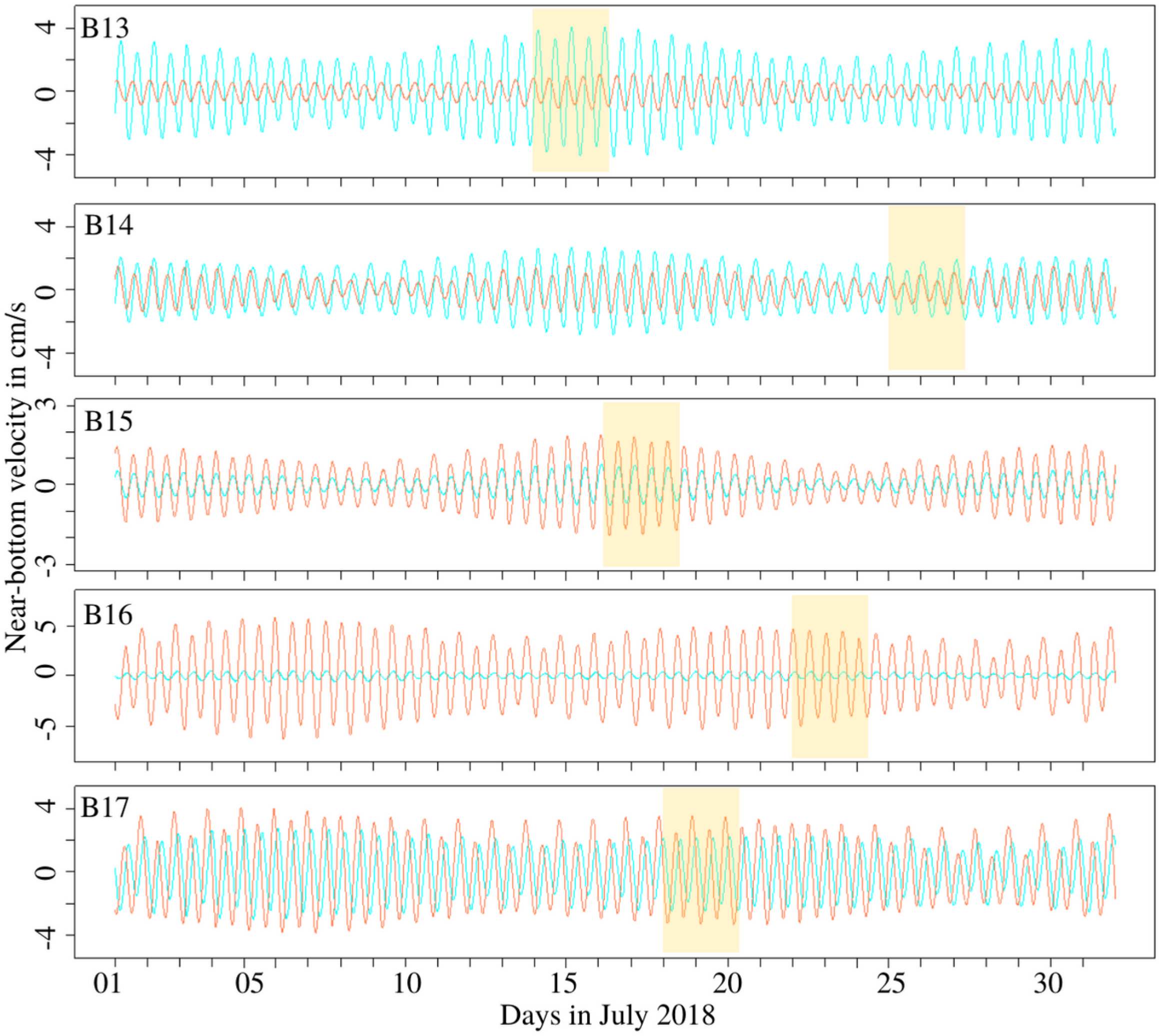

Figure 29: Near-bottom tidal flow in 2018, East-West component in blue, North-South component in red; dates during which the stations were visited are marked in yellow

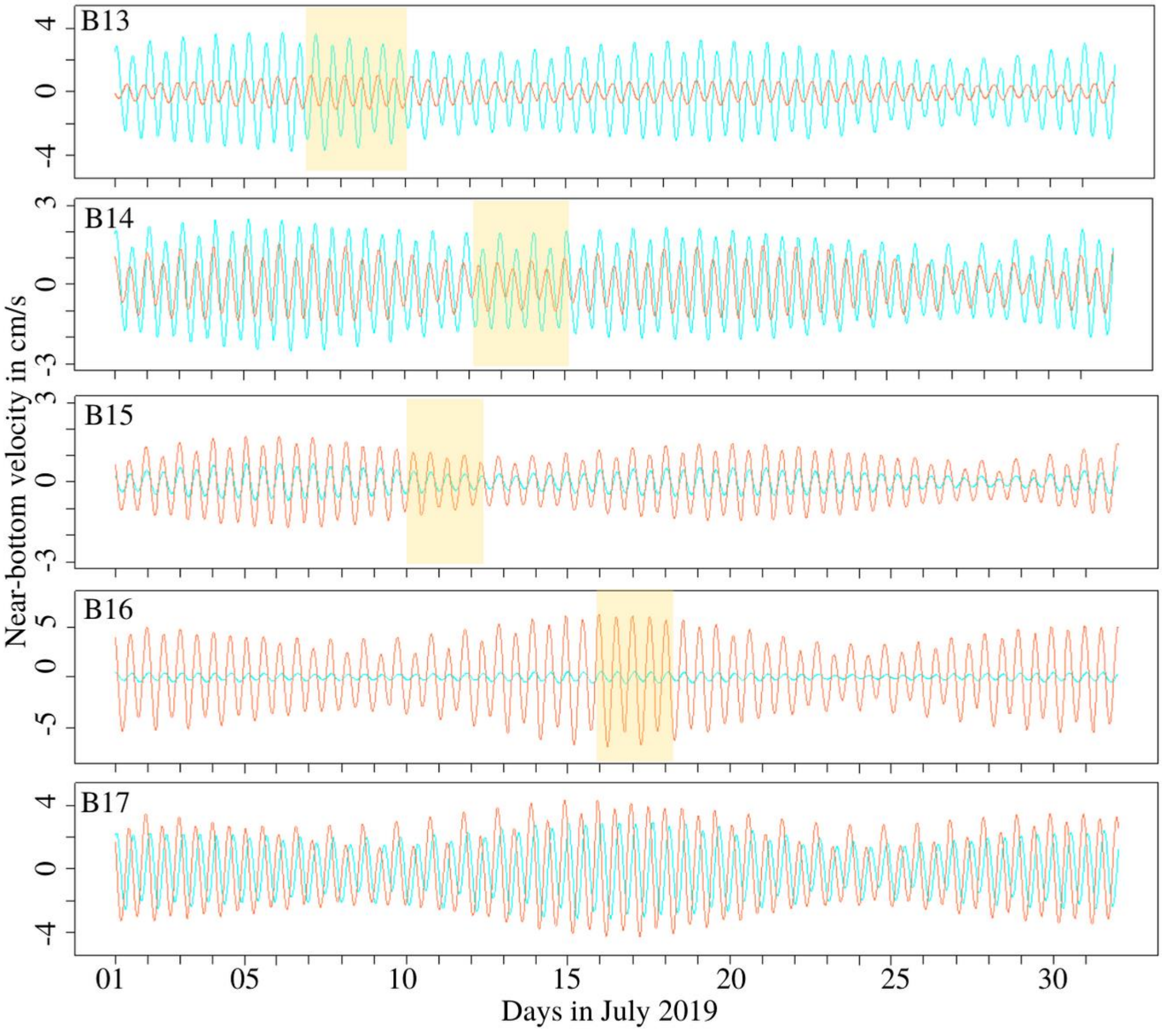

Figure 30: Near-bottom tidal flow in 2019, East-West component in blue, North-South component in red; dates during which the stations were visited are marked in yellow

Comparing the modelled tidal flow with the ADCP measurements taken during the 2019 cruise shows that tidal currents can account for more than half of the flow speed at B13, B15 and B16, and almost all at B14 (see Figure 31). The differences between tidal flow and critical erosion velocities shows that tidal flow within the benthic boundary layer alone is likely insufficient to induce resuspension (see Figure 31).

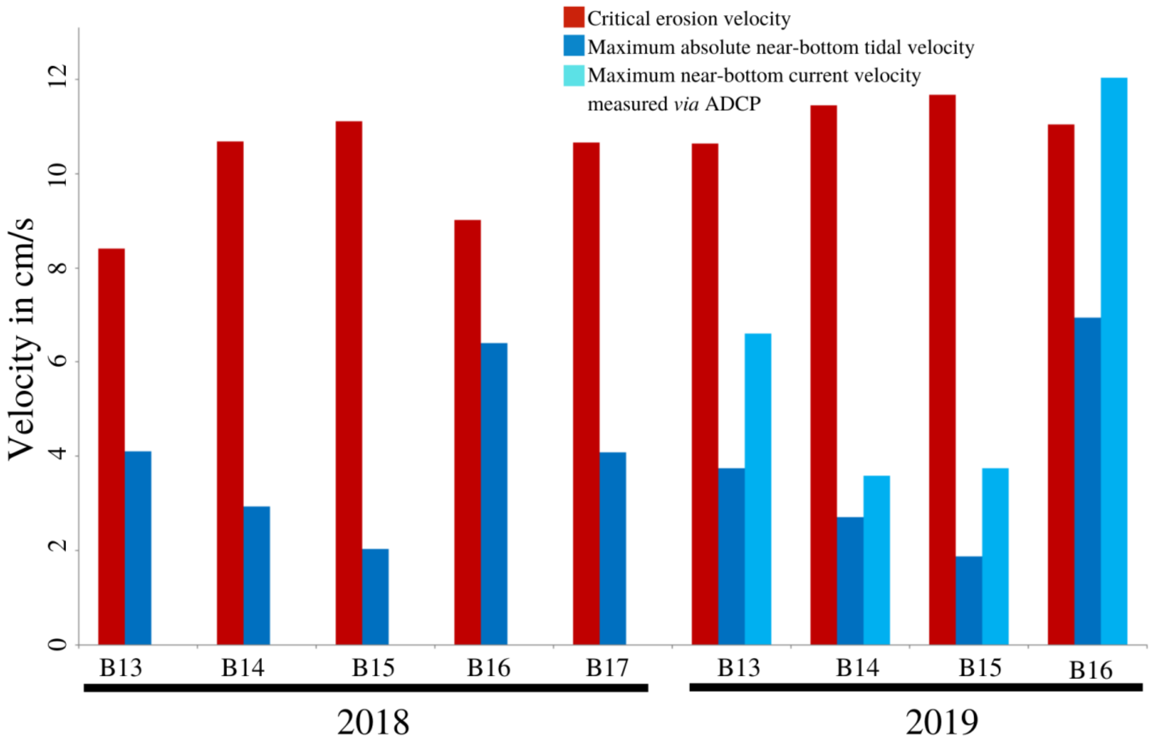

Figure 31: Maximum absolute near-bottom tidal velocities and overall current velocities measured with the ADCP (see Equation (C)) and critical erosion velocities (see Equation (A)) at each station in both years

ADCP current measurements in 2019 however show that in this year, overall current speeds were high enough to cross the critical erosion point at station B16, and presumably trigger associated advective and resuspension-driven B/P fluxes. As mentioned in the methods section, ADCP data had not been collected during the 2018 cruise, which is why no comparison between modelled tidal flow and measured current velocities can be made for this year. Because of this, it is uncertain whether the exceedance of the critical erosion velocity by ambient current velocities observed at B16 in 2019 is a common occurrence or an exceptional circumstance. The non-tidal components of the overall current velocities measured *via* ADCP in 2019 showed residual east-ward flow of roughly 2 cm/s at B13, residual south-east flow of 4-6 cm/s at B14, north-west residuals of around 1 cm/s at B15 and north-easterly residual flow of 1-1.5 cm/s at B16. Each site was visited at a different point in the spring-neap cycle, and S-N range in tidal velocities differed between sites.

4.3.1.7 Fishing *versus* Sea ice

Sea ice cover in April, when the ice extent is on average at its maximum, was correlated with landings data (Pearson's, t = 3.3124, p = 0.007847) but September sea ice cover (least extensive on average) did not correlate to the landings data (Pearson's, t = 0.14794, p = 0.8853). Based on AIS data, the average number of annual hours of trawling was highest at B13 (117.69 hours) and lowest at B16 (0 hours; see Table X for more detail). Trawling hours were negatively correlated to percentage sea ice cover at the stations (Pearson's, t = -4.3336, p = 0.0001293) in this seven year period.

Table X: Annual trawling effort at each station, based on 2012-2018 AIS records within the grid boxes surrounding the sample stations as specified in Table II; As no AIS data was available for 2019, I was unable to determine whether the sites had been trawled in that year prior to sampling, especially at B13 and B14, trawling events more recently than this are highly likely based on the seasonal timing of the trawling at these stations recorded in the other years

Station	**Average hours of trawling per year**	**Number of months during which site is trawled annually**	**Number of years in which site was trawled between 2012 and 2018**	**Average number of trawling incidents per year (average, maximum and minimum)**	**Time since last trawling incident at time of sampling**	
					2018	**2019**
B13	117.69 (stdev 70.09)	1 - 6 (average 3.86)	7 / 7	207.14 (max 666, min 46)	16 days	215 days (likely less)
B14	68.18 (stdev 79.47)	1 - 5 (average 3)	7 / 7	47.86 (max 128, min 6)	59 days	411 days (likely less)
B15	2.79 (stdev 2.83)	1 - 3 (average 1.29)	5 / 7	11 (max 38, min 1)	273 days	245 days
B16	0	0	0 / 7	N/A	N/A	N/A
B17	0.69 (stdev 1.26)	0 - 1 (average 0.29)	2 / 7	2.5 (max 3, min 2)	551 days	N/A

4.3.2 Quantifying B/P exchange of POM and Nutrients

4.3.2.1 DM B/P exchange

At the two southern, Atlantic dominated, stations (B13 and B14) the overall flux of DM was directed downward, from the pelagic towards the benthos. At the three Arctic-influenced stations on the other hand (B15-B17), DM fluxes were directed upward (See Figure 32).

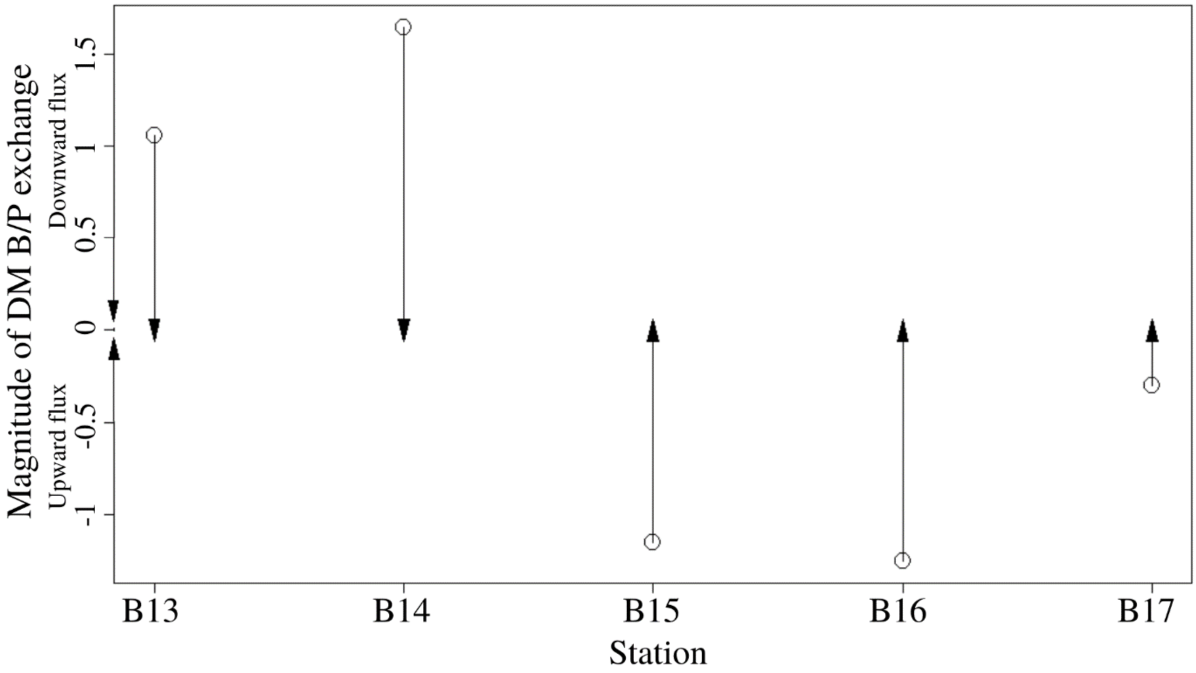

Figure 32: DM B/P exchange potential at each of the stations

Though differences between the stations were not significant in the inter-station OPLS model, it confirmed the 2-way split between southern (B13 and B14) and northern stations B15-B17 (Model 1, R2X = 0.535, R2Y = 0.93, Q2 = 0.604, pR2Y = 0.15, pQ2 = 0.1; see Appendix C, 4d, for VIP scores >1). Modelling the transect according to this bilateral divide showed that there were distinct differences between the two groups (Model 2, R2X = 0.678, R2Y = 0.971, Q2 = 0.762, pR2Y =

0.1, pQ2 = 0.05), attributable to differences in geophysical and biogeochemical parameters (sediment grain size, Phosphate concentration and shear-stress driven Phosphate flux), biological parameters (bioturbation depth and biodiffusion coefficient), and anthropogenic pressures (annual trawling hours spent at the sites; see Appendix C, 4d, Model 2 for all VIP scores > 1). This suggests, that both passively driven differences in DM exchange potential along the transect caused by a concentration gradient between benthic and pelagic environments and variability in sediment grain size, and active exchange processes through biological sediment reworking, the placement of solutes in the water column through anthropogenic disturbances (trawling) as well as the potential for shear-stress driven nutrient fluxes must be considered. The relative importance of each of the driver groups towards these fluxes varied between the stations, though diffusion and advection-driven B/P exchanges were generally the most important, while the influence of physical resuspension was small across the whole transect. Biological mixing had more impact on DM B/P exchanges than bioirrigation. The fact that ambient Phosphate concentration was an important factor while Silicate concentration was not, even though both were considered equally, indicates the clarity of distinction in microbial Phosphate uptake and processing between the South and the North, identified by Downes *et al.* (2020) from samples taken on the same 2018 cruise (Solan, 2018). Atlantic influxes supply large amounts of Phosphate to the Barents Sea from the South, which is then taken up and retained by the pelagic phytoplankton (dominated by coccolithophores) and microbial community. Locations dominated by Arctic water on the other hand, at which the phytoplankton community is dominated by phaeocystis species, show overall lower ambient Phosphate concentrations and lower microbial uptake rates, but also an emission of organic phosphorous compounds by the microbial community

(Downes *et al.*, 2020). Thus, the net downward fluxes recorded at the southern stations and net upward fluxes in the North correspond to the respective concentration gradients in Phosphate between benthic and pelagic environments.

4.3.2.2 PM B/P exchange

PM B/P exchanges were dominated by upward flux at B13 and downward flux at all other stations (see Figure 33). Upward and downward transport were roughly equally important at all sites except for B13, where upward fluxes were dominant.

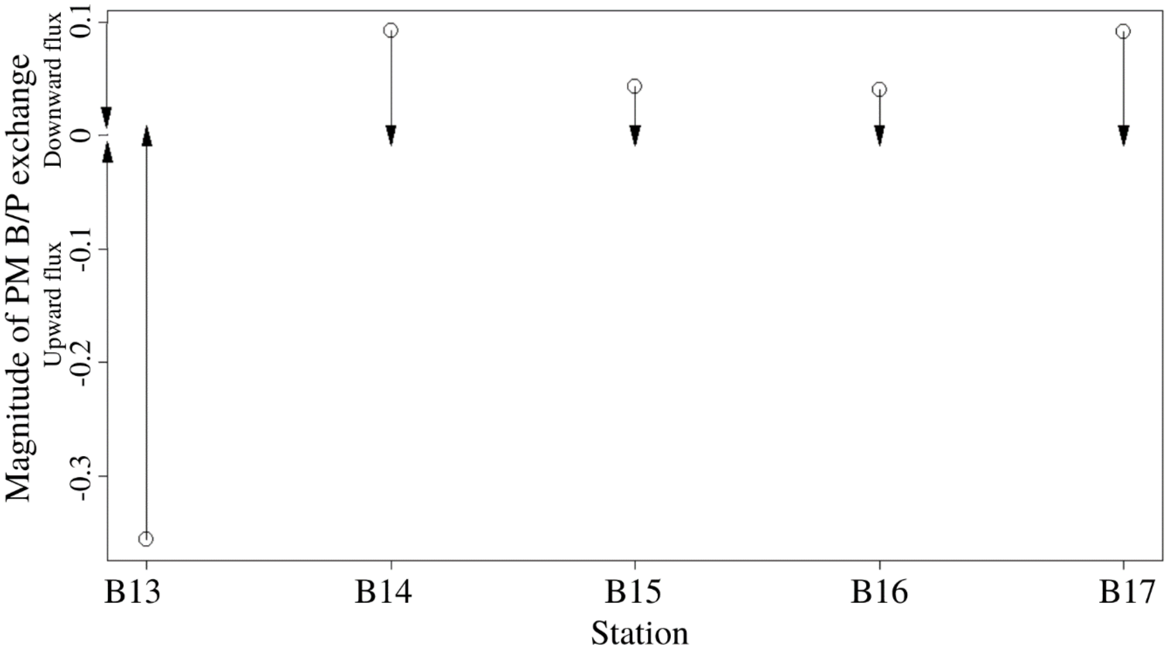

Figure 33: PM B/P exchange potential at each of the stations

This more southerly bilateral divide was reflected in the inter-station OPLS model (Model 3, R2X = 0.594, R2Y = 0.824, Q2 = 0.606, pR2Y = 0.15, pQ2 = 0.1, see VIP scores > 1 in Appendix C, 4d, Model 3). Re-modelling the division between B13 and the rest of the stations showed that differences in ambient SPM and suspended OC, biological activity and annual trawling hours were the main reasons for the bilateral split (Model 4, R2X = 069, R2Y = 1, Q2 = 0.902, pR2Y =

0.05, pQ2 = 0.05; see VIP scores > 1 in Appendix C, 4d, Model 4). This suggests that although physical anthropogenic disturbances play a significant role in this environment, they do not overshadow benthic biological activity, which also contributes significantly to PM B/P exchanges. The significance of differences in ambient SPM and suspended OC between the South and the North may be seen as representative of the importance of the pelagic OM production. Alternatively, it may be connected to the increased trawling effort in the South, causing higher levels of turbidity (see Palanques *et al*., 2001).

The overall potential for PM flux was much lower than that for DM flux, which suggests that DM B/P exchanges are of a greater magnitude and importance than PM exchanges in this environment. The processes factoring into B/P exchange at this arctic Barents Sea location are illustrated in a simplified graphic in figure 34.

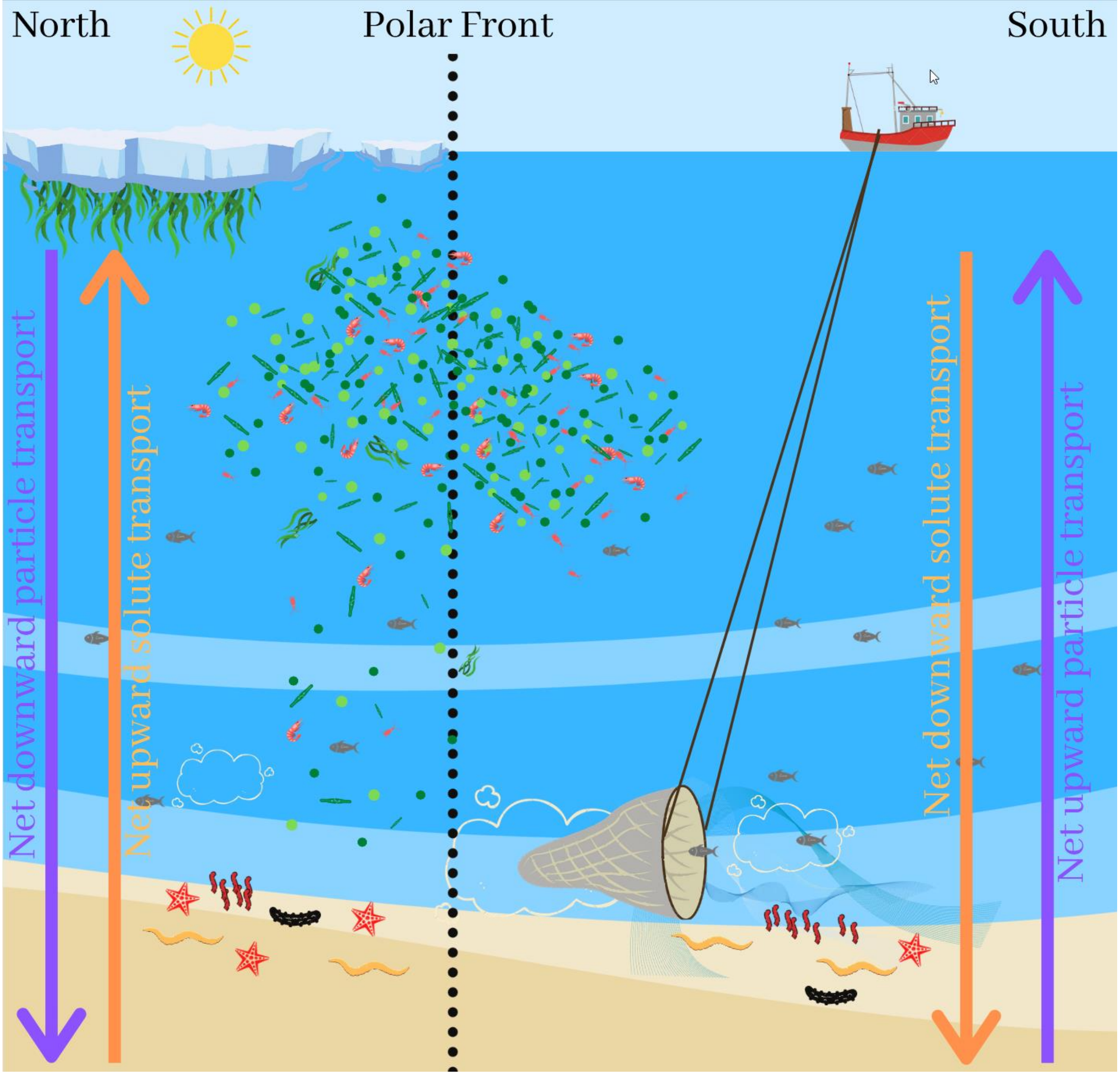

Figure 34: Conceptual graphic of the environment, and factors influencing benthic-pelagic exchanges north and south of the Polar Front in the Arctic, including the direction of respective net PM and DM exchanges

4.4 Discussion

Factors driving the differences between the Atlantic-dominated and the Arctic-dominated stations can be split into direct, and indirect drivers of DM B/P exchange. The direction of DM flux is linked to ambient Phosphate concentrations, thereby also to the community composition of pelagic primary producers, which also depends on temperature (Downes *et al.*, 2020). Thus, a climate driven shift in the magnitude and dominant direction of passive Phosphate B/P exchanges is highly likely. This could lead to changes in the composition, diversity and abundance of pelagic primary producers. Biologically driven active DM exchange processes are dependent on macrofauna community composition and biodiversity, both of which have been found to vary between Atlantic and Arctic dominated benthic environments and are likely to be affected by climate change (Carroll and Ambrose Jr, 2012; Cochrane *et al.*, 2012; Jørgensen *et al.*, 2015). A northward shift of the Polar Front and corresponding increase in pelagic primary production in the northern parts of the Barents Sea are predicted to cause an increase in benthic biomass in the North (Cochrane *et al.*, 2009). This could increase bioturbation depths and surface boundary roughness in these areas, thereby raising the potential for biologically-driven B/P exchanges. It is unlikely that the heightened small-scale topographic diversity will cause a rise in advective fluxes however, because the cohesive sediment matrix within Barents Sea glacial troughs does not promote this mechanism (Maiti *et al*., 2010; Rühl *et al.*, 2020). At the southern stations however, the northward shift of the Polar Front may benefit the pelagic environment, and be detrimental to the benthos in areas which are currently covered by sea ice for part of the year (Søreide *et al*., 2013).

Present-day observations show a contrast between high trawling efforts at the southern stations, which are either infrequently, or never covered by sea ice, with little to no trawling in the North. Fishing fleets can be expected to exploit the increasingly available fishing grounds following the retreat of the ice and northward shifting distribution of commercially important boreal species (Fossheim *et al.*, 2015; Misund *et al.*, 2016). As trawling is one of the main drivers of the current differences in DM B/P exchange direction and magnitude, the resulting re-distribution of trawling activity is likely to cause changes to these processes as well. It is possible that the trawling-induced increase in solute release into the water column could cause a shift from net upward to net downward fluxes (Morin and Morse, 1999; Kalnejais *et al*., 2010). The dragging of trawling gear through surface sediment layers is known to cause resuspension and winnowing out of finer particles, including organic matter (Ferré *et al.*, 2008). It is therefore likely that the significance of mean grain size in distinguishing Atlantic and Arctic environments is a secondary effect of the heavier trawling of the Atlantic-dominated stations. Through this, the potential for shear-stress driven DM fluxes, which are linked to grain size, may also be increased at the northern stations, where current speeds are already higher than in the South.

Factors contributing most to the differences in PM B/P exchange between the southern, upward transport dominated, and the northern, downward dominated, Barents Sea, were measures of suspended matter, bioturbation and anthropogenic sediment disturbance. The climate-driven increase in both benthic biomass and trawling effort in the northern Barents Sea suggests that B/P exchange conditions in the North are likely to change towards a state of more net upward fluxes (*e.g.* Carroll *et al.*, 2008; Jørgensen *et al.*, 2015; Misund *et al.*, 2016). If this was applied to the whole of the northern Barents Sea, half the area thus affected would be at least equivalent in size to the country of Ukraine (roughly 603700 km^2).

Previous findings, that sedimentary particle mixing in glacial trough environments is predominantly biologically driven (Maiti *et al.,* 2010), had not taken anthropogenic drivers into account. Considering that trawling is also known to impact on the structure of benthic macrofauna communities (Puig *et al.*, 2012), and suspended matter concentration (Palanques *et al.*, 2001), this factor is likely doubly important in determining climate-driven changes in PM B/P exchange. In the southern Barents Sea, the predicted decrease in benthic biological activity could lead to higher rates of long-term OC burial due to lower biogenic Carbon processing efficiency (Søreide *et al.*, 2013; Stevenson and Abbott, 2019). At present date, the Barents Sea is the largest sink of OC of all Arctic shelf seas, and Carbon assimilation and sedimentation rates are higher in the North than in the South (Carroll *et al.*, 2008). Future conditions may promote a reversed Carbon processing balance, limiting upward fluxes south of the Polar Front.

Under current conditions, ambient suspended OC levels in near-bottom water were highest at the southernmost station and in ice-free conditions, both SPM and suspended OC concentrations decreased with increasing latitude. This could mean that with the retreating sea ice and northward shift in the Polar Front, SPM and OC concentrations in the North may rise, creating a heightened potential for downward PM fluxes through passive sinking processes. It is difficult to weigh up whether this will be sufficient to counter-act the increased upward fluxes through biological and anthropogenic drivers.

By demonstrating the potential for climate change to switch the dominant direction of net PM B/P exchange, this study requires us to rethink our current perceptions of Arctic B/P coupling. So far, most studies have focussed on the downward directed flux of organic matter produced in the pelagic and supplied to the benthic environment (*e.g.* Grebmeier *et al*., 1988; Grebmeier, 1993; Ambrose and Renaud, 1995; Dunton *et al.*, 2005; Tamelander *et al.*, 2006; Morata, 2007; Renaud *et al.*, 2008; Søreide *et al.*, 2013; Stasko *et al.*, 2018). The current study integrates both top-down and bottom-up B/P exchange processes and includes not only their biological drivers, but also their biogeochemical, physical and anthropogenic ones. In addition, of the existing studies of climate-change effects on B/P coupling in the Arctic, most tend to also focus only on the consequences of reduced organic matter input due to sea ice loss (*e.g*. Thamdrup and Fleischer, 1998; Mattlin *et al.*, 2000; Fortier *et al.*, 2002; Marcin Węsławski *et al.*, 2011; Birchenough *et al.*, 2015). While this is also addressed in the current study, the transdisciplinary approach taken here facilitated the detection of other likely climate change impacts such as the potential switch in the prevalent direction of B/P exchanges. There are a handful of previous studies which explore climate change effects in the Arctic while incorporating oceanographic and geophysical, as well as biological elements (Carroll and Carroll, 1990; Nishi and Tabeta, 2007; Søreide *et al.*, 2013), although none of them have also considered the effects of a potential increase in anthropogenic pressures.

A limitation of the current study is that it captures a mere snapshot of two years. Without the backdrop of previous studies or long-term records for most of the variables (excluding sea ice cover (Cryo, 2019), trawling effort (Global Fishing Watch, 2020) and sediment grain size (Norges Geologiske Undersøkelse, 2020)), there is little indication of whether, or how much, the conditions recorded in this study have already been altered due to climate change effects. Furthermore, the specific nature of conditions found within glacial trough areas limits how applicable the findings of this study are to the Barents Sea Shelf in general (see *e.g*. Chochrane *et al.,* 2012).

The work carried out in this study should be used as a basis for future studies of the same processes in a more diverse selection of Arctic habitats, to allow conclusions about climate-driven changes to B/P exchange drivers and processes in the wider Barents Sea and overall Arctic area. The results of this study may be used to inform management strategies and thereby mitigate the impact of anthropogenic actions on B/P exchanges in the future.

Chapter 5

General discussion and conclusion

5.1. Introduction

Direct drivers of benthic-pelagic exchange can be identified from the existing literature as shown in Chapter 1, but their variability across various temporal and spatial scales impedes our ability to assess their relative influences on overall exchange processes (*e.g.* Graf, 1992; Jones *et al.*, 1998; Chauvaud *et al.*, 2000; Mattlin *et al.*, 2000; Marcin Węsławski *et al.*, 2011; Tonkin *et al.*, 2017). In this thesis, B/P exchanges were investigated over short term seasonal, medium-term inter-annual/multiannual, and proxy long-term climate driven temporal scales, through case studies.

5.2. Seasonal variability in B/P exchange processes

In temperate environments, many of the biological, chemical and physical processes that are known to affect the exchange of particulate and dissolved matter between the seafloor and the water column, follow cyclical patterns associated with seasonal variation. Chapter 2 assessed the extent to which these individual seasonal cycles affect specific direct drivers of seafloor-water exchanges, how drivers interact with one another throughout the year, and what the resulting seasonal variation in the exchange processes themselves is. It was determined that, in an average year for a temperate coastal ecosystem, there are two periods of upward dissolved matter flux, and one period of downward flux. The flux periods were three, two and a half, and three and a half months long respectively and driven primarily through diffusion, biological activity and a mix of biological activity and hydrodynamics, respectively. Particulate matter flux exhibited a clear winter-time efflux from the sediment into the overlying water (resuspension), driven by the highly physically active hydrological environment; and two periods of depositional flux from the water column sown onto and then into the seafloor, during and after the main phytoplankton bloom. The first particulate matter deposition event was purely biologically driven, while the second was derived through a mixture of benthic and pelagic faunal activity and increasing riverine influx and wave action. Even though the seasonally cyclical and alternating biological and physical/meteorological influences overlapped in several instances, dominant drivers within each season could be identified. The seasonal patterns and interactive relationships between environmental variables, drivers and exchange processes identified at the study-site (Station L4, Western Channel Observatory), therefore build the basis for a deeper understanding of ecosystem processes at intra-annual time scales. This information can then for example be used to inform ecosystem models and management decisions. In the case of the former, trophic or elemental cycling modelling can benefit from seasonal ecological contextualisation as an additional variable to provide more accurate outputs at a finely resolved temporal scale. Ecosystem management guidelines too could be based on incorporating season-specific measures, fine-tuned to the prevalent processes in different parts of the year, as identified in studies such as this one.

5.3. Inter- and multiannual variability in B/P exchange processes

The seasonal patterns detected in Chapter 2 are based on the premise of an average year, but in the natural environment any individual year is influenced by inter-annual variability, and the occurrence of stochastic extreme events. Therefore, in Chapter 3, the multi-year temporal patterns of dissolved and particulate matter benthic-pelagic exchanges at Station L4 were investigated, to assess connections between inter- and multiannual processes, and characterise their nature and what drives them. It was determined that, on a decadal time scale, extreme events such as unusually large or long-lasting storms and phytoplankton blooms have the capacity to cause both inter-annual and multi-annual variability in B/P exchange processes. Throughout the decade investigated in this chapter, an unnaturally large and long-lasting spring plankton bloom (Zhang *et al.*, 2015), two sequential years with extreme storm events (Masselink *et al.*, 2016) and recurrent instances of co-occurring synergistic positive NAO and El Niño episodes (NOAA, 2019) occurred. All of these events shaped the inter-annual variation and multi-annual trends detected in the B/P exchange time series. Chapter 3 therefore highlights the importance of multi-parameter long-term observatories, such as the Western Channel Observatory, and demonstrates the use of transdisciplinary time-series datasets to identify individual events which have large ecosystem-level impacts.

5.4. Climate-change driven long-term shifts in B/P exchange processes

The temporal variability in B/P exchange processes on medium length time scales described in Chapter 3, are characterised by stochastic variations from regularly occurring conditions, such as the ones described in Chapter 2. Although these occasional events may occur suddenly, they are typically followed by a gradual return to pre-event conditions. Long-term environmental changes can be gradual too, yet if a tipping point is crossed, systems can abruptly be fundamentally changed. One such scenario is illustrated in Chapter 4. Here, the effects a climate-driven switch from an ice covered, Arctic water dominated system, to an Atlantic-dominated ice free one, is likely to have on seafloor water exchanges, were investigated. Results showed that sea ice reduction and northward shift of the Polar Front have the potential to cause a switch in the direction of net dissolved and particulate matter benthic-pelagic exchanges in the Arctic part of the Barents Sea. A distinction between southern, Atlantic dominated, and northern, Arctic dominated regions was detected in physical, biological and anthropogenic drivers of benthic-pelagic fluxes. Sediments south of the Polar Front were siltier and more erodible, and contained lower levels of infaunal biodiversity, resulting in differences in benthic biological activity between the northern and southern Barents Sea regions. The latter, in combination with higher amounts of trawling activity south of the Polar Front, were of particular importance in the differentiation between northern and southern conditions. In today's conditions, DM fluxes were found to be dominated by net downward transport in the South, and upward in the North, while PM exchanges were the opposite. Based on the differences identified between the two systems, a likely result of the northward shift in the position of the Polar Front would be that the northern Barents Sea conditions would become more similar to those in the South of this region. In practice, this could mean more DM downward and PM upward fluxes in the North, shifting the overall balance. The inclusion of anthropogenic, physical and hydrodynamic variables in this approach shifted the focus in Arctic benthic-pelagic coupling research to a balanced view of both upward and downward exchanges, in contrast to many previous studies of benthic-pelagic coupling processes which focused on downward fluxes (*e.g.* Grebmeier *et al.*, 1988; Grebmeier, 1993; Ambrose and Renaud, 1995; Dunton *et al.*, 2005; Tamelander *et al.*, 2006; Morata, 2007; Renaud *et al.*, 2008; Søreide *et al.*, 2013; Stasko *et al.*, 2018). A switch in benthic-pelagic exchange directions in Arctic environments under future conditions could have wide-reaching consequences for other ecosystem processes (*e.g*. changes to the benthic macrofauna community (Nordic Council of Ministers, 2007) and localised organic Carbon burial rates (Stevenson and Abbott, 2019)). The importance of anthropogenic actions revealed in the results of this study could be used to inform sustainable management strategies for Arctic shelf environments, and thereby minimise cumulative impacts that interact with those of climate change, where possible.

5.5. Practical implications of the co-occurrence of variability at different time-scales

In the natural environment, temporal variability in ecosystem processes such as benthic-pelagic exchanges co-occurs simultaneously on different time-scales. The effects of each of the temporal variations can therefore overlap, altering the overall variations caused to the ecosystem. Analytical techniques, such as the Seasonal Decomposition of Time Series outlined in Chapter 3, can be used to assess their relative impact on the overall patterns observed in the data, if the time-series in question is long and comprehensive enough. The minimum time-series length may depend on the time-scale of local multi-annual or multi-decadal trends (see *e.g.* the 65 year minimum time series length specified in Wu *et al*. (2007)), and in some areas, such as the Arctic, less time is needed to identify trends (less than 30 years, see Henson *et al.* (2016)). The presence of inter-annual as well as inter-decadal fluctuations suggests the need for time series of at least three decades to reveal long-term trends, with data sets covering at least 50 % of the required predicted time period (Ghil and Vautard, 1991; Splinter *et al*., 2013; Williams and Esteves, 2017). In order to reliably model and predict the occurrence of extreme events such as the ones outlined in Chapter 3, time series should be as long as possible, to correctly identify and capture frequency patterns.

The overlap between short, medium, and long-term variability can lead to misguided implications, such as the effects of one being mistaken for those of another. The observations made in Chapter 4 for example, of a substantially lower sea ice extent during the second year’s cruise than during the first, could have been mistaken for a sign of an extreme case of climate-induced sea ice loss.

Thanks to the long-term record indicating the normality of such extreme inter-annual variability unrelated to climate trends, this possibility could however be placed in an appropriate ecological context. For environments in which, for example, both seasonal and inter-annual variability of the same parameter exist (*e.g*. organic matter supply quality and quantity; Grebmeier, McRoy and Feder, 1988), a sampling campaign to determine inter-annual temporal variability would have to take place consistently within the same season, to produce conclusive results. Alternatively, a record spanning all seasons, subsampled and analysed in within-season periods, can be equally conclusive as demonstrated in Chapter 3. An attempt to record medium or long term temporal patterns could otherwise easily be a simple miss-interpretation of patterns and trends on shorter time scales.

5.6. Previous studies and novel contributions

Previous literature provides a thorough image of most aspects of benthic-pelagic exchanges, including details on individual drivers and processes. However, as noted in the literature review in Chapter 1, Section 1.1, there are few published studies that assess the variability and compare the relative influences of these drivers and processes across different temporal scales. The research presented in this thesis has contributed fundamentally to closing this knowledge gap by covering variability in B/P exchange processes on three different time scales: seasonal (short term), inter- and multi-annual (medium term), and climate-driven (long term).

As mentioned in Chapter 2, there are previous studies on seasonal variability in benthic-pelagic coupling (*e.g*. Graf, 1992; Jones *et al.*, 1998; Lee *et al.*, 2002; Chipman *et al*., 2012; Ubertini *et al.*, 2012; Tonkin *et al.*, 2017), none of which however take hydrological drivers into account to the same extent to which they are addressed in this thesis. Similarly, there are publications on long-term variability in benthic-pelagic exchanges (Grebmeier *et al*., 1988; Berger and Wefer, 1990; Chauvaud *et al.*, 2000; Smith *et al*., 2006), as well as the effect of extreme events (Zhang *et al.*, 2015; Collins and Sutherland, 2019). The approach taken in Chapter 3 incorporates both, thereby providing a more complete image of natural conditions. Of the previous studies of B/P coupling in the Arctic, almost all focused on top-down processes (Grebmeier e*t al.*, 1988; Grebmeier, 1993; Ambrose and Renaud, 1995; Dunt*on et al*., 2005; Tamelander *et al*., 2006; Morata, 2007; Renaud *et al*., 2008; Søreide *et al*., 2013; Stasko *et a.*, 2018). Although there are several investigations of the effects of climate change on Arctic benthic-pelagic exchange processes (Thamdrup and Fleischer, 1998; Mattlin *et al.*, 2000; Fortier *et al.*, 2002; Marcin Węsławski *et al.*, 2011; Birchenough *et al.*, 2015), few incorporated oceanographic and geophysical as well as biological elements (exceptions: Carroll and Carroll, 1990; Nishi and Tabeta, 2007; Søreide *et al.*, 2013). The work presented in Chapter 4 incorporates both physical and biological variables, covers both top-down and bottom-up processes and is the first to directly link the predicted climate-induced increases in trawling effort on the northern Arctic shelf to changes in B/P coupling processes.

The overall novelty of this work thus lies, not only in its investigation of temporal variability along varying time scales, but also in its transdisciplinary approach. This thesis has highlighted that, through the transdisciplinary combination of long-term monitoring with targeted high resolution data sets, the contributions of biological, biogeochemical, oceanographic, geophysical, anthropogenic and meteorological drivers to temporal variability in benthic-pelagic exchange processes can be detected. The results presented in this thesis show the importance of considering the temporal ecological context of ecosystem processes. The near-equal inclusion of biological and non-biological environmental variables in this work, brings the importance of hydrological, meteorological and anthropogenic drivers of temporal variability in benthic-pelagic exchange processes into focus. This is a shift, away from the biologically-centred approaches taken by much of the previously published benthic-pelagic coupling research, and towards a holistic, real-life ecosystem approach. In addition, we now have a better grasp of how the different drivers of benthic-pelagic exchanges interact on different time-scales, and can implement driver-process and driver-driver interactions and relationships deduced from the observations made in Chapters 2 – 4 in similar ecosystems locally or on a global scale. The result is an improved understanding of ecosystem processes in their temporal ecological context, on which future work can be based.

5.7. General limitations

On top of the limitations outlined in the individual data chapters, there are a number of overarching limitations to the research presented in this thesis.

Firstly, it was not possible to investigate variation on all three time scales (seasonal, inter-annual, long-term climate trend) within the same environment. As mentioned in Chapter 3, the decadal records at the temperate study site were too short to reliably capture any true long-term trend. Some of the variables in the Western Channel Observatory database have been recorded for multiple decades and may be used to detect more long-term temporal patterns (*e.g.* Highfield *et al.*, 2010). However, the benthic record is thus far of insufficient length to permit a balanced, multi-decadal investigation of B/P exchanges at this site. Due to the resulting combination of temperate (Chapters 2 and 3) and Arctic environments (Chapter 4), it was unfeasible to draw quantitative conclusions about the implications of co-occurring variability on all three time scales in Section 5.5. However, while the differences between intra- and inter-annual time-scales are small, and interactions between the two can reasonably be expected, climate-driven trends are on a different scale as they can cause permanent baseline shifts (*e.g*. Fulweiler and Nixon, 2009; Griffiths *et al.*, 2017). Moreover, comparing one temperate site with a transect in the Arctic poses no real scope for generalised comparisons or conclusions between the two. In recording at least short and medium-term variability at the same site, the work presented in this thesis at least covers the two that are most closely linked. Thus, the baseline for temporal variability in the ecosystem was established, and the overall aim of the thesis, to investigate the interactions of B/P exchange drivers and processes on a range of temporal scales, was met.

Secondly, although similar methods were used across all time scales due to their shared utility to answer the respective research questions in each chapter, the available data sets were not equal. In Chapters 2 and 4, comprehensive combinations of long-term records and highly resolved *in-situ* and experimental observations were compiled. In Chapter 3 however, a long-term time-series data set was used which had not been collected with the B/P exchanges in mind. Because of this, some of the relevant measurements included in the other two studies could not be included. As already mentioned in Chapter 3, Section 3.4, this may have led to an omission of variables which had been identified as being key drivers of benthic-pelagic exchanges on other temporal scales (*e.g*. Critical Shear Stress, see Chapter 2). Through the grouping of variables into the driver groups defined in Chapter 1, the effects of potential omissions could however be somewhat mitigated. In this way, all direct drivers were represented in each study, regardless of the secondary environmental variables included in the driver groups.

Further, the lack of spatial variability of the locations investigated throughout this thesis limits the transferability of its results. Further studies which cover a wider range of benthic communities and physical environments need to be investigated on similar time scales to contextualise the results in a broader, global, context.

Finally, the examples used to study temporal patterns in dissolved matter benthic-pelagic exchange drivers and processes differed between short-term intra-annual (Chapter 2; Dissolved inorganic Nitrogen), and long-term climate-induced variability (Chapter 4; Phosphate and Silicate). This was mainly due to differences in the availability of the data. Using the same example in both would have increased the comparability between the two chapters. Nevertheless, the driver-process relationships identified in each of the studies hold up to scrutiny, and the differences between dissolved inorganic Nitrogen, and Phosphate and Silicate benthic-pelagic exchanges are not as extensive as those between, for example, dissolved inorganic Nitrogen and Oxygen, or Carbon (Emerson and Hedges, 2003).

5.7.1 Practical limitations

As mentioned in several instances throughout the previous chapters, there were limitations to the sampling design and execution of some of the work presented in this thesis. In-situ sampling, as carried out for Chapters 2 and 4, can be highly dependent on factors that are out of any individual’s control, such as the weather. Consequently, scientists have to accept this fact and potentially adapt projects and redefine their aims accordingly. In the case of the field work carried out for the seasonal study presented in Chapter 2, more frequent resuspension experiments had for example been planned throughout the year, which would have provided a more even coverage of information on seafloor resuspendability and shear-stress driven fluxes. The limitations in sample collection opportunities were the cause of a re-definition of the time periods analysed throughout the year, from the original plan of a month-by-month analysis to the selection of the five phenological periods presented in Chapter 2. Fortunately, the temporal coverage was broad enough to capture inter-periodic variability throughout the year nonetheless. Instruments that are needed for laboratory-based sample analysis are also at times fragile. In the case of this thesis' work, this meant the unexpected underrepresentation of biogenic sediment cohesion measurements due to the fact that the samples that had been collected could simply not be analysed.

Another practical limitation, faced mainly by small projects such as carried out throughout a doctoral or postdoctoral research appointment, is that only limited working hours are available as it is usually up to a single person to carry out the research. In the case of a subject of research which relies heavily on collecting records of a multitude of parameters from various disciplines (*e.g.* the biological, geophysical, biogeochemical, anthropogenic and oceanographic variables affecting B/P exchanges), this limitation is likely to lead to uneven coverage. A single person can become an expert in one, or even a few disciplines, but is unlikely to master all and is thus likely to overlook, or underrepresent something.

5.8. Practical applications of results presented in this thesis

The results presented in this thesis detail temporal variability of key ecosystem processes at three different time scales, thereby providing an important temporal ecological context for applications such as ecosystem management and modelling. Intra- and inter-annual variations in nutrient and organic matter availabilities for example, including the effects of extreme events shown in Chapter 3, could be included in ecosystem modelling approaches to improve their accuracy in terms of temporal variability. Such additional variables in ecosystem modelling could not only be applied at this specific site or in this particular time period, but as transferrable variables that can be applied to other systems too. The resulting output would resemble the natural state of the ecosystem more closely than current models, which are often unnaturally regular and consistent.

An indication of the direction of long-term trends or potential sudden changes to important ecosystem functions, are highly useful for ecosystem and fisheries management planning for the coming decades. The results of Chapter 4, indicating a potentially large impact of fishery-seafloor interactions on overall benthic-pelagic exchange processes under future climate conditions, could specifically be used, to inform policy to keep fishing fleets in check, and thereby limit their impact. Knowledge generated in this thesis could also be included in the reports of independent and/or intergovernmental bodies such as the Intergovernmental Body on Climate Change (IPCC). This would place the research presented here into a broader context with related work, and help to inform legislative decision-makers and management agencies around the world.

The effective use of transdisciplinary data sets throughout this thesis highlights the utility of combining data inputs of all relevant disciplines, thereby evidencing the recommendation of the continued application of this approach in modelling, ecosystem management and future scientific studies.

5.9. Recommendations for future research

Future research of the drivers and processes of benthic-pelagic exchanges should be based on the combination of long-term monitoring and targeted highly resolved data as the work presented in this thesis is, to provide both a broad temporal context and enough detail to characterise individual ecosystem processes. To this end, the implementation of multidisciplinary long-term observatories, and maintenance of existing ones, to facilitate the placement of ecosystem process investigations in the right temporal ecological context, are recommended (see also Chapter 3, Section 3.4). Newer technologies, such as the analysis of environmental DNA (eDNA) could also be incorporated with data sets of older, well-established, methods to this end.

One of the short-comings of this thesis' research, outlined in Section 5.7, sheds light on an opportunity for further research: an investigation of variability in benthic-pelagic exchanges on short, medium and long-term temporal scales, at the same location. This would allow for a true quantitative assessment of the implications of co-occurring temporal variation, and improve our understanding of their interactivity. There are no publications of this nature to date. For example, an awareness of the exact interactions between multi-year patterns and true long-term trends at the same location, would help to assess the magnitude and nature of the trend accurately, avoiding under- or overestimations.

The implementation of the methods used in Chapters 2 – 4, and the driver-process relationships described throughout this thesis, in other kinds of environments would be beneficial to expand our understanding of benthic-pelagic exchanges globally. Environments in which seasonality doesn't follow the temperate cycle described in Chapter 2 (*e.g.* Arctic (Olli *et al.*, 2002) or Mediterranean (Coma *et al.*, 2000)), would likely have different, or additional drivers of seasonal variability in benthic-pelagic exchange that were not considered here. It is even unclear whether the insights into temporal variation in the temperate environment investigated in this thesis are transferrable to other temperate sites. Another temperate location in an otherwise comparable environment may yet have enough differences in sediment properties, faunal communities, riverine influences, or other environmental characteristics to lead to fundamental differences in benthic-pelagic exchanges on seasonal and/or inter-annual time-scales. Once temporal variation in benthic-pelagic exchanges has been studied repeatedly in various environments, a global model may be constructed, balancing benthic-pelagic fluxes on seasonal, inter-annual and long-term scales.

Finally, an investigation of long-term trends in locations where true baseline data (dating back to pre-industrial times) as well as long-term records exist, would allow a quantitative assessment of their impact. There are some observatories with extensive enough records to assess purely pelagic processes (see AWI (2020) and POGO (2020) for comprehensive lists of and links to long-term observatories, globally) but unfortunately none with a long enough record of the benthic environment. The Bermuda Institute of Ocean Science for example has records of pelagic physical, biological and chemicals properties dating back to 1988 (BIOS, 2020a) and an Oceanic Flux Programme spanning more than four decades that recorded vertical particle fluxes (BIOS, 2020b). These could be used to investigate multi-decadal patterns in particulate benthic-pelagic exchanges. Unfortunately, as no benthic records exist, it would still be impossible to identify some of the drivers of exchange and assess their relative impacts.

Thus, this final recommendation for future research concerns not the imminent, but the more distant future. In a few decades, if more benthic monitoring has been incorporated into existing time-series and when enough data have been recorded of both benthic and pelagic processes (records spanning multiple decades, as mentioned in Section 5.5), long-term investigations of benthic-pelagic exchange processes grounded in an environmental baseline and based on time-series records will be possible. Then, we will be able to get a grasp of multi-decadal, and in time perhaps even centennial temporal patterns in benthic-pelagic exchange drivers and processes.

Glossary of Terms

Term	Definition/description of the term
Advection	The transfer of heat or matter by the flow of a fluid, especially horizontally in the atmosphere or the sea
Aerobic	Relating to, involving or requiring free oxygen
Anthropogenic	Originating in human activity
Barotropic fluid	A fluid whose density is a function of pressure only
Bedform	A feature that develops at the interface of fluid and a moveable bed
Benthivore	Feeding on benthic organisms
Benthos	The flora and fauna found on the bottom, or in the bottom sediments, of a sea or lake
Biofilm	A thin but robust layer of mucilage adhering to a solid surface and containing a community of bacteria and other microorganisms
Bivalve	An aquatic mollusc which has a compressed body enclosed within a hinged shell, such as oysters, mussels, and scallops
Byssal	Strong, silky filaments by which certain bivalve molluscs, such as mussels, attach themselves to rocks and other fixed surfaces
Continental shelf	The area of seabed around a large land mass where the sea is relatively shallow compared with the open ocean
Convection	The movement caused within a fluid by the tendency of hotter and therefore less dense material to rise, and colder, denser material to sink under the influence of gravity, which consequently results in transfer of heat
Copepod	A small or microscopic aquatic crustacean of the large class Copepoda
Diagenesis	The physical and chemical changes occurring during the

	conversion of sediment to sedimentary rock
Diurnal	Daily; during the day
Eddy	A circular movement of water causing a small whirlpool
Epifauna	Animals living on the surface of the seabed or a riverbed, or attached to submerged objects or aquatic animals or plants
Flocculate	Form or cause to form into small clumps or masses
fluidisation	A process similar to liquefaction whereby a granular material is converted from a static solid-like state to a dynamic fluid-like state
Flume	An artificial channel conveying water
Fluvial	Of or found in a river
Geo-polymerisation	The process of combining many small molecules into a covalently bonded network
Geostrophic	Relating to or denoting the component of a wind or current that arises from a balance between pressure gradients and coriolis forces
Glacimarine	Areas where sediment is deposited in the sea after release from glacier ice
Granulometry	The measurement of the size distribution in a collection of grains
Gravimetric	Relating to the measurement of weight
Hydrographic	Of or relating to the characteristic features of bodies of water
Infauna	The animals living in the sediments of the ocean floor
Interannual	Occurring between, relating to, or involving two or more years
Intra-annual	Occurring on a time scale of between one month and one year
Luminophore	Particles coated in luminescent dye

Macrofauna	Macrofauna are benthic which are retained on a 0.5 mm sieve
Meroplankton	A floating mass of eggs and larvae of organisms that are nektonic or benthic in their adult stage
Mesocosm	An experimental set-up containing the physical features and organisms of an ecosystem but restricted in size
Metabolite	A substance formed in or necessary for metabolism
Microphyte	Microscopic algae
Mineralisation	A process where an inorganic substance precipitates in an organic matrix
Multi-annual	A time-span including multiple years
Nepheloid	The organic fluff layer in permanent suspension immediately above the seafloor
Nitrification	The biological oxidation of ammonia to nitrite followed by the oxidation of the nitrite to nitrate
Oscillation	A movement, back and forth, in a regular rhythm
Pelagic	Water column environment
Phytoplankton	Plankton consisting of microscopic plants
Polydispersity	A measure of the distribution of molecular mass in a given polymer sample
Polysaccharide	A carbohydrate (e.g. starch, cellulose, or glycogen) whose molecules consist of a number of sugar molecules bonded together
Primary production	The synthesis of organic compounds from atmospheric or aqueous Carbon dioxide
Pseudo-faeces	Particles rejected by a mollusc as unsuitable for food and expelled without passing through the digestive tract
Remineralise	Restore the depleted mineral content
Secondary production	The formation of living mass of a heterotrophic population or group of populations over some period of time

Stochastic	Having a random probability distribution or pattern that may be analysed statistically but may not be predicted precisely
Synchronous	Existing or occurring at the same time
Taxon	A taxonomic group of any rank, such as a species, family, or class
Topography	The arrangement of the natural and artificial physical features of an area
Zooplankton	Plankton consisting of small animals and the immature stages of larger animals

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Appendices

A) Chapter 2 Appendices

2a: Sources of supplemental data sets

Variable	Temporal availability of data	Data source	Data acquisition method or reference for methods details	Location of sampling
Total and Organic Particulate Carbon (TPC and POC) concentrations	2009-2013	WCO time series	Thermoquest Flash EA 1112 elemental analyser	L4
Total and Organic Particulate Nitrogen (TPN and PON) concentrations	2009-2013	WCO time series	Thermoquest Flash EA 1112 elemental analyser	L4
CDOM concentration	2009-2013	WCO time series	L4 buoy in-situ sensor	L4
Suspended particulate matter concentration	2009-2013	WCO time series	L4 buoy in-situ sensor	L4
Oxygen concentration	2009-2017	WCO time series	L4 buoy in-situ sensor and CTD measurements	L4
Phytoplankton abundance	2009-2014	WCO time series	(Widdicombe *et al.*, 2010)	L4
Phytoplankton biomass	2009-2014	WCO time series	(Widdicombe *et al.*, 2010)	L4
Zooplankton abundance	2009-2016	WCO time series	(Eloire *et al.*, 2010)	L4
Benthic macrofauna abundance and biomass	2009-2013	WCO time series benthic survey	Box coring Sediment and sieving out	L4 benthic station
Benthic fluorescence and	2010-2016	WCO time series	CTD measurement	L4

chlorophyll				
Solar radiation	2009-2013	PML MET station	Weather station stationary sensor	PML (see Figure 3)
Photosynthetically active radiation	2009-2013	PML MET station	Weather station stationary sensor	PML (see Figure 3)
Air pressure	2011-2013	Rame Head MET station	Weather station stationary sensor	Rame Head (see Figure 3)
Rain	2011-2013	Rame Head MET station	Weather station stationary sensor	Rame Head (see Figure 3)
Wave height	2009-2017	Looe buoy	In-situ buoy sensor	Looe (see Figure 3)
Benthic temperature	2010-2016	WCO time series	CTD measurement	L4
Benthic photosynthetically active radiation (PAR)	2010-2016	WCO time series	CTD measurement	L4
Sediment grain size	2009-2012	WCO time series benthic survey	Particle Size Analysis	L4 benthic station
River flow	2009-2016	National River Flow Archive	Flow check gauge	Gunnislake, Tamar (see Figure 3)
Tidal state	2009-2017	Permanent Service for Mean Sea Level	Tidal gauge	Devonport Tidal station (see Figure 3)

2b: Sampling campaign of data collection throughout the 2017/2018 seasonal cycle

Variable	**Field sampling method**	**08 / 2017**	**11 / 2017**	**12 / 2017**	**01 / 2018**	**02 / 2018**	**03 / 2018**	**04 / 2018**	**05-06 / 2018**
Resuspension / erosion thresholds	Box corer	✓	✓					✓	✓
Bioturbation	Box corer	✓	✓	✓	✓	✓	✓	✓	✓

Water column SPM and POC	Rosette sampler	✓	✓	✓	✓	✓	✓	✓	✓
Nepheloid SPM and POC	Multi-corer	✓	✓	✓	✓	✓	✓	✓	✓
Sediment grain size	Box corer	✓	✓	✓	✓	✓	✓	✓	✓
Sediment density	Box corer	✓	✓	✓	✓	✓	✓	✓	✓
Sediment OC content	Box corer	✓	✓	✓	✓	✓	✓	✓	✓
Water column temperature	CTD	✓	✓	✓	✓	✓	✓	✓	✓
Water column fluorescence	CTD	✓	✓	✓	✓	✓	✓	✓	✓
Water column density	CTD	✓	✓	✓	✓	✓	✓	✓	✓
Water column salinity	CTD	✓	✓	✓	✓	✓	✓	✓	✓

2c: Flume programmes

K-index	Dwell time in minutes	Velocity in m/s	Shear stress in Pa
0	10	0.000128103	0.017409884
1	10	0.001195501	1.516262444
2	10	0.002013365	4.300506215
3	10	0.002856191	8.654637122
4	10	0.003718308	14.66780767

5	10	0.00470084	23.44365984
6	10	0.005713836	34.63618521
7	10	0.006607689	46.32054397
8	10	0.007540815	60.32690907
9	10	0.008451207	75.77255817
10	10	0.009468514	95.11260725
11	10	0.010376729	114.2339979

2e: Results of the OPLS models

Model	**R2X**	**R2Y**	**Q2Y**	**pR2Y**	**pQ2Y**
Model 1	0.683	0.989	0.945	0.05	0.05
Model 2	0.694	0.971	0.623	0.15	0.2
Model 3	0.657	0.775	0.655	0.05	0.05
Model 4	0.476	0.76	0.417	0.15	0.05
Model 5	0.954	0.975	0.87	0.05	0.05
Model 6	0.901	0.982	0.959	0.05	0.05
Model 7	0.449	0.775	-0.241	0.15	0.5
Model 8	0.604	0.57	-0.222	0.7	0.345
Model 8a	0.749	0.865	0.048	0.15	0.3

2f: VIP scores of the OPLS models

OPLS model	**Driver**	**VIP score**
Model 1: All variables	PAR at 50 m	1.0065
	Salinity at 50 m	1.0272
	Wave height	1.7049
	Wave peak period	1.3445
	Wave peak duration	1.6255
	River flow	1.6560

	τ0crit	1.1906
	Tidal flow	1.2797
	Phytoplankton abundance	1.5386
	Phytoplankton biomass	1.3547
	Fluorescence at 50 m	1.2176
	[Chlorophyll a] at 10 m	1.4930
	SPM at 0 m	1.4934
	SPM at 10 m	1.1250
	Sediment [OC] (1-2 cm)	1.1556
	Sediment [OC] (2-3 cm)	1.1881
	Sediment density (3-5 cm)	1.0465
	Macrofauna biomass	1.0794
	Overall Nitrite/Nitrate ratio	1.5283
	Nitrite/Nitrate ratio at 50 m	1.3568
	Overall [Ammonia]	1.5250
	[Ammonia] at 50 m	1.4055
	Overall [Silicate]	1.7070
	[Silicate] at 50 m	1.6048
	Overall [Phosphate]	1.5311
	[Phosphate] at 50 m	1.3186
Model 2: Biological mixing of DIN	Water temperature at 50 m	1.5024
	D50 (0-1 cm depth)	1.3281
	D50 (1-2 cm depth)	1.5478
	BPc	1.576
	Bioturbation activity	1.0365
Model 3: Advective flushing of DIN	Wave height	1.5092
	Wave peak period	1.6552

	Wave peak duration	1.5910
	Sediment density (1-2 cm)	1.2024
Model 4: Bioirrigation of DIN	Water temperature at 50 m	1.524
	Macrofauna biomass	1.5295
Model 5: Diffusive flux of DIN	Sediment density (0-1cm)	1.6774
	Sediment density (1-2 cm)	1.0986
	[Nitrite] at 50 m	2.3159
	[O_2] at 50 m	1.6200
Model 6: Physical resuspension of DIN	Wave peak period	1.4890
	Wave peak duration	1.7244
	τ_{0crit}	1.3518
	Tidal flow	1.0494
Model 7: Resuspension of POC	Wave height	1.6738
	Wave peak period	1.5877
	Wave peak duration	1.7352
	τ_{0crit}	1.5206
	Sediment [OC] (2-3 cm)	1.0534
	Sediment density (2-3 cm)	1.4673
	Macrofauna abundance	1.0193
	Bioturbation depth	1.2217
	[POC] at 50 m	1.1074
Model 8: Deposition of POC including SPM	Water temperature at 50 m	1.2550
	Tidal flow	2.0048
	River flow	1.0944
	[SPM] at 0 m	1.6994
	[SPM] at 10 m	1.3421
	[SPM] at 20 m	1.2413
	[SPM] at 30 m	1.6096

	[SPM] at 40 m	1.2767
	[POC] at 10 m	1.7630
	[POC] at 20 m	1.7489
	[POC] at 30 m	1.8626
	[POC] at 40 m	1.9624
Model 8a: Deposition of POC without SPM	Copepod abundance	1.1891
	Wave height	1.1263
	Riverflow	1.4385
	Chlorophyll at 10 m	1.3620
	Tidal flow	1.5175
	POC at 0 m	1.2785
	POC at 20 m	1.7559
	POC at 30 m	1.1427
	POC at 40 m	1.4492

B) Chapter 3 Appendices

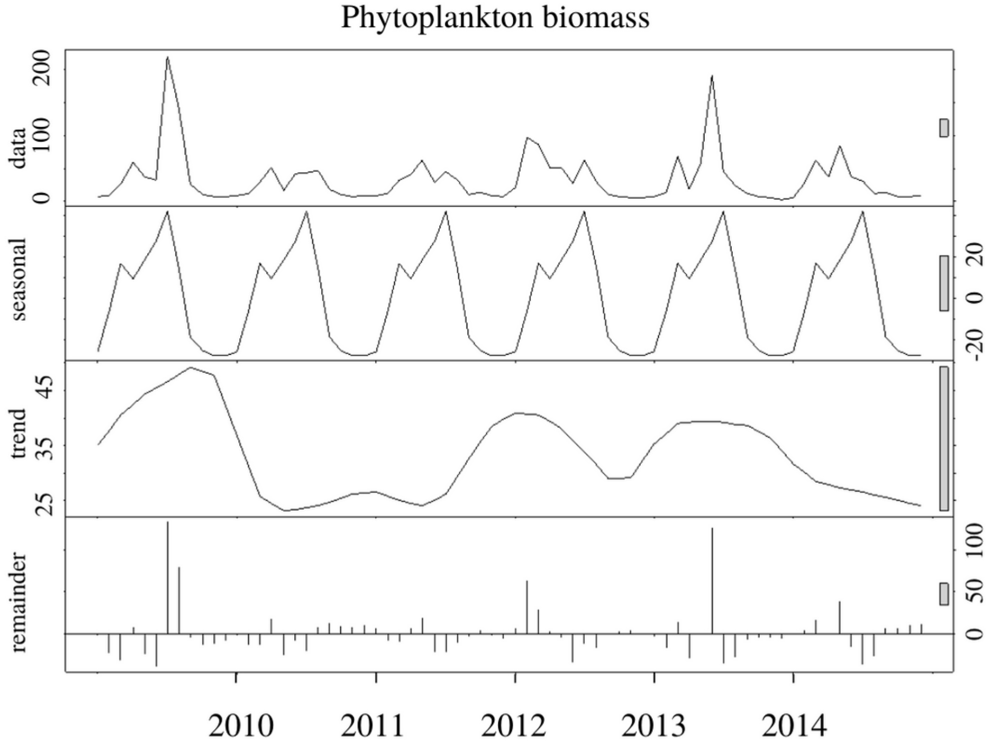
3a: Selection of driving factors for each direct driver of DM and PM exchange, as well as the overall exchange processes

Process → ------------------------- - **Driving variables** ↓	PM Resuspension	PM Deposi-tion	Absolute PM flux	Diffusion-driven DM exchange	Phys. Resuspension driven DM	Advection-driven DM exchange	Biological mixing driven DM	Bioirriga-tion-driven DM	Absolute DM flux
Particulate Organic Carbon (POC)		✓	✓						
Total Particulate Carbon (TPC)		✓	✓						
Total Particulate Nitrogen (TPN)		✓	✓						
Particulate Organic Nitrogen (PON)		✓	✓						
Coloured dissolved organic matter (CDOM)		✓	✓						
Suspended particulate matter (SPM)		✓	✓						
Oxygen (O_2)				✓	✓	✓	✓	✓	✓
Phytoplankton abundance and biomass		✓	✓						
Zooplankton abundance		✓	✓						
Meroplankton abundance	✓		✓						
Copepod abundance		✓	✓						
Benthic macrofauna abundance and biomass	✓		✓				✓	✓	✓
Benthic fluorescence		✓	✓				✓	✓	✓

Chlorophyll a		✓	✓				✓	✓	✓
Rainfall		✓	✓						
Max wave height, T_{peak} and T_z	✓		✓		✓	✓			✓
Water temperature	✓		✓				✓	✓	✓
Salinity		✓	✓						
Sediment grain size	✓		✓	✓	✓	✓			✓
River flow		✓	✓						
Tidal flow	✓	✓	✓		✓	✓			✓
Nitrate				✓	✓	✓	✓	✓	✓
Nitrate/Nitrite ratio				✓	✓	✓	✓	✓	✓
Ammonia				✓	✓	✓	✓	✓	✓
Silicate				✓	✓	✓	✓	✓	✓
Phosphate				✓	✓	✓	✓	✓	✓

3b: Seasonal time-series decomposition figures of individual variables

Figure 1: STL decomposition of phytoplankton abundance and biomass data sets


Phytoplankton biomass

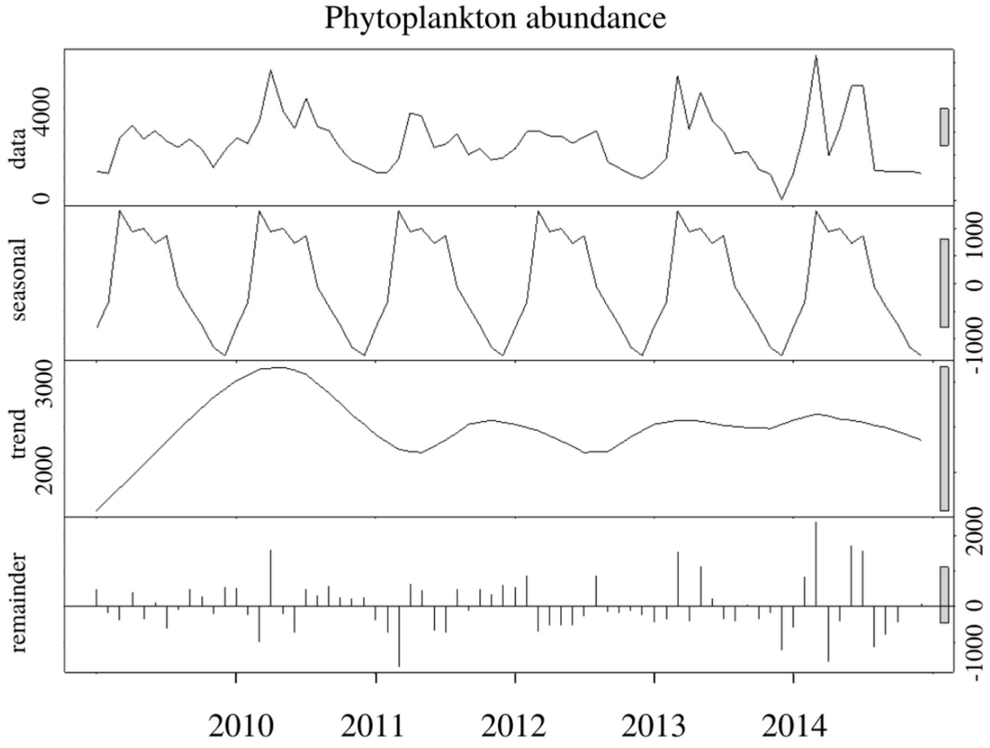
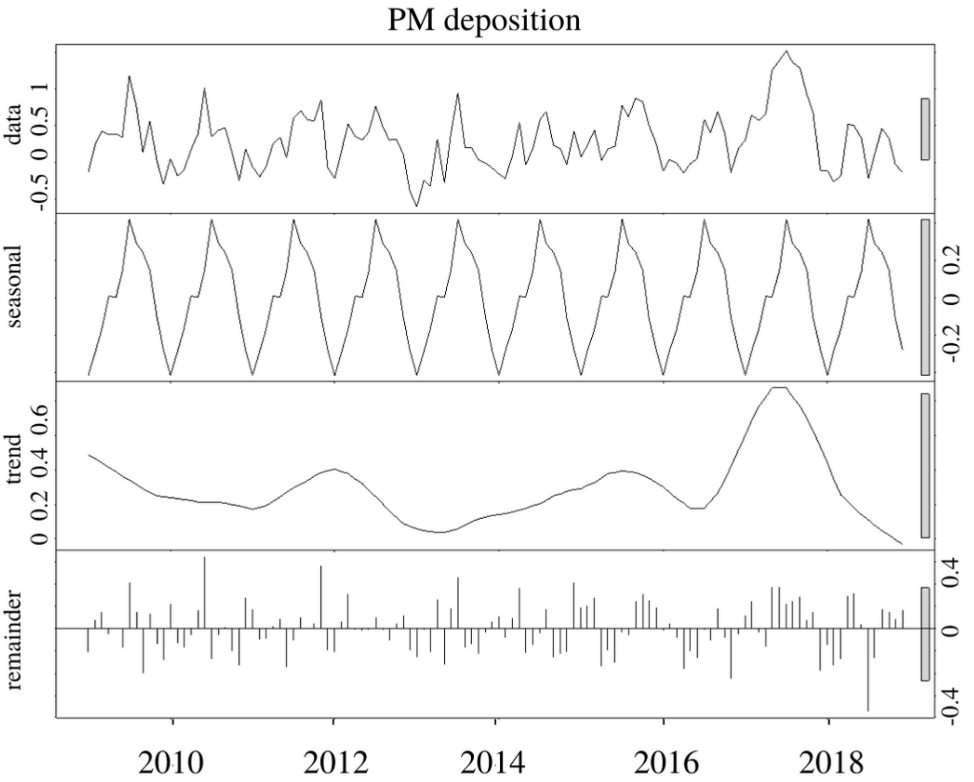

Phytoplankton abundance

Figure 2: STL decomposition of PM deposition and resuspension



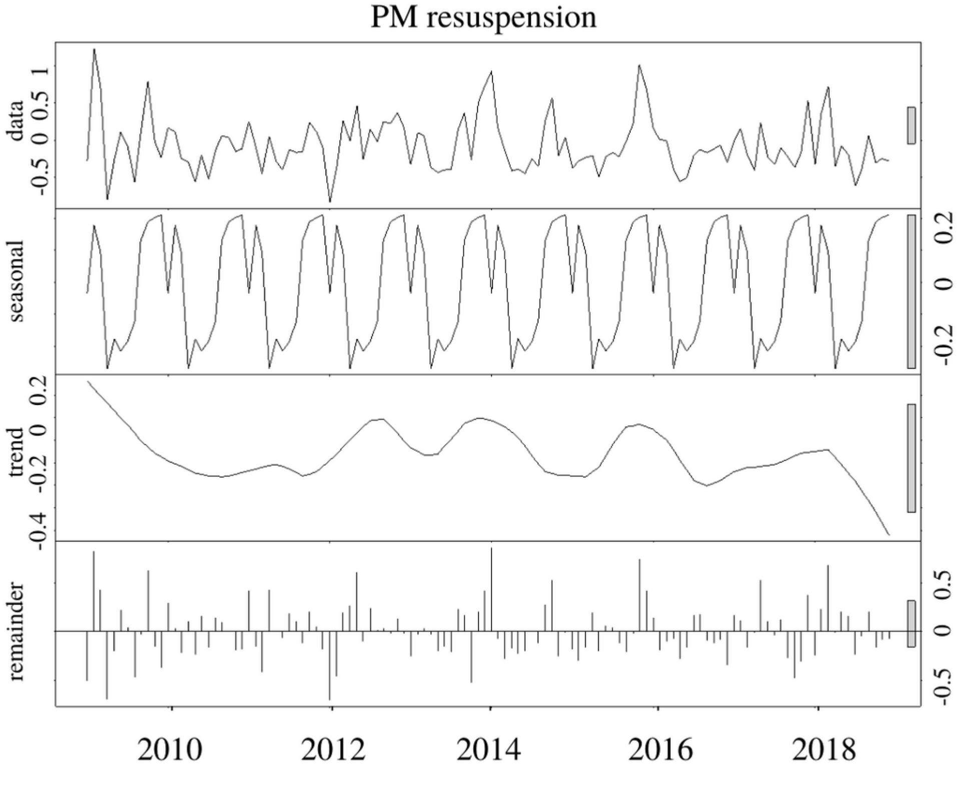


Figure 3: STL decomposition of DM exchange through bioirrigation and biological mixing

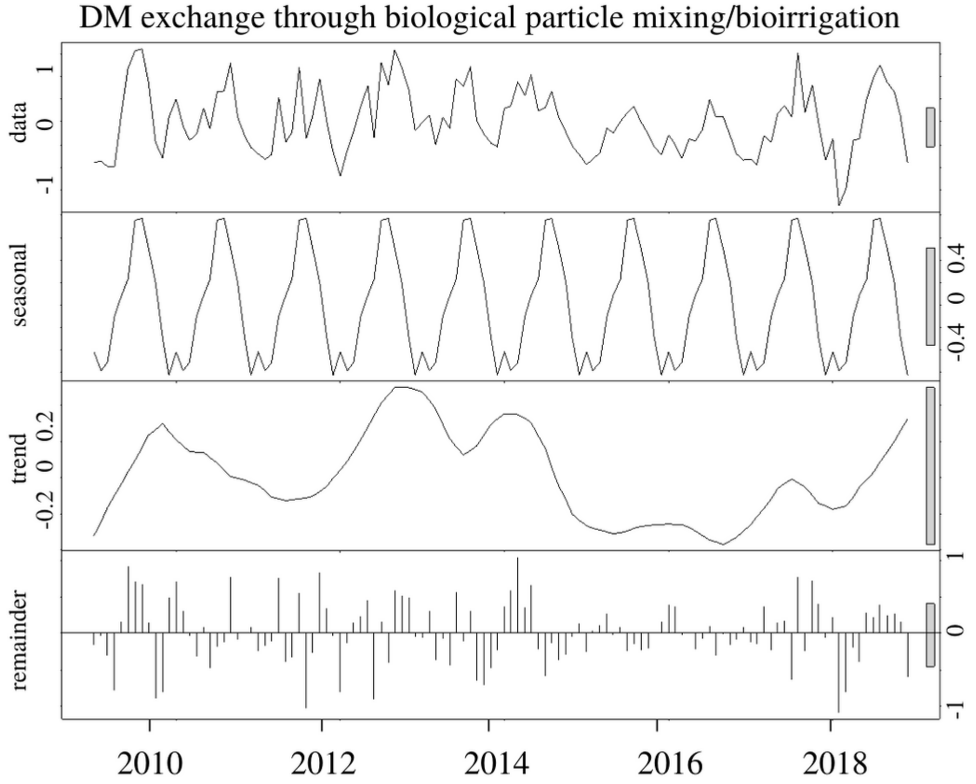
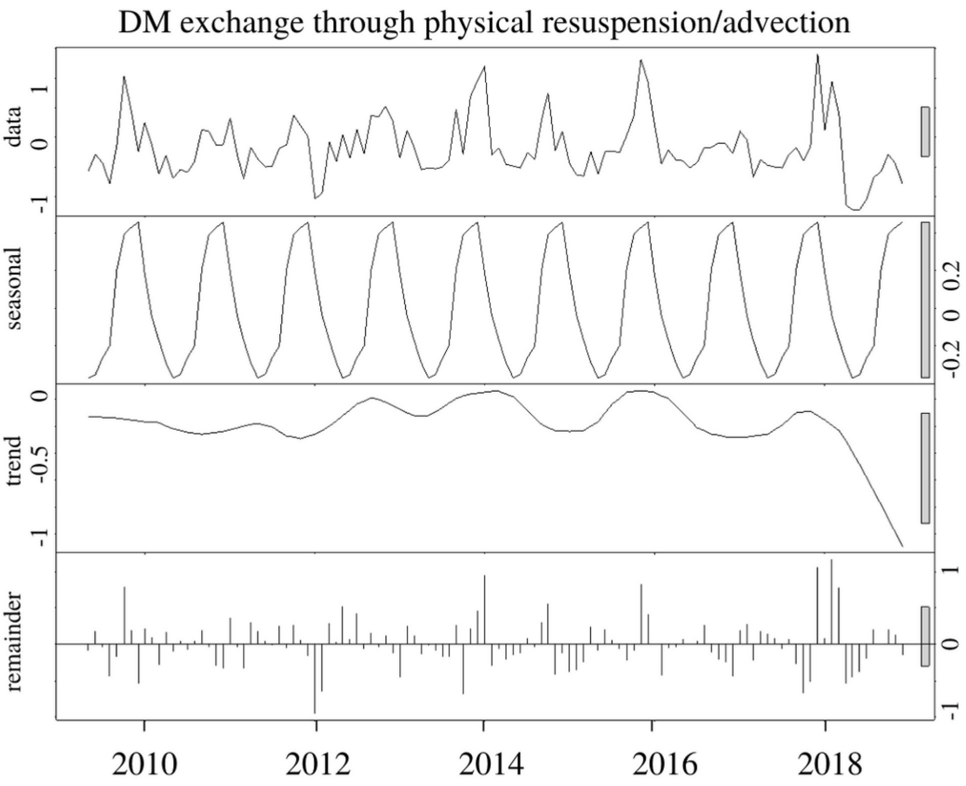


Figure 4: STL decomposition of DM exchange through physical resuspension / advection and diffusion



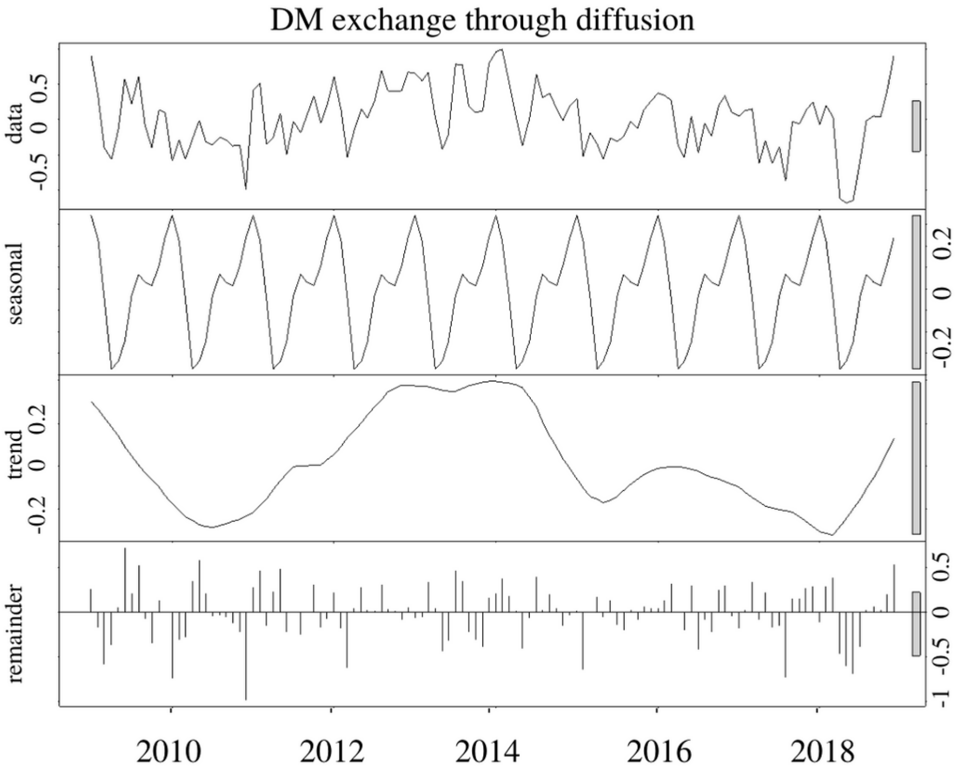
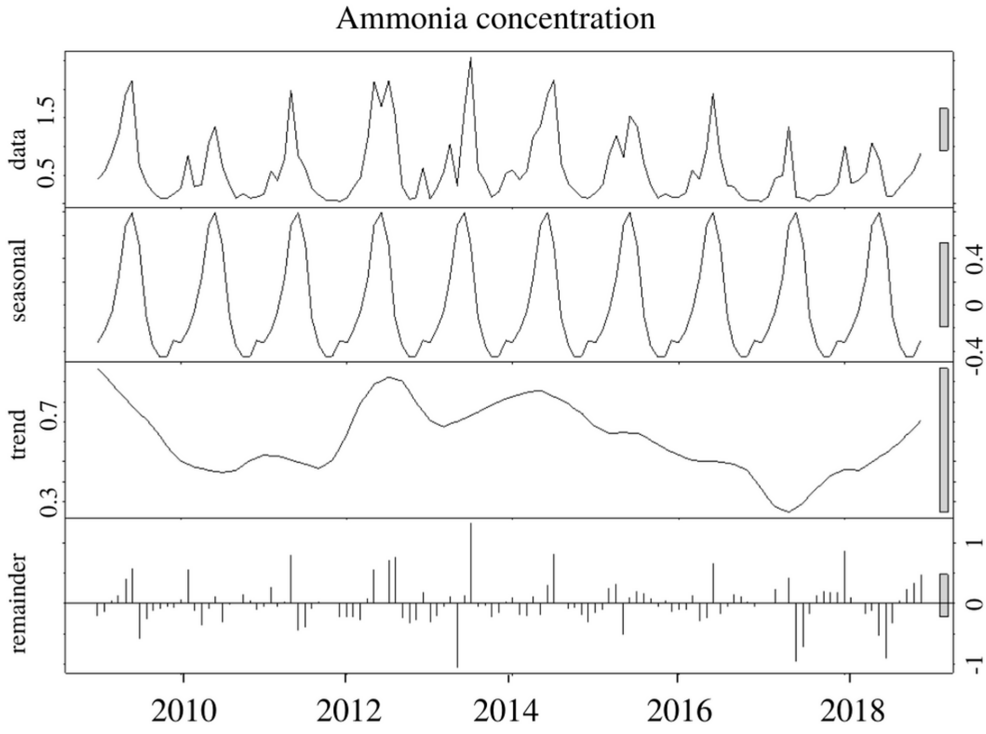


Figure 5: STL decomposition of Ammonia and Silicate concentration



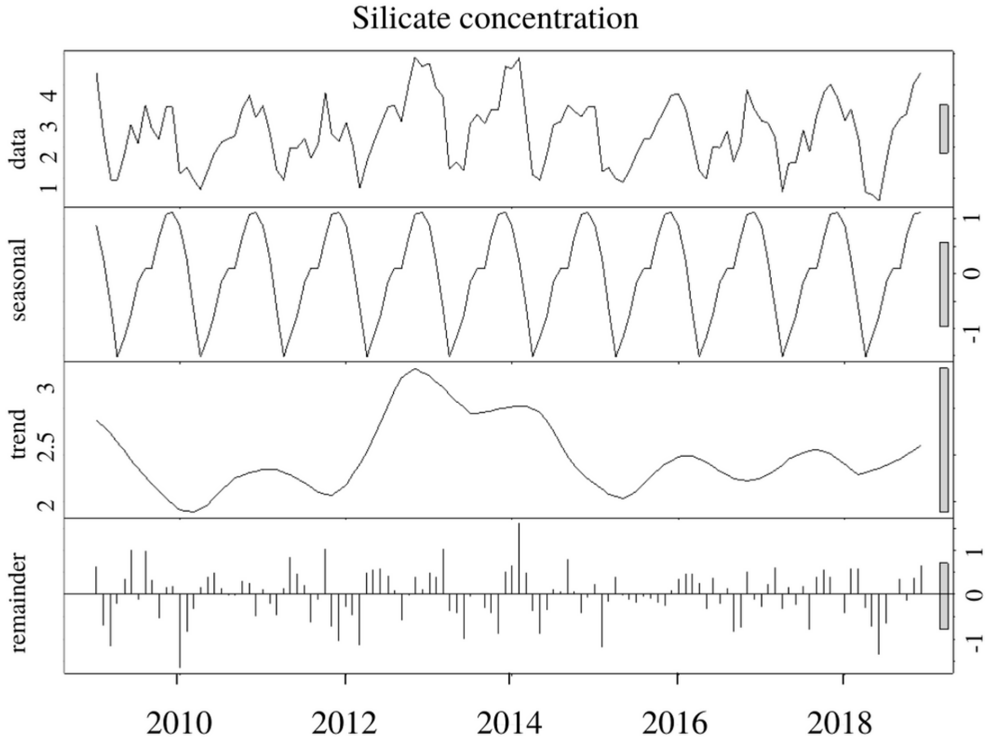
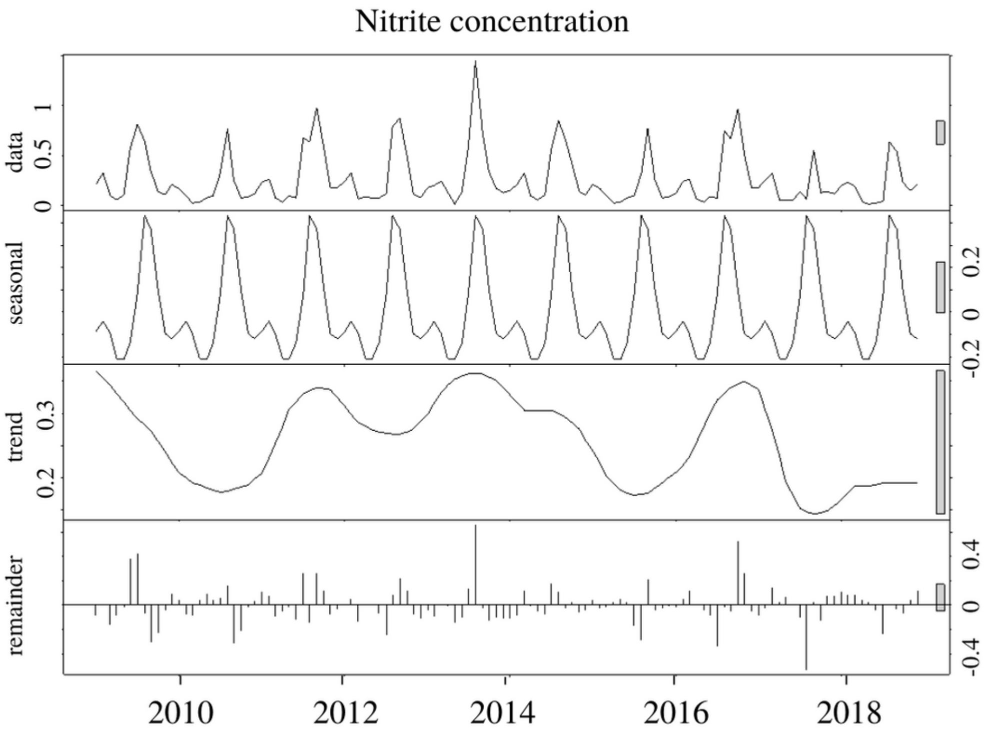


Figure 6: STL decomposition of Nitrite and Phosphate concentration



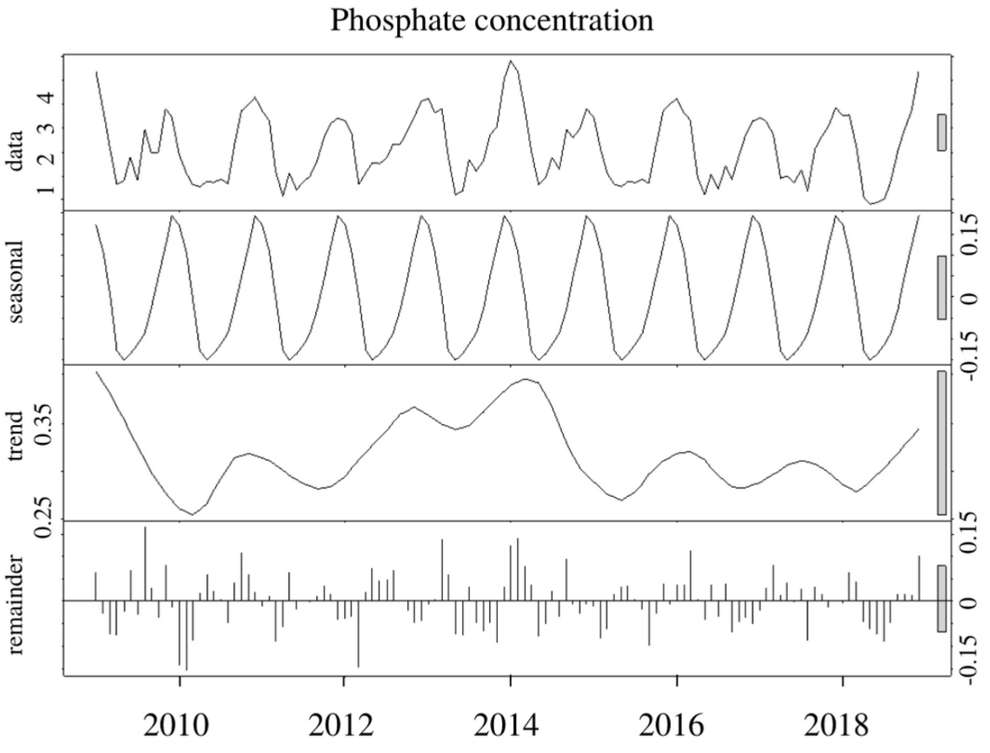
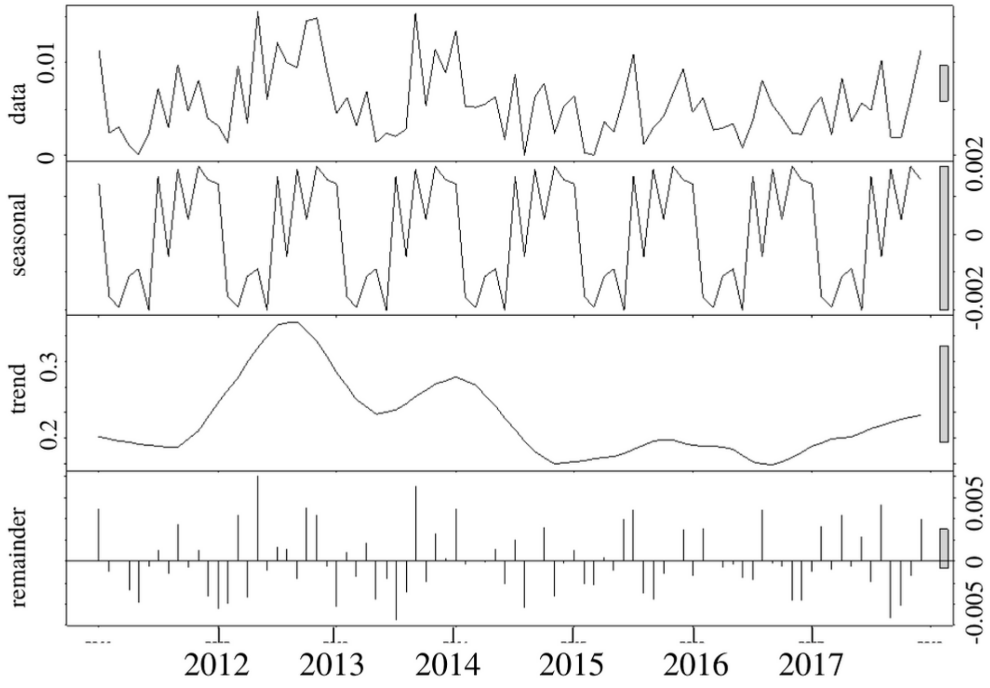


Figure 7: STL decomposition of rain fall and river flow

Rain fall



River flow

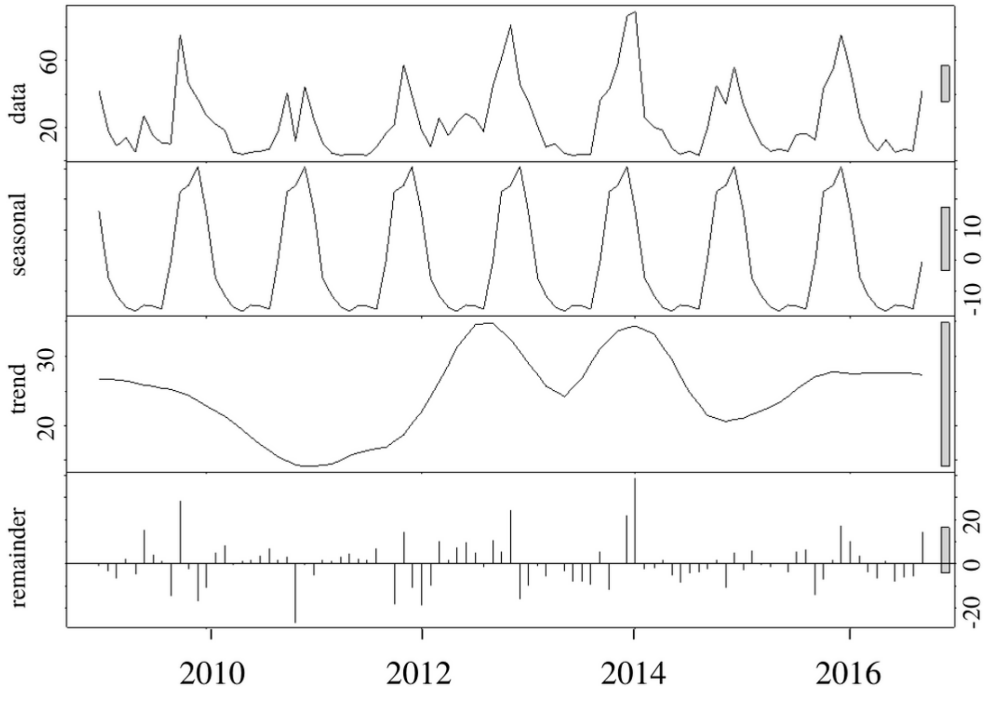


Figure 8: STL decomposition of wave height and T_z

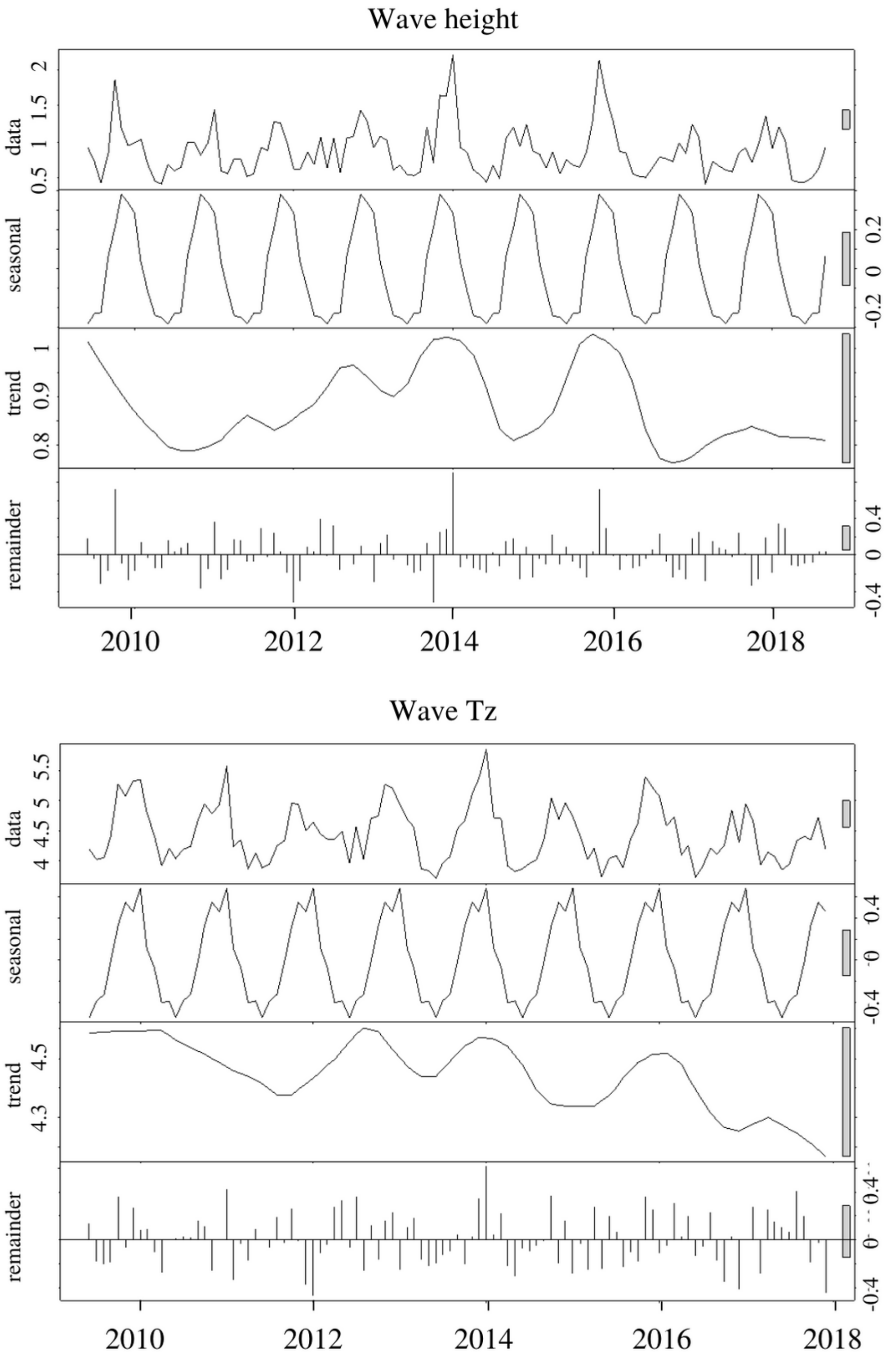
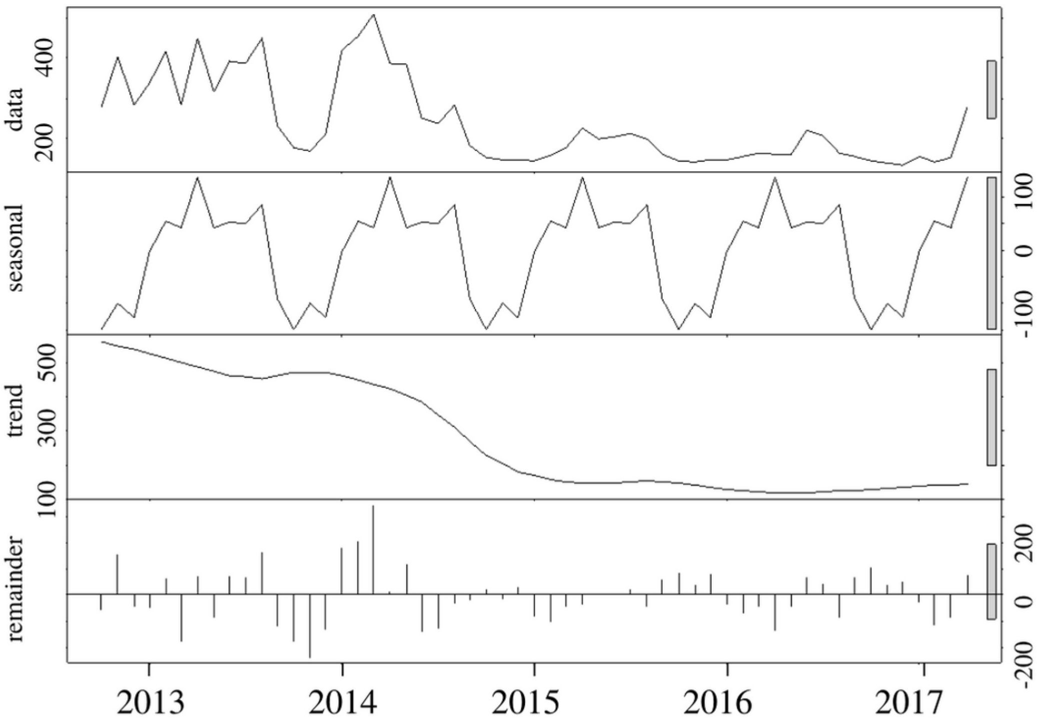


Figure 9: STL decomposition of POC concentration and tidal flow

POC concentration



Tidal flow

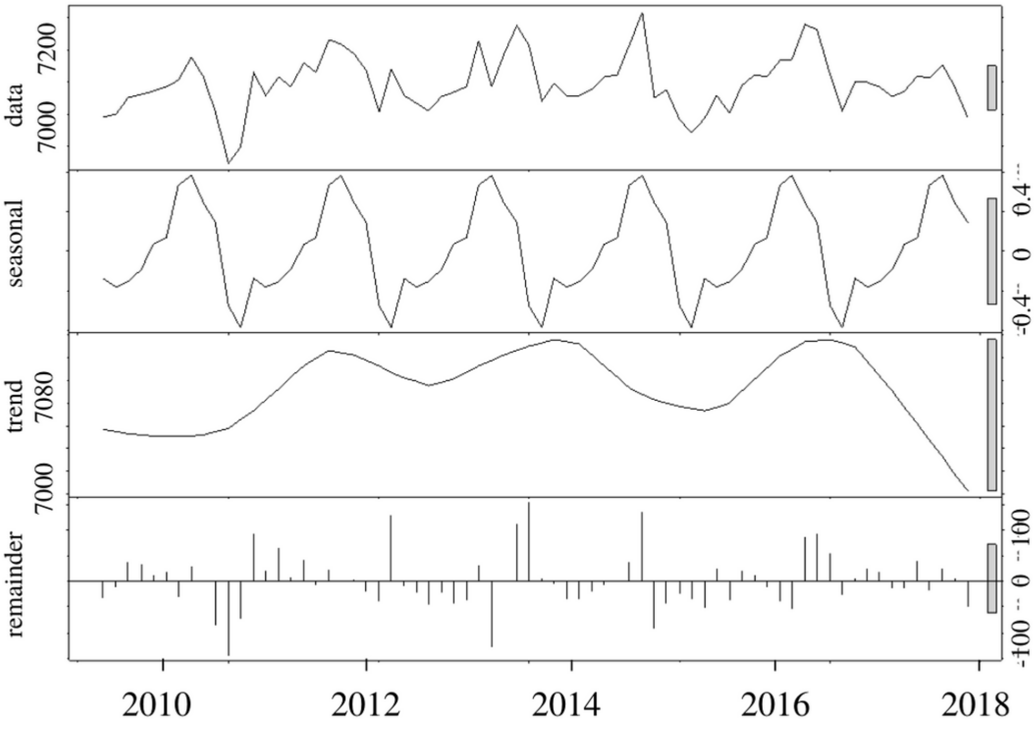


Figure 10: STL decomposition of within-season DM B/P exchanges

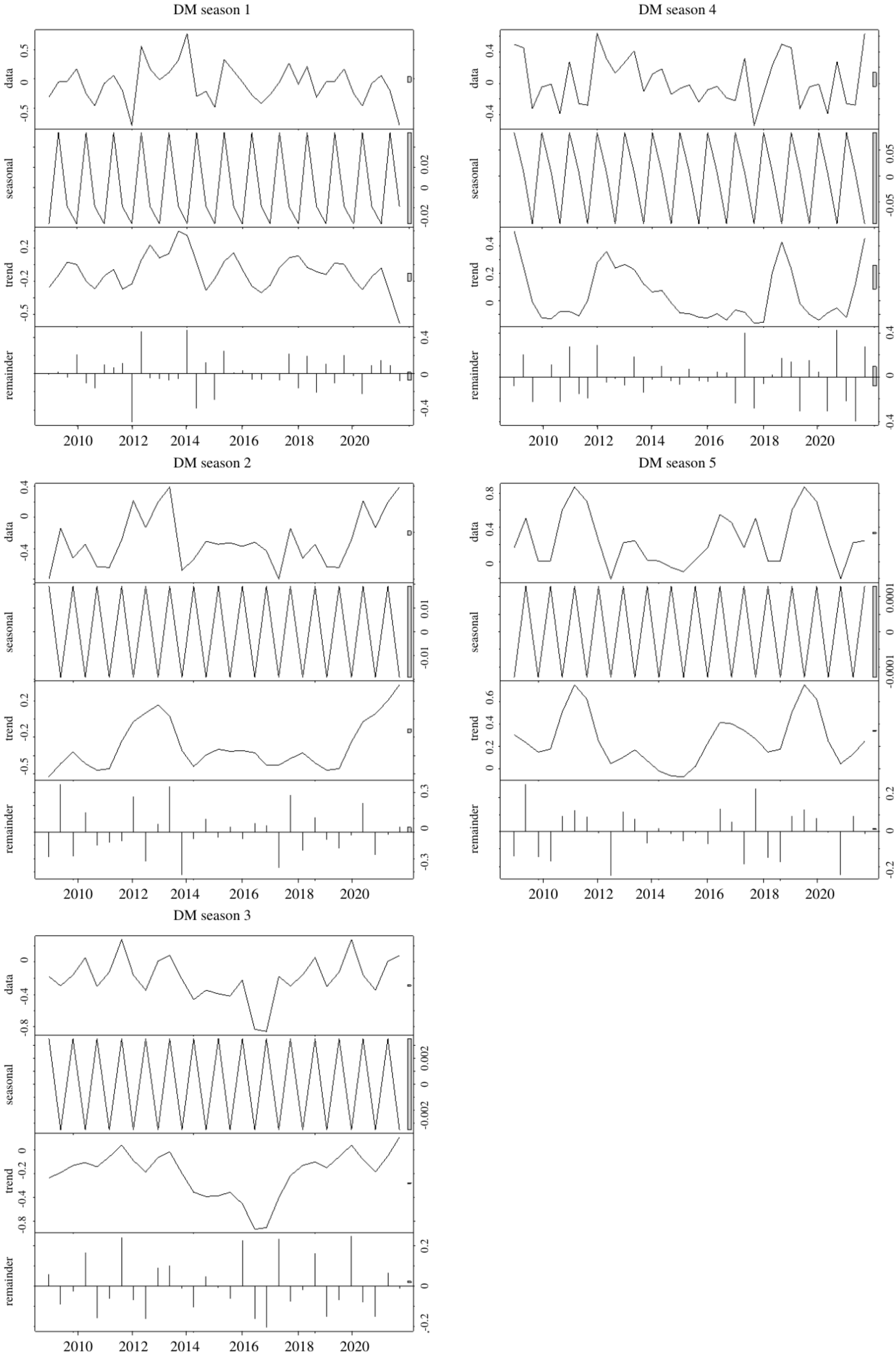


Figure 11: STL decomposition of within-season PM B/P exchanges

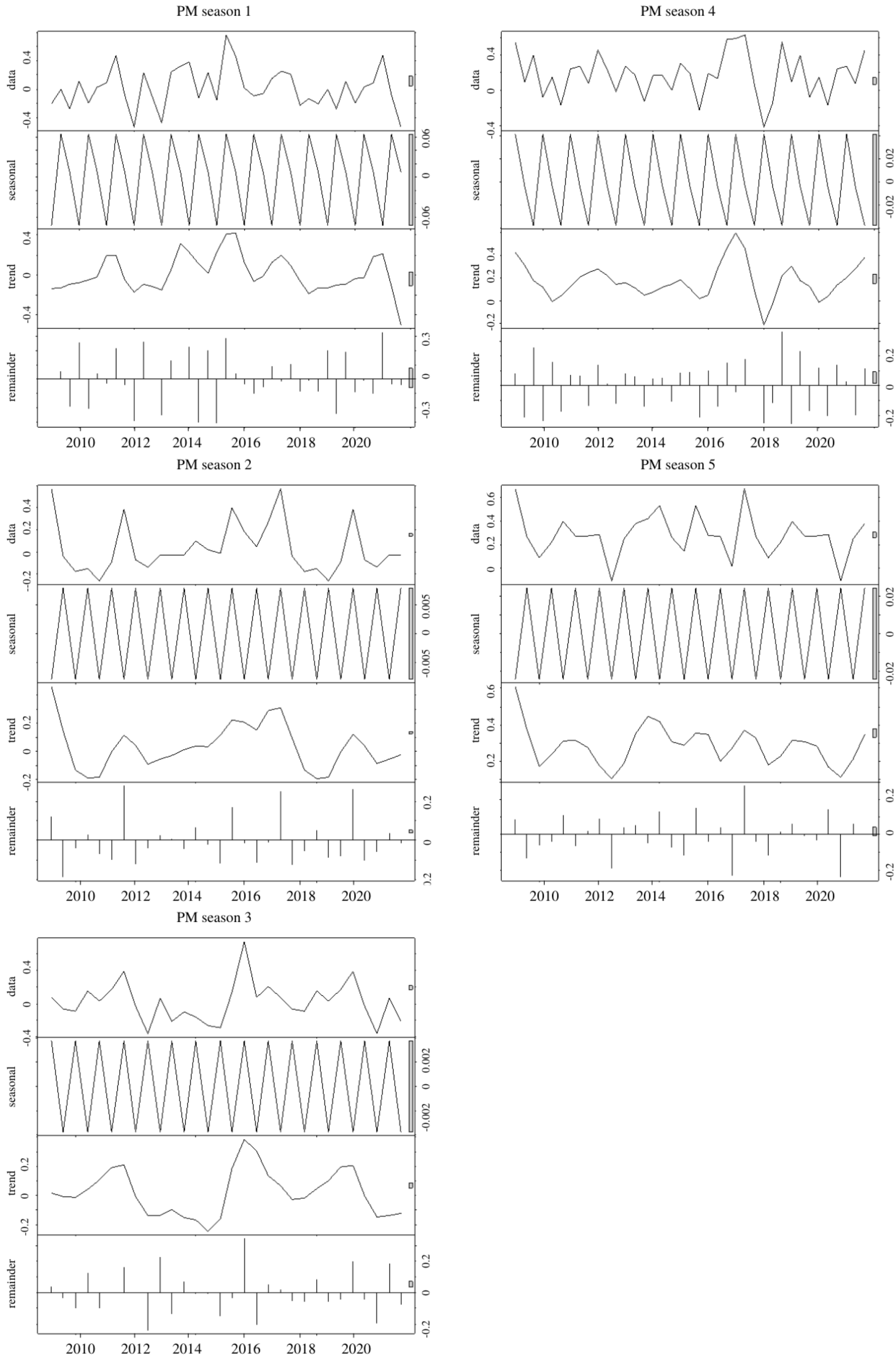


Figure 12: STL decomposition of SPM and salinity

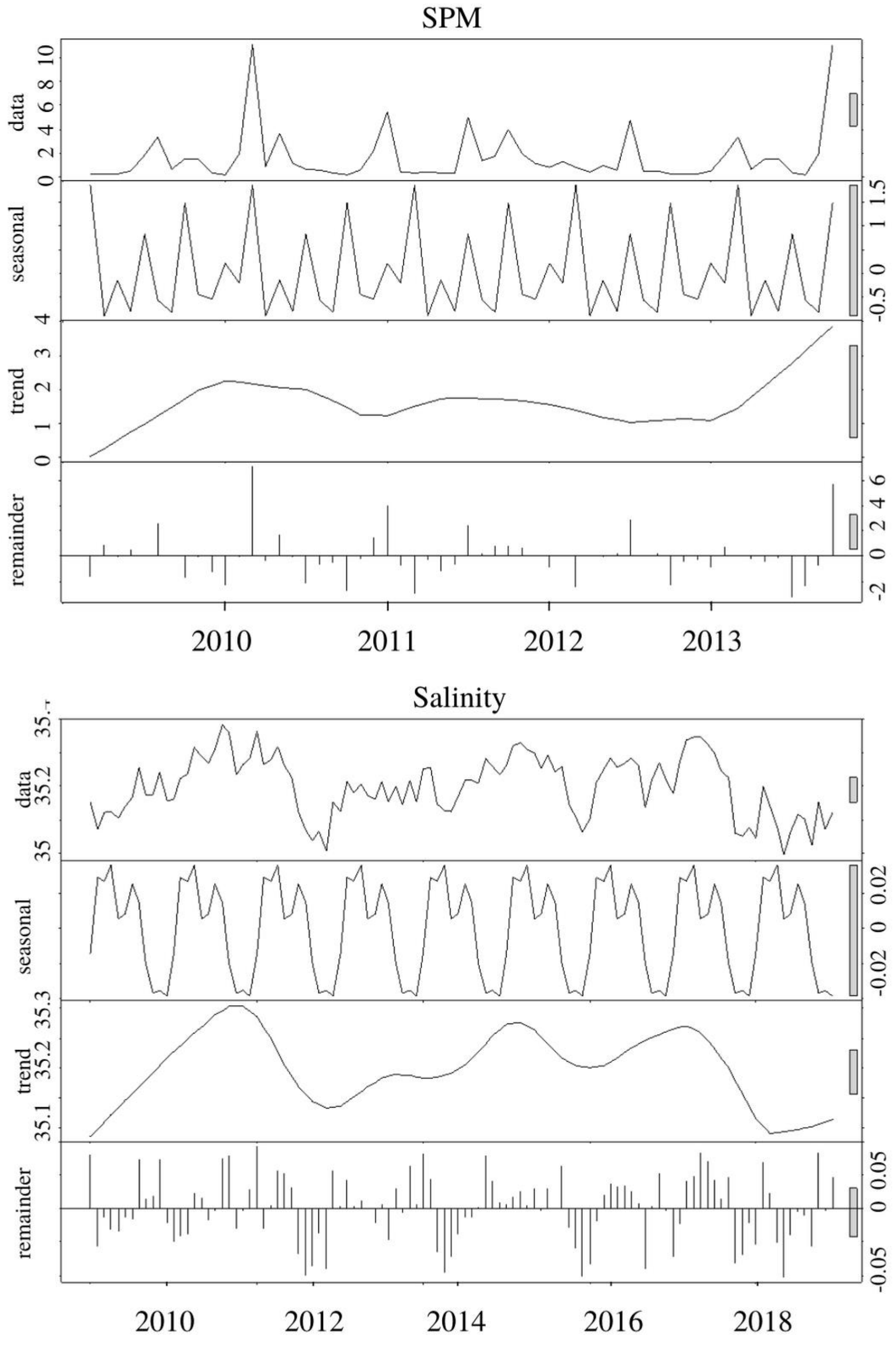
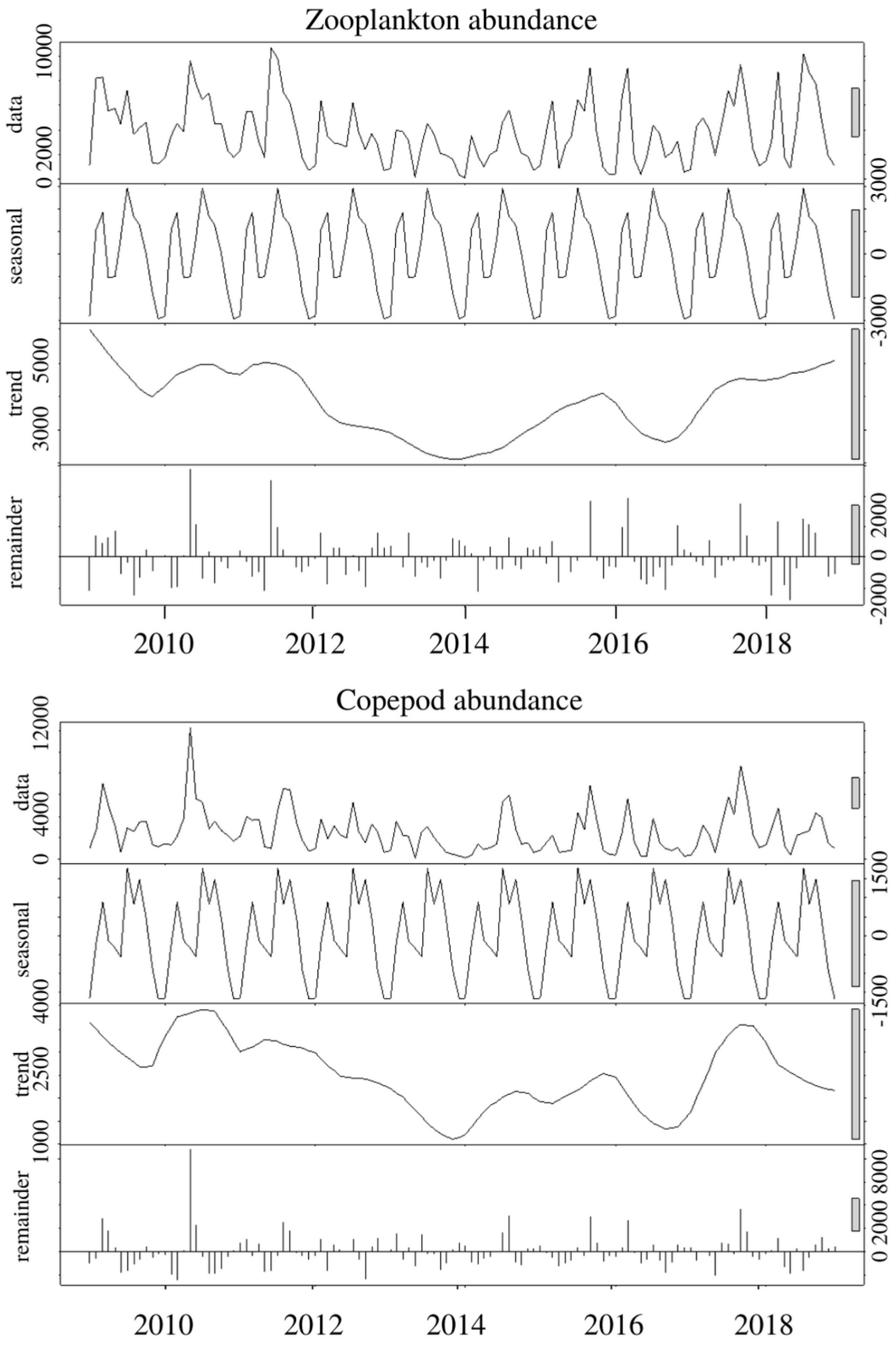


Figure 13: STL decomposition of zooplankton and copepod abundance



3c: Results of the OPLS models

Model	R2X	R2Y	Q2Y	pR2Y	pQ2Y
Model 1: Entire data set all seasons	0.244	0.386	0.172	0.05	0.05
Model 2: Entire data set season 1	0.27	0.623	0.152	0.2	0.05
Model 3: Entire data set season 2	0.381	0.719	-0.423	0.1	0.5
Model 4: Entire data set season 3	0.309	0.829	0.458	0.1	0.05
Model 5: Entire data set season 4	0.325	0.771	0.509	0.05	0.05
Model 6: Entire data set season 5	0.402	0.862	0.456	0.05	0.05
Model 7: DM diffusion season 1	0.555	0.0203	-0.194	1.05	0.4
Model 8: DM diffusion season 2	0.75	0.39	0.0114	0.1	0.25
Model 9: DM diffusion season 3	0.618	0.321	0.244	0.15	0.1
Model 10: DM diffusion season 4	0.612	0.196	0.154	0.35	0.15
Model 11: DM diffusion season 5	0.71	0.288	-0.225	0.5	0.45
Model 12: PM deposition season 1	0.341	0.517	0.114	0.15	0.15
Model 13: PM deposition season 2	0.352	0.582	-0.866	0.5	0.85
Model 14: PM deposition season 3	0.332	0.696	0.179	0.2	0.05
Model 15: PM deposition season 4	0.27	0.836	0.702	0.05	0.05
Model 16: PM deposition season 5	0.425	0.766	0.584	0.05	0.05

3d: VIP scores of the OPLS models

Model	**Variable**	**VIP**
Model 1: Entire data set all seasons	PAR at 50 m	2.523
	Wave height	1.063
	Wave peak	1.748
	Wave duration	1.438
	Rainfall	1.614
	Fluorescence at 50 m	1.702
	BPc	1.037
	BiPc	1.250
	[POC]	2.523
	[PON]	2.290
Model 2: Entire data set season 1	Wave height	1.082
	River flow	1.459
	Phytoplankton abundance	1.123
	Phytoplankton biomass	1.037
	Meroplankton abundance	1.023
	Macrofauna abundance	1.582
	Macrofauna biomass	1.288
	BPc	1.763
	BIPc	2.837
	[Silicate]	1.202
	[PON]	1.563
Model 3: Entire data set season 2	Fluorescence	1.909
	Macrofauna abundance	1.7516
	Macrofauna biomass	2.512
	BPc	1.252
	BIPc	1.204
	Cohesive sediment	1.422
	d50 at 0-1 cm sediment depth	1.422
	[Nitrate]	1.223
	Nitrate-Nitrite ratio	1.327
	[PON]	1.096
	[O_2]	2.042
Model 4: Entire data set season 3	PAR	1.638
	T peak	1.678
	Copepod abundance	2.081
	Zooplankton abundance	2.048

	Fluorescence	1.451
	Macrofauna abundance	2.081
	BPc	1.390
	Tidal flow	1.946
	[O_2]	1.738
Model 5: Entire data set season 4	PAR	1.796
	Temperature	1.170
	Phytoplankton abundance	1.175
	Meroplankton abundance	1.498
	Fluorescence	1.405
	Macrofauna biomass	1.232
	BIPc	1.336
	Tidal flow	1.404
	[POC]	2.426
	[PON]	2.543
Model 6: Entire data set season 5	PAR	2.029
	T_{peak}	1.324
	T_z	1.157
	Rain fall	1.912
	Phytoplankton abundance	1.219
	Fluorescence	1.583
	[POC]	2.904
	[PON]	2.082
Model 7: DM diffusion season 1	[Nitrite]	1.078
	Nitrate/Nitrite ratio	1.448
	[Ammonia]	1.054
	[Silicate]	1.177
	[Phosphate]	1.449
	[O_2]	1.048
Model 8: DM diffusion season 2	[Nitrate]	1.025
	Nitrate/Nitrite ratio	1.426
	[Silicate]	1.058
	[Phosphate]	1.281
	[O_2]	1.675
Model 9: DM diffusion season 3	[Ammonia]	1.252
	[Silicate]	1.702
	[O_2]	1.683
Model 10: DM diffusion season	[Nitrate]	1.407

4	Nitrate/Nitrite ratio	1.460
	[Silicate]	1.552
	[Phosphate]	1.432
Model 11: DM diffusion season 5	Nitrate/Nitrite ratio	1.087
	[O_2]	2.034
Model 12: PM deposition season 1	Meroplankton abundance	1.056
	River flow	1.796
	Phytoplankton abundance	1.739
	Phytoplankton biomass	1.678
	Fluorescence	1.048
	PAR	1.649
	Temperature	1.253
	[PON]	1.332
Model 13: PM deposition season 2	Copepod abundance	1.010
	River flow	1.467
	Fluorescence	2.498
	Temperature	2.211
	CDOM	1.876
Model 14: PM deposition season 3	Copepod abundance	1.955
	Fluorescence	1.572
	PAR	1.661
	Tidal flow	1.887
	Zooplankton abundance	2.054
Model 15: PM deposition season 4	Fluorescence	1.011
	PAR	1.647
	Temperature	1.119
	Tidal flow	1.656
	[POC]	2.260
	[PON]	2.270
Model 16: PM deposition season 5	T peak	1.246
	T_z	1.014
	Phytoplankton abundance	1.060
	Fluorescence	1.180
	PAR	1.610
	[POC]	2.342
	[PON]	1.796
	Rain fall	1.2670

C) Chapter 4 Appendices

4a: Exact locations of replicate box cores

Cruise	Station	Repetition	Latitude	Longitude	Depth in m
JR17007	B13	1	74.49993	29.9996	358
JR17007	B13	2	74.49995	29.99891	358
JR17007	B13	3	74.49945	29.9983	367
JR17007	B13	4	74.49931	29.99792	367
JR17007	B13	5	74.49923	29.99841	364
JR17007	B14	1	76.49956	30.49896	292
JR17007	B14	2	76.49949	30.49837	292
JR17007	B14	3	76.49934	30.49808	292
JR17007	B14	4	76.49925	30.49869	293
JR17007	B14	5	76.49934	30.49927	293
JR17007	B15	1	78.52122	29.99896	312
JR17007	B15	2	78.25095	29.99772	311
JR17007	B15	3	78.25098	29.99917	311
JR17007	B15	4	78.25114	29.999	311
JR17007	B15	5	78.25123	29.99972	312
JR17007	B16	1	80.11607	30.06703	279
JR17007	B16	2	80.116	30.06609	278
JR17007	B16	3	80.11581	30.06556	283
JR17007	B16	4	80.11595	30.06635	283
JR17007	B16	5	80.11597	30.06514	284
JR17007	B17	1	81.28125	29.3254	334
JR17007	B17	2	81.28114	29.32433	334
JR17007	B17	3	81.28089	29.32487	334
JR17007	B17	4	81.281	29.32565	335
JR17007	B17	5	81.28107	29.32666	335
JR18006	B13	1	74.46575	30.11817	353.93

JR18006	B13	2	74.46589	30.11805	353.89
JR18006	B13	3	74.46596	30.11818	353.74
JR18006	B13	4	74.46602	30.11822	355.72
JR18006	B13	5	74.46609	30.11837	354.36
JR18006	B14	1	76.55236	30.61845	281.32
JR18006	B14	2	7655217	30.61811	281.53
JR18006	B14	3	76.552	30.61769	281.39
JR18006	B14	4	76.55183	30.6173	281.74
JR18006	B14	5	76.55177	30.61711	281.11
JR18006	B15	1	78.26153	30.20271	312
JR18006	B15	2	78.26137	30.20164	313
JR18006	B15	3	78.26126	30.20075	313
JR18006	B15	4	78.26125	30.20045	343
JR18006	B15	5	78.26117	30.19994	313
JR18006	B16	1	80.06242	29.92257	296
JR18006	B16	2	80.07458	29.92959	293
JR18006	B16	3	80.08279	29.93968	300
JR18006	B16	4	80.08899	29.95215	299
JR18006	B16	5	80.10068	29.98869	296

4b: Locations and depths of the CTD bottom water samples and distances between replicate box cores

Cruise	**Station**	**Latitude**	**Longitude**	**Depth in m**	**Average distance between reps in m**
JR17007	B13	74.3	30.0002	359/357	207.427
JR17007	B14	76.3	30.30011	292	25.424
JR17007	B15	78.15111	29.5995	313	28.599
JR17007	B16	80.07	30.04115	280	22.99

JR17007	B17	81.16895	29.19592	334	28.943
JR18006	B13	74.3	30.0002	359.1	18.712
JR18006	B14	76.3	30.30011	295.4	38.251
JR18006	B15	78.15111	29.5995	318.4	35.818
JR18006	B16	80.07	30.04115	288.4	2120.684

4c: Dates and times of arrival and departure at each station in both cruises

Cruise	**Station**	**From**	**To**
JR17007	B13	14/07/2018 07:38	15/07/2018 12:27
JR17007	B14	25/07/2018 01:53	26/07/2018 01:26
JR17007	B15	16/07/2018 11:37	17/07/2018 10:37
JR17007	B16	22/07/2018 10:18	23/07/2018 19:01
JR17007	B17	18/07/2018 06:37	19/07/2018 19:33
JR18006	B13	07/07/2019 16:18	09/07/2019 16:40
JR18006	B14	12/07/2019 17:49	14/07/2019 10:14
JR18006	B15	10/07/2019 16:59	12/07/2019 03:13
JR18006	B16	16/07/2019 03:51	17/07/2019 09:25

4d: OPLS models significant VIP scores

Model	**Variable**	**VIP score**
Model 1, DM all factors, stations as class	d_{50}	1.2783
	Bioturbation depth	1.5904

	Surface boundary roughness	1.2309
	Biodiffusion coefficient	1.7143
	Annual trawling hours	1.8260
Model 2, DM all factors, North/South divide (B13-14/B15-17) as class	d_{50}	1.2636
	Ambient Phosphate concentration	1.0398
	Shear-stress driven Phosphate flux	1.0160
	Bioturbation depth	1.1795
	Biodiffusion coefficient	1.6920
	Annual trawling hours	1.9417
Model 3, PM all factors, stations as class	d_{50}	1.1546
	Sediment TOC content	1.3245
	Ambient SPM concentration	1.1551
	Ambient suspended OC concentration	1.2778
	Bioturbation depth	1.3669
	Annual trawling hours	1.6733
Model 4, DM all factors, North/South divide (B13/B14-17) as class	Ambient SPM concentration	1.6059
	Ambient suspended OC concentration	1.6171
	Bioturbation depth	1.1862
	Surface boundary roughness	1.2424
	Annual trawling hours	1.6474

D) Published papers associated with sections of this thesis

ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2020), doi:10.1093/icesjms/fsaa060

Review Article

Missing links in the study of solute and particle exchange between the sea floor and water column

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Rühl, S., Thompson, C., Queirós, A. M., and Widdicombe, S. Missing links in the study of solute and particle exchange between the sea floor and water column. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsaa060.

Received 10 October 2019; revised 28 February 2020; accepted 15 March 2020.

Exchanges of solutes and solids between the sea floor and water column are a vital component of ecosystem functioning in marine habitats around the globe. This review explores particle and solute exchange processes, the different mechanisms through which they interact at the ecosystem level, as well as their interdependencies. Solute and particle exchange processes are highly dependent on the characteristics of the environment within which they takes place. Exchange is driven directly by a number of factors, such as currents, granulometry, nutrient, and matter inputs, as well as living organisms. In turn, the occurrence of exchanges can influence adjacent environments and organisms. Major gaps in the present knowledge include the temporal and spatial variation in many of the processes driving benthic/pelagic exchange processes and the variability in the relative importance of individual processes caused by this variation. Furthermore, the accurate assessment of some anthropogenic impacts is deemed questionable due to a lack of baseline data and long-term effects of anthropogenic actions are often unknown. It is suggested that future research should be transdisciplinary and at ecosystem level wherever possible and that baseline surveys should be implemented and long-term observatories established to fill the current knowledge gaps.

Keywords: benthic/pelagic exchange, biogeochemistry, particle, sea floor, solute

Introduction

More than 70% of the Earth's surface is covered by water. If the water were to be removed, marine sediments would cover more global surface area than all other ecosystems combined (Snelgrove *et al.*, 1999). This marine benthos (sea floor) can have extremely varied geological, physical, and chemical characteristics and supports a diverse range of life forms. It also acts as an important source and sink of energy and matter, which are exchanged with the overlying water (Morris and Howarth, 1998). Thanks to new technologies, tackling formerly inaccessible areas of the ocean, it is now known that the benthos is an important asset of marine ecosystems globally, which is tightly coupled with other marine environments (e.g. Marcus and Boero, 1998; Navarrete *et al.*, 2005). In this review, this connection of benthic and pelagic (water column) environments will be explored by assessing exchange processes between the two.

A wide diversity of physically and biologically mediated benthic/pelagic solute and particle exchanges (hereafter "B/P exchanges") exists. The potential for, and nature and magnitude of, B/P exchanges depends strongly upon the physical characteristics of the sediment, such as its grain size, cohesion, permeability, and porosity (Kalnejais *et al.*, 2010). A sediment bed may be described as cohesive when it contains at least 10–30% clay and/or silt content, particles which are <63 µm in grain size; and non-cohesive otherwise (Winterwerp, 2011). Permeable sediment can be defined as having a permeability of $> 10^{-12}$ m^2 (see Huettel *et al.*, 2014). While cohesion mostly affects particle exchange processes, more permeable environments have larger solute exchange potentials. Sediment properties may in turn be modified through physically and biologically mediated sediment mixing and ventilation, thereby passively and actively altering exchange rates (Volkenborn *et al.*, 2010). In many cases, the effects of biological processes are particularly influential in the absence of large-scale physical disturbances (e.g. Widdows *et al.*, 1998a; Andersen and Pejrup, 2002; Paarlberg *et al.*, 2005). For instance, the degree of cohesion and fluidizations of sediments may fundamentally reflect the activity of its biological community (Widdicombe and Austen, 1999). In turn, biological communities are often shaped by their physical and chemical environments as many organisms occupy specific niches (Snelgrove, 1999).

In addition to biogenic and physical influences on B/P exchanges, anthropogenic (human) interventions can play an important role. The effects of anthropogenic interaction with the marine environment are often synchronous and can act synergistically, making it difficult to put preventative and counter-active measures in place (Caddy, 2000). Impacts are not only concentrated in coastal shelf areas where anthropogenic activity is prevalent but can be spread further (Martín *et al.*, 2008). For example, the form and extent of effects of bottom trawling on benthic communities are also dependent on the respective sediment types they occur in, which also in themselves affected by this activity (Hiddink *et al.*, 2006; Queirós *et al.*, 2006; Hale *et al.*, 2017). The relative impact of anthropogenic interferences compared to naturally occurring processes on B/P exchanges can thus be hard to quantify, as the two can have similar consequences (Pusceddu *et al.*, 2005) but cause different effects on different types of organisms (e.g. meiofauna: Schratzberger *et al.*, 2009; and macrofauna: Fang *et al.*, 2019).

In the course of this review, the complexity of particle and solute B/P exchange processes, as well as particular driver interactions, will be explored. Solute and particle exchanges will be reviewed individually, with solute exchange subsections designed to highlight the main drivers of exchange, and particulate exchange subsections structured to highlight downward and upward directed exchange processes. Interdependencies between solute- and particle-specific processes will be explored using the example of organic matter cycling, which is a biologically vital process that crucially depends on both types of exchange. Knowledge gaps in the current research will be highlighted throughout each section and finally reviewed in combination with recommendations for future research.

Solutes

Solutes in the marine environment can broadly be defined as substances dissolved in sea water. Throughout the water column, solutes may be transported through eddy and molecular diffusion (Boudreau, 2001), as well as convection (Webster *et al.*, 1996). When biologically important elements such as oxygen (O_2), carbon (C), and nitrogen (N) are in solution, they are readily available for processes such as respiration, photosynthesis, calcification, diagenesis, and direct nutrient uptake (all of which will be elaborated upon below), which is why their transport across the pelagic and benthic environments and exchange between the two are essential.

O_2 is perhaps the most biologically important solute moving across the sediment–water interface. The depth to which O_2 penetrates the sediment controls the depth distribution of O_2-dependent biogeochemical oxidation reactions, such as nitrification and sulphide oxidation (Rysgaard, 1994), as well as the oxidization of organic matter (OM; Cai and Sayles, 1996). On the whole, the availability of dissolved oxygen in sediment drives aerobic OM degradation rates, a reduction in the concentration of dissolved organic C, and can decrease molecular dissolved OM diversity (Seidel *et al.*, 2015). O_2-driven diagenesis (mineralization, dissolution and geo-polymerization during burial; Lindqvist, 2014) is intensified in the presence of marine organisms, which produce enzymes that catalyze those reactions (Lindqvist, 2014). In the absence of biological interactions, the penetration depth of O_2 in the sediment has been shown to depend on the O_2 concentration in the overlying water (Revsbech *et al.*, 1980; Rasmussen and Jorgensen, 1992). Anthropogenic disturbance, such as trawling, can cause a reduction in dissolved O_2 (Tiano *et al.*, 2019). The displacement of the oxygenated sedimentary surface layer through trawling equipment lessens biogenic O_2 consumption and causes deeper O_2 penetration depths in the affected areas, thereby effectively changing the sedimentary biogeochemical environment (Tiano *et al.*, 2019).

Nutrients are another ecologically important solute group in the marine system, as their availability and cycling throughout the environment can be limiting to many organisms (e.g. Howarth, 1988). Intermittence in nutrient concentrations in the water column, and thus at the sediment–water interface, is driven, among other processes, by seasonal changes in temperature (Pomeroy and Deibel, 1986), fluvial and terrestrial input (Justic, 1995; Burnett *et al.*, 2003; Milliman and Farnsworth, 2013), water column mixing, and sea bed resuspension. The latter is often initiated by stochastic storm events (Corte *et al.*, 2017). Temporal patterns of denitrification and nutrient flux dynamics also depend upon the sediment type, as sandy sediments exhibit seasonal changes primarily driven by temperature and irradiation, while silty sediments are additionally influenced by aforementioned stochastic resuspension events (Seidel *et al.*, 2015) and meteorologically induced upwelling events (MacIntyre, 1998). The resulting supply of nutrients from the benthos to the pelagic environment is a crucial factor controlling phytoplankton blooms at times of the year when the water column is not stratified in non-eutrophic systems, as the mixing of water from depth and surface layers can place nutrients from benthic sources within reach of the pelagic organisms (Barnes *et al.*, 2015). This, in turn, fuels zooplankton productivity and can give rise to knock-on effects throughout the entire marine food web (Eloire *et al.*, 2010). Increased pelagic productivity, on the other hand, leads to increased nutrient influx rates to the benthos from sinking OM, which is why the benthic community and its activity typically flourish in response to large seasonal plankton blooms (e.g. Queiros *et al.*, 2015; Tait *et al.*, 2015). Other nutrient sources to benthic sediment–water interactions include atmospheric input (Krishnamurthy *et al.*, 2010), anthropogenic terrestrial sources (Justic, 1995; Burnett *et al.*, 2003), dredge-spoil dumps (e.g. Harvey, Gauthier and Munro, 1998), and the addition of dead cells and faecal pellets from pelagic organisms, sinking onto the sea floor (Van Duyl *et al.*, 1992). The relative impact of each of these depends on factors such as proximity to the coast and the extent of local pelagic primary productivity, and lateral transport fuelled by circulation patterns can alter their relative importance (e.g. Walsh, 1991; Williams and Follows, 1998). Most of the organically available nutrients near the seafloor are extracted and processed diagenetically by the benthic microbial community, or directly consumed by deposit and suspension feeding fauna, degrading and mineralizing the floccules' contents. The latter can generally be described as the return of nitrogen (N) and phosphorous (P) to inorganic forms after having been incorporated in organic molecules, or (re-)mineralization (Williams and del Giorgio, 2005). Within the sediment, diagenesis is fuelled by the enrichment of the sediment matrix with O_2 (Emerson and Hedges, 2003).

The B/P exchange of not only O_2 and nutrients but also all solutes is governed by a number of direct and indirect drivers (Figure 1), and the current understanding of each in the literature will be detailed throughout this section.

It is difficult to definitively determine the relative importance of the different driver groups and important factors within each on B/P, as they can be highly variable across spatial and temporal scales. Seasonal variation, for example can cause shifts in the relative importance of biological and physical influences (Howarth *et al.*, 1993; Schlüter *et al.*, 2000); biogenically induced spatial variation in sediment properties can cause differences in the main drivers of solute B/P exchange on both small (Wethey and Woodin, 2005) and large (Fang *et al.*, 2019) spatial scales. This variability constitutes a knowledge gap, which has to be filled on a situational basis, specific to the system, location, and time period of each study within which such processes are investigated. For the purposes of this review, the main drivers of solute B/P exchange are therefore elaborated upon in no particular order.

Diffusive flux

Water close to the sediment surface within the benthic boundary layer is directly affected by friction at the seabed, which promotes solute transport *via* diffusion. Cohesive sediments, with high clay content, tend to be more difficult to percolate due to a generally smaller degree of permeability, thus impeding the flux of solutes (Yang and Aplin, 2010; though this is not necessarily true for cohesive environments with low clay content, see, e.g. Winterwerp and Kesteren, 2004). In such conditions, molecular diffusion of pore-water solutes across the sediment–water interface prevails, leading to more gradual solute fluxes (Berner, 1980; Forster *et al.*, 1999) in the form of ion transfer between pore water and near-bottom water or as a result of the reactivity of solid surfaces (Kalnejais, Martin and Bothner, 2010). Other physical environmental variables, such as pressure differentials driven by tides, have been shown to lead to short-term temporal variability of diffusive fluxes (Van Der Kamp and Gale, 1983). The potential depth of diffusive processes is, theoretically, only limited by time. In some cases, however, diffusive distances can be altered, driven, and extended through an increase in sediment permeability, promoted by benthic biological activity. Sedimentary O_2 uptake, for instance is only a function of physical penetration depth, which is determined by time in the absence of biological activity and OM (Revsbech *et al.*, 1980). What is hitherto unknown is whether there are ways in which biological or anthropogenic interactions may be directly inhibitive of solute diffusion across the sediment–water interface. As diffusion does not necessarily occur in isolation from other drivers of solute exchange, a differentiation between relative contributions of each driver would be of interest to correctly quantify each pathway. However, while the balance between, for example diffusive and advective solute B/P exchange

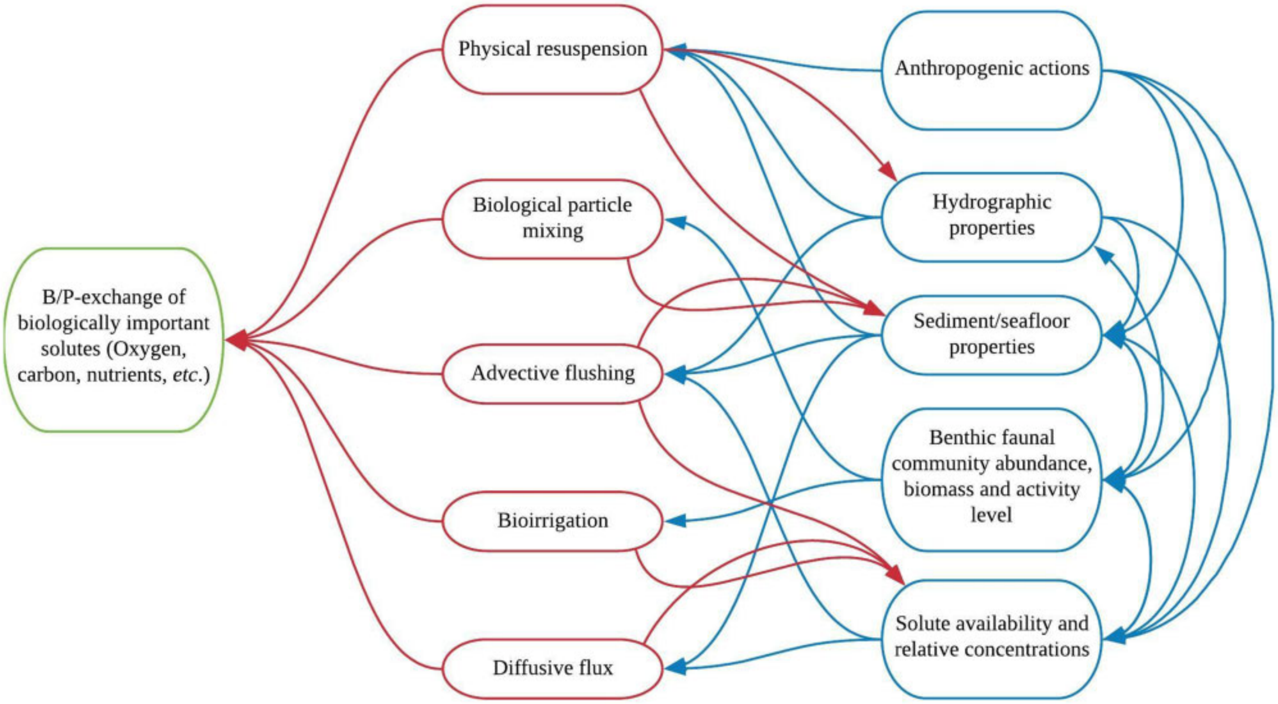

Figure 1. Flow chart of direct (red, middle) and indirect (blue, right) drivers of solute B/P exchange (green, left); arrows indicate which factors affect others and are colour-coordinated with the driver they originate from.

may be calculated in theory (Anderson and Cherry, 1979; Taigbenu and Liggett, 1986), *in situ* measurements that take both into account and clearly differentiate between their respective contributions have so far not been successful.

Advection and physical resuspension

Abiotically driven fluctuations into (and out of) the sediment matrix can also occur through mechanically driven water transfer into and out of the sediment pores. With increasing shear stress and turbulence, benthic boundary layer thickness typically decreases (though there are some exceptions), and with it, the resistance of solute transfers into and out of the sediment (Lohse *et al.*, 1996). This decline continues into the top sediment layers (Ahmerkamp *et al.*, 2017). In turbulent conditions, under strong enough shear stress or in the presence of sediment surface obstacles, solute transport is prevalent through advection and physical resuspension. Obstacles can include protruding solid objects (rocks, shells, etc.), man-made structures, biogenic sediment structures (e.g. polychaete tubes), or simply a three-dimensional bedform, all of which lead to pressure differentials that drive water through the sediment and significantly enhance the exchange of solutes (Huettel and Gust, 1992; Ziebis, Huettel and Forster, 1996; Hutchinson and Webster, 1998). The flushing action from advective processes can winnow smaller particles from the sediment matrix, leading to an overall coarser environment that can be percolated more easily (Malarkey *et al.*, 2015), and the less cohesive and more permeable the seabed is, the more likely is the occurrence of active ejections of solutes into the water column through physically driven advective currents (Lohse *et al.*, 1996; Cook *et al.*, 2007). Resuspension events, driven by either biological activity or abiotic interactions, can enhance solute exchange processes through an increase in the sediment surface area availability for dissolution through the placement of particulates in the water column, re-oxygenation of formerly diagenized elements, and the direct flushing out of interstitial water (Morse, 1994; Morin and Morse, 1999; Saulnier and Mucci, 2000; Kalnejais *et al.*, 2010). Turbulent hydrodynamic forces close to the sea bed thus catalyze the oxygenation of the surface sediment layers through partial resuspension as well as flushing action (Malan and McLachlan, 1991; Couceiro *et al.*, 2013). And B/P solute exchange through physical processes, such as advection and resuspension, further contributes to the breaking down of OM and subsequent supply of biologically important solutes (Franke *et al.*, 2006). In intertidal sandy areas, for example, which typically contain low concentrations of particulate OM due to seasonal hydrodynamic removal (POM; Rusch *et al.*, 2000), pore-water nutrients may be supplemented through advective flushing (Seidel *et al.*, 2015).

Clearly, although there is already a large body of literature covering physically driven solute exchange processes, there are still areas requiring further exploration. Temporal variability in advective transport, for instance is poorly understood and has therefore so far not been taken into account in most studies (Cook *et al.*, 2007). As the hydrographic drivers of advection and resuspension may be consistent (e.g. currents), and/or regularly occurring (e.g. tidal flow), and/or stochastic in nature (e.g. storm events), even *in situ* measurements only capture a snapshot of events, and the potential overlap between time scales impedes our ability to differentiate between them. Long-term monitoring of physically driven B/P solute exchanges may offer a solution to this, though so far this has not been undertaken. The extent to which boundary layer flow dynamics impact physically driven solute B/P exchange has also yet to be definitively quantified, especially in an *in situ* context, including physical and biological interactions.

Bioirrigation and biological particle mixing

Biological mediation of solute exchange across the sediment–water interface is constant and inherent to sedimentary life, but in environments in which physically mediated transport is minimal, processes such as faunal flushing of pore waters can determine the rate and characteristics of B/P exchange of solutes (Mermillod-Blondin and Rosenberg, 2006; Volkenborn *et al.*, 2010). In addition, the sediment depth to which solutes are transported biologically can be multiple times that which may be reached through purely physical means (Volkenborn *et al.*, 2010). The biological exchange of solutes can take the form of bioirrigation, the active displacement of liquid and solutes by benthic organisms (Volkenborn *et al.*, 2007) linked to respiration, metabolite excretion, and other individual-based processes; or bioadvection, the induction of additional pore water through burrowing organisms' physical activity into the surrounding sediment (Volkenborn *et al.*, 2012). Biologically mediated exchange rates strongly depend on the characteristics of the associated faunal and microbial community (see e.g. Waldbusser *et al.*, 2004). Both bioirrigation and bio-advection are at least equally as important as, and often largely exceed, the rates of molecular diffusion in the upper sediment layers of biogenic environments (Berg *et al.*, 2001). The large spatial extent to which the hydraulic forces generated by bioadvectors and bioirrigators propagate through the sediment can lead to effects, which far exceed the immediate vicinity of their burrows (Wethey and Woodin, 2005). This can in some instances have significant effects at the landscape scale (Fang *et al.*, 2019), though more often it leads to small-scale spatial variation with hot spots of altered oxygenation nutrient and carbon concentrations in the immediate vicinity of the bioirrigative activity. The release of O_2 from root systems in submerged macrophytes can even create three-dimensional spatial variability in variable diffusion potential and solute distribution (Sand-Jensen *et al.*, 1982).

Pore-water O_2 content in particular is typically increased through bio-advection (N Volkenborn *et al.*, 2010; Volkenborn *et al.*, 2012) as many burrowing animals actively oxygenate the surrounding sediment by ventilating their burrows with bottom water (Volkenborn *et al.*, 2007). Due to this, the thickness and volume of the sedimentary oxidizing phase are largely extended, thus ameliorating conditions and promoting the occurrence of other aerobic life forms (Mermillod-Blondin and Rosenberg, 2006; Glud, 2008). This can in some cases lead to seasonal variations in O_2 availability linked to organisms' own seasonal lifecycle processes (Glud *et al.*, 2003). Significant variation is also observed between sediment types (Hicks *et al.*, 2017). Through the particle movement and disruption of sediment layering, biogenic particle mixing (bioturbation) strengthens B/P coupling as it increases the fluxes of nutrients, metals, C, O_2, and other microparticles, which would otherwise remain buried (Caliman *et al.*, 2007; Hale *et al.*, 2017). At the local scale, the presence of infaunal bioturbators has been shown to increase natural denitrification rates by at least 160% (Gilbert *et al.*, 1998). Generally, N-mineralization rates are faster in more permeable substrates and may be enhanced by macrofauna influence, irrespective of organic enrichments, due to the O_2 enrichment (Hansen and Kristensen, 1998; Huettel *et al.*, 2014). The associated modified supply of nutrients can also strongly affect microbial community structure (Yingst and Rhoads, 1980). This can be traced back to a combination of factors, one of which is the input of macrofaunal metabolic waste products, which provides additional sources of nutrients to microbial communities (e.g. Reichardt, 1988), thereby adding to the overall flux and cycling of solutes, and their bio-catalyzing effects on the microbial community (e.g. Yazdani Foshtomi *et al.*, 2015). The polysaccharide protein lining the burrows of many invertebrates has a filtering effect on the water flushing across and, through it, affects exchange processes by preferentially selecting against anionic solutes due to their own net negative charge (Aller, 1983). Burrowing macrofauna can in some cases actively culture the microbial community associated with their burrows, which then in turn affects the rates and direction of solute exchange within the burrows (Kristensen, 1988). Fishing pressure can passively affect C and nutrient fluxes mediated by benthic macrofauna by altering the community composition, though these effects are mediated by sediment type and the kind of fishing gear deployed (Hale *et al.*, 2017). Changes in benthic community can also be induced through the installation of offshore wind farms (Coates *et al.*, 2014) and other solid substrates or through dredging (e.g. Thrush *et al.*, 1995). Sources of pollution can affect benthic community diversity (e.g. Kingston, 1992) and thereby also passively lower biogenic B/P solute exchange rates.

Due to many organisms' temporally variable behaviours, rates of biologically mediated solute transport can vary on scales of minutes to seasons (e.g. Schlüter *et al.*, 2000). Despite this seasonality being a well-studied phenomenon, there is an important consideration that has thus far not been investigated: The assumption and assessment that in some areas physical pressures are strong enough to drown out the effects of biological processes (as assumed in e.g. Andersen *et al.*, 2002; Paarlberg *et al.*, 2005) may not be true at all times as the balance may swing the other way during biologically active seasons. This is a crucial knowledge gap that warrants further research. Spatial variability too should be considered more often when assessing the relative importance of physical *versus* biological drivers of B/P exchange, as small-scale patchiness and large-scale B/P exchange budgets may differ.

Particles

In contrast to solutes, particles are not transported uniformly as they occur in a variety of materials, sizes, shapes, and concentrations. Particle exchange between benthic and pelagic environments may be driven by water flow, occurring regularly (such as through currents or tides); stochastically (such as through storm events and faunal activity); or *via* direct disturbance of the sea bed through biological activity or anthropogenic interference. Biologically and physically mediated particle transport processes often occur simultaneously and non-independently from one another, on separate or concurrent spatial and temporal scales. Within the sediment, particle reworking occurs mainly through sources of biotic and abiotic mixing rather than resuspension and deposition. The main drivers of exchange between the seabed and the water column can be grouped into upward transport from the benthos to the pelagic environment, in the form of resuspension, and downward transport from the pelagic environment to the benthos through deposition (Figure 2). These two routes include various biological, physical, and anthropogenic pathways, which will be elucidated in this section.

As previously mentioned, the relative importance of individual drivers of B/P exchange is context dependent. The occurrence of large phytoplankton blooms (e.g. Zhang *et al.*, 2015) or dredge-spoil dumps (e.g. Moon *et al.*, 1994), for example leads to an abundance of suspended material, the sinking of which is likely to locally dominate particle exchange processes. In storm-heavy seasons, or during the occurrence of extreme stochastic storm events, on the other hand, upward particle fluxes are likely to be dominant (e.g. Madsen *et al.*, 1993). Outside of such extreme events, the relative importance of physical and biological drivers of B/P exchange is dependent on location (e.g. Dellapenna *et al.*, 1998). This situation and location dependence of the relative importance of B/P particle exchange drivers constitutes yet another gap in our knowledge of these processes. Past studies may be used to estimate each driver's importance to warrant its inclusion in future studies, though this assessment has to be made in each instance, taking into account the scale, location, and timing of the sampling effort, as well as the occurrence of extreme events close to the time of sampling (Hewitt *et al.*, 2007). Because of this complexity, and for the sake of simplicity, these drivers of particle exchange are reviewed subsequently moving focus from the water column and towards the sediment, without necessarily reflecting their relative importance.

Downward flux and deposition

Throughout the water column, particles stay in suspension when the ascending vertical components of turbulent eddy velocity fluctuation are greater than the corresponding particle settling velocity (Komar, 1976a, b). Physical and chemical barriers in the water column, for instance in the form of haloclines and thermoclines, can change and inhibit the rates at which matter fluctuates from the water column to the benthos and *vice versa* (e.g. Biggs and Wetzel, 1968; Qiao *et al.*, 2011). While dissolved matter can still readily diffuse across the thermocline (e.g. Emerson *et al.*, 1997), particulate matter up to a critical negative buoyancy threshold is unlikely to cross a thermodynamic barrier. In the majority of cases, the deposition of particles occurs in combination with other processes; turbulence and upward-mixing can make the settling process considerably unpredictable (Winterwerp and Kesteren, 2004). Mass settling flux may thus be defined as a product of matter concentration and settling velocity (Manning and Bass, 2006). The latter is mainly affected by the size and density in which OM flocs occur (Maa and Kwon, 2007) while the former depends on the rates at which particles are supplied through resuspension or release within the water column. In cohesive sediment settling conditions, high concentrations of suspended particles may flocculate while in suspension (Einstein and Krone, 1962; Stolzenbach and Elimelech, 1994). Flocculation is a constant yet dynamic balance of aggregation and disaggregation (Tsai *et al.*, 1987) driven by physical or chemical attraction, and particle polydispersity (Sun *et al.*, 2018). The typical primary source of cohesion and hence flocculation is the effect of salinity on charged clay particles through mass-attractive London-van der Waals forces and electrostatic bonding, though this may not be the most important factor driving flocculation in a biological context (Parsons *et al.*, 2016). Flocculated particles are relatively large in size and tend to settle more readily than primary particles, depending on their size and density, but may be broken up

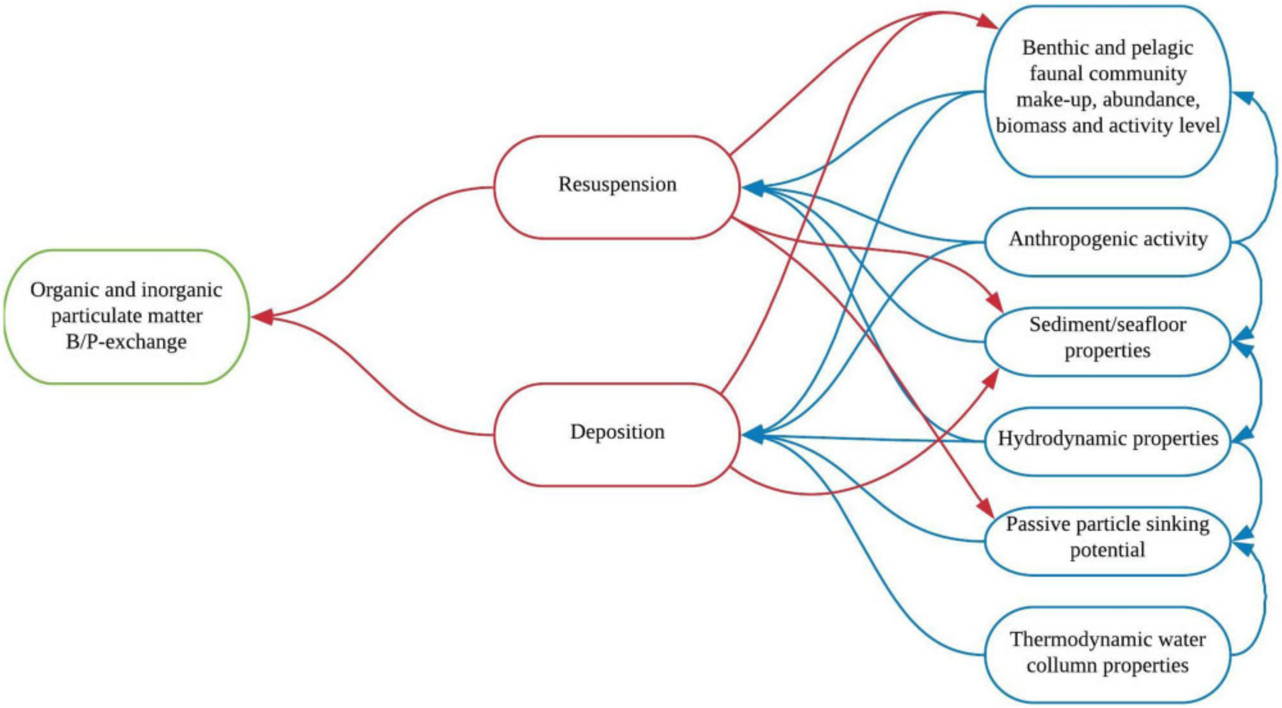

Figure 2. Flow chart of direct (red, middle) and indirect (blue, right) drivers of particle B/P exchange; arrows indicate which factors affect others and are colour-coordinated with the driver they originate from.

again easily by applied shear stress (Winterwerp, 2011). Regardless of particle size or nature, materials can be moved around the water column through turbulent water flow and trapped in biological (e.g. Gambi *et al.*, 1990) or man-made (e.g. Simons and Şentürk, 1992) near-bottom structures. Lateral transport throughout water bodies can be hard to track, and only some studies attempt to trace the origins of suspended matter collected in sediment traps (e.g. Narita *et al.*, 1990). There is much to discover yet about the sources of suspended particulates and the pathways they take through the water column.

Biological drivers of particle deposition can act both actively and passively. Some zooplankton groups, such as Copepods, migrate vertically through the water column on a diurnal basis. The transport of OM through diel vertical migration constitutes an active downward transport, as organisms come towards the upper water layers to feed at night and return to deeper water where the OM is returned to the system in the form of excretions, or as decaying carcases (Packard and Gómez, 2013). The presence of OM and microorganisms suspended in the water column (generally termed "marine snow") can enhance benthic community metabolism rates and nutrient mineralization (Van Duyl *et al.*, 1992). Marine snow aggregates can include any combination of dead and living matter of highly variable spatial complexity, density, and consequently, sinking rate (Alldredge and Gotschalk, 1988). It serves as a microhabitat and food source to pelagic organisms during its sinking (Lundgaard *et al.*, 2017) and is a source of OM to benthic organisms (e.g. Townsend *et al.*, 1992). In low turbulence, fluff-like OM, which is not immediately incorporated into the sediment matrix, may form a layer that rests on the sediment surface along with fine sediment particles (termed nepheloid layer; e.g. Durrieu de Madron *et al.*, 2017). Within this layer, particulates may be transported laterally across large distances and even exported off the continental shelf (Inthorn *et al.*, 2006). Particle residence times within the nepheloid layer can be vast and warrant further study.

Deposition of particulate matter on the seafloor is catalyzed by roughness elements, which result in interfacial flow dynamics and cause descending vertical sweeps (Huettel *et al.*, 1996). Biogenic structures, such as bivalve byssal structures and seagrasss blades, can trap suspended particles, reduce near-bed water velocity, and increase turbulence in the benthic boundary layer (e.g. Widdows *et al.*, 1998b). In addition, filter feeders can actively move water and the particles suspended in it, towards the sea floor, causing increased particle fluxes towards the benthos, preventing subsequent resuspension through ingestion, trapping in structures (such as tubes and gills), and pelletization of the descended matter (e.g. Widdows *et al.*, 1998b; Denis *et al.*, 2007). Selective sediment particle processing, through the actions of biodiffusing bivalves, for example can lead to long-lasting changes in granulometry over large spatial scales, thereby changing the environment and creating specific habitats for other organisms (Montserrat *et al.*, 2009). Around mussel beds, biodeposition is further catalyzed and accelerated through the production of pseudofaeces, which leads to an increase in the annual deposition of sediment, C, and nutrients (Kautsky and Evans, 1987). Macroalgae and seagrasses have been shown to shield the sea bed from turbulence and lower water velocities, thereby increasing net deposition rates (Fonseca *et al.*, 1982; Gambi *et al.*, 1990). The rate at which this filtering of suspended material flowing through the fronds occurs depends strongly upon the morphology of the macrophytes (Hendrick *et al.*, 2016). Obstacle-induced flow turbulence can effectively filter suspended particulate matter from the water column by driving parts of the flow through the sediment matrix, thus leading to their deposition within the sediment (Hutchinson and Webster, 1998). B/P exchange may further be affected by animals that increase sediment cohesion by building protruding tubes and byssal mats. These act similarly to sea grass and algal fronds by altering the flow and trapping sediments when they occur in high densities. *Lanice conchilega* presence, for example can lead to a reduction in erosion potential when occurring in high enough densities (Denis *et al.*, 2007; Borsje *et al.*, 2014). The addition of small particles to the sediment matrix through active or passive filtering may lead to a change in sediment granulometry and, effectively, cohesion (e.g. Widdows *et al.*, 2000; Volkenborn *et al.*, 2007). During the deposition of already cohesive sediments, though particles of all sizes may be deposited (Lau and Krishnappan, 1994), a sorting process can occur, thus leading to vertical and horizontal particle size gradients (Mehta, 1988).

The availability of depositable particulate material in the water column may also be affected by anthropogenic structures and actions, including dredge-spoil dumping (Moon *et al.*, 1994; Pilskaln *et al.*, 1998; Mikkelsen and Pejrup, 2000) and the installation of offshore wind farms (Baeye *et al.*, 2011; Coates *et al.*, 2014; Dannheim *et al.*, 2019). Although the former constitutes a rapid and intense input of non-native particulate matter to the water column, this does not always affect the benthic community or local sediment properties directly (Smith and Rule, 2001). It can, however, introduce additional organic carbon and new species to the dredged site (Morton, 1977; Wildish and Thomas, 1985), which is likely to have knock-on effects on the biogeochemical composition of the affected environments and B/P exchange potentials. Although some monitoring studies have investigated short-to-medium term effects of dredge-spoil dumping on drivers of B/P exchange, few of these studies include an adequate assessment of the benthic environment prior to the commencement of the dumping and the number of long-term monitoring studies to date is insufficient to draw meaningful conclusions. Other activities, such as active bottom fishing practices (dredging, trawling), can also cause increases in SPM. For instance, trawling can increase SPM concentrations up to six times that of the background levels (Tiano *et al.*, 2019). In the case of offshore wind farms, SPM plumes up to five times the background level in concentration have been shown to be generated through tidal resuspension of fine-grained materials accumulated and produced by epifauna associated with the wind farms' solid structures (Baeye and Fettweis, 2015). The changes in granulometry and OM content in the sediment (Coates *et al.*, 2014) are mostly attributable to the fauna's filtering activity and the production of faeces and pseudofaeces, which can lead to a shift in microbenthic community structure and diversity. In addition, the solid structures constituting the wind turbine's foundations introduce roughness elements to the water column, thereby creating eddies, vortexes, and turbulent flow dynamics and increasing the probability of resuspension (Grashorn and Stanev, 2016). Considering the extensive coverage of offshore wind farms in some areas, such as throughout the North Sea, this change in circulation, seafloor community, and sediment properties may constitute shifts in B/P exchange pathways at large spatial scales.

In contrast to several well-studied offshore wind farms impacts, such as seabird collisions, settlement of encrusting fauna and flora, and electromagnetic disturbances, not much research has been carried out to test their effects on B/P exchange processes (Dannheim *et al.*, 2019). Furthermore, the investigation of anthropogenic impacts often happens in retrospect and the addition of more baseline studies would undoubtedly add much to our understanding of anthropogenic impacts on particle deposition.

Upward flux and resuspension

Particle deposition is rarely final, as particulates can be eroded away from the sediment surface. Generally speaking, the erosion of non-cohesive sediments is constant with applied shear stress and a product of fluid stresses and grain stresses only affected by the excess shear stress, bed roughness, grain size and orientation, particle sorting and packing, and bed configuration (Julien, 2010). On an exclusively physical basis, low-level forces applied to the sediment lead to rolling or sliding of particles along its surface, medium levels prompt a hopping motion called saltation, and strong forces cause particles to be drawn from the bulk sediment into complete suspension. In turbulent environments, particles exchange momentum with the surrounding fluids and are thereby swept across or ejected from the sediment surface (Gordon, 1974; Kassem *et al.*, 2015). Physical erosion patterns in cohesive environments depend strongly upon the way in which the bed was originally formed (Ariathurai and Arulanandan, 1978). Erosion processes in cohesive environments are depth-limited, and erosion rates are reduced in deeper layers, due to the consolidation of particles with depth (Aberle *et al.*, 2004). There are three different types of physical erosion (Amos *et al.*, 1992, 1997), and all three may be displayed in parallel in cohesive sediments, making the process notoriously hard to model.

An additional factor that complicates our understanding of the erosion process is the interference of biotic elements. The extracellular polymeric substances (EPS) produced by marine biofilms, for example reduce the sediment surface roughness and frictional drag, thereby increasing cohesion (Sutherland *et al.*, 1998). EPS distribution throughout the sediment is one of the key components controlling bed form dynamics where it appears in high enough concentrations (Malarkey *et al.*, 2015). There are other biological mechanisms affecting sediment erosion and resuspension such as animal tracking, grazing, (Nowell *et al.*, 1981; Borsje *et al.* 2008; Kristensen *et al.*, 2012), and faecal pellet production (Andersen and Pejrup, 2002) affecting bed roughness as well as resuspension potentials.

Benthic organisms can also drive transport that counters gravimetric deposition by actively ejecting OM and sediment grains into the water column during feeding and other activities, as well as their gametes and larvae to initiate pelagic stages in their development (e.g. the polychaete burrowers *Nereis virens*; Bass and Brafield, 1972). Other organisms known as ecosystem engineers modify, maintain, and create habitats by causing physical state changes in biotic or abiotic materials, thereby modulating resource availabilities directly and/or indirectly (e.g. reef-building bivalves and macrophytes; Jones *et al.*, 1994). The extent to which different areas of the ecosystem in question are impacted depends upon the strength and nature of the respective engineering species (Bouma *et al.*, 2009; Meadows *et al.*, 2012). They may, for example alter their environment and change flow dynamics around the sea bed, thereby altering erosion and deposition rates in various ways (Coleman and Williams, 2002) and thus dictating the sediment type present in an area (Ginsburg and Lowenstam, 1958). Increases in bulk sediment grain size and permeability caused by the bioengineers then promote altered B/P exchange rates (Ziebis *et al.*, 1996). Erosion thresholds may also be affected, in some cases seasonally varying between increase and decrease (Grant and Daborn, 1994; Paarlberg *et al.*, 2005). These and other biologically mediated particle movements can affect particle distributions from micro to landscape scale (Van Hoey *et al.*, 2008; Montserrat *et al.*, 2009).

Bioturbation (the biogenic movement of particulate matter throughout the sediment matrix) can play an important role in localized particle displacement (Berg *et al.*, 2001) as well as landscape-scaled effects on particle distributions by affecting sedimentary structure, biogeochemical gradients and fluxes, and the composition of associated communities of auto- and heterotrophs (Van Hoey *et al.*, 2008; Bouma *et al.*, 2009; Montserrat *et al.*, 2009). Each bioturbating species may affect particle exchanges differently, depending on their functional traits, mediated by species performance in response to the environment in which they occur (e.g. Mermillod-Blondin *et al.*, 2004; Solan *et al.*, 2004; Maire *et al.*, 2006; Braeckman *et al.*, 201), sediment characteristics (Bernard *et al.*, 2019), and temporal patterns such as seasonal cycles (Queirós *et al.*, 2015). The main impacts that bioturbation activity has on upward B/P exchange processes are (i) that it generally destabilizes the sediment, lowering critical erosion and resuspension thresholds in the process (Widdows *et al.*, 1998c; De Deckere *et al.*, 2001), and (ii) the biogenic physical ejection of particulate matter into the water column (Davis, 1993). Co-occurrence of bio-stabilizing and destabilizing organisms is known to have variable effects on sediment matrix properties (Queirós *et al.*, 2011). Such duality may even exist within the effects of a single species, such as has been shown in the deposit-feeder *Peringia ulvae*, which destabilizes sediment surfaces through grazing while simultaneously excreting pellets with increased settling velocity compared to the original sediment, thereby having both destabilizing and stabilizing effects (Andersen and Pejrup, 2002). In some cases, an organisms' effect on sediment erosion thresholds may even reverse in sync with seasonal environmental changes, leading to alternating stabilization and destabilization of the surrounding sediment (e.g. Grant and Daborn, 1994). Overall, the magnitude at which biological processes affect sediment transport and solute exchange is tightly dependent upon the density of active organisms and the magnitude of their effects relative to that of ecosystem attributes or processes also affecting the transport of sediment and solutes (Queirós *et al.*, 2011; Erik Kristensen *et al.*, 2012). The net effect of co-occurring bio-stabilizing and destabilizing benthos, and how this balance may shift on different temporal and spatial scales, has thus far only been investigated in small, location-specific studies and should be investigated at the ecosystem level.

Once buried, particles may be stored and consolidated or recycled (Graf and Rosenberg, 1997). Within the benthic matrix, the complex materials that are not permanently buried are broken down chemically *via* oxidation and biologically by benthos and bacteria, allowing them to re-enter the cycling of elements. In permeable sediments, even living microphytes may be advectively flushed into deeper sediment layers and trapped there, leaving them to be mineralized more swiftly than they would be at the sediment surface when they die, thereby fuelling the recycling of nutrients and C (Ehrenhauss *et al.*, 2004). Advective flushing of particulate OM throughout permeable sediment distributes it evenly, thereby alleviating concentrated hot spots and spreading the OM to a larger microbial community (Franke *et al.*, 2006). Diagenetic reactions vary in speed and, consequently, affect the environment on different scales: very slow reactions occur mostly at depth and are of importance at geological time scales, while rapid ones define the biogeochemical conditions of the benthic boundary layer without having interfered in the sediment matrix at any significant depth (Aller, 2014). The major roles that biological processes play in mineralization do not only extend to the direct impacts of microbes, which catalyze and drive the process itself but also the effects of larger organisms, which modify OM burial rates and contribute to its break-down through grazing (Tait *et al.*, 2015; Queirós *et al.*, 2019). The translocation of particles and potential homogenization of surface sediment layers, as well as the introduction of fresh O_2 and OM to deeper layers by bioturbators, bioirrigators, and even benthivores, is a crucial determinant of diagenetic processes (Lindqvist, 2014).

Direct anthropogenic causes of particle resuspension include dredging, trawling, mining, anchoring, and many others. Repeated dredging can lead to long-term modification of local sediment properties and particle and solute transport rates at the dredged site (Moon *et al.*, 1994; Pilskaln *et al.*, 1998; Mikkelsen and Pejrup, 2000), and the use of trawls and similar types of mobile fishing gear can have comparable effects (e.g. Palanques *et al.*, 2001; Jennings and Kaiser, 2006). The removal of fine-grained particles from continental shelves through anthropogenic resuspension on a global scale is estimated to be up to six times as large as it would be through purely natural causes of resuspension, closely matching the input of fine-grained material from riverine sources (Oberle *et al.*, 2016). On a local level, however, this may not be the case (e.g. Schoellhamer, 2002; Ferré *et al.*, 2008). Mobile fishing gear can furthermore lead to the removal or disruption of micro- and macro-phytic communities that would otherwise inhibit resuspension, as well as modification of the benthic macrofauna community composition (Hiddink *et al.*, 2006; Hiddink *et al.*, 2006), and burial of sediment surface chlorophyll a content (Tiano *et al.*, 2019). Biogeochemical impacts of trawling are more pronounced in naturally muddy than in sandy environments (Sciberras *et al.*, 2016), although some sandy sediments are likely to occur due to long-term granulometry changes resulting from chronic bottom trawling pressure (Hiddink *et al.*, 2006). Long-term biogeochemical changes in seafloor habitats associated with anthropogenic interactions, and associated shifts in B/P exchange processes remain, thus far, largely unknown. This is, among other reasons, due to a lack of data on baseline conditions collected prior to anthropogenic intervention.

Interactions and interdependencies

Most of the B–P coupling processes described in this review are difficult to consider individually, as they either interact very closely with others or have a wide range of effects and dependencies, making them hard to assign to any one section. Each is part of a feedback mechanism and interacting with others, thereby producing the overall effect on sediment and water column structures, which results in altered rates of sediment and solute transport (Borsje *et al.*, 2008). The combination of interacting processes and the scales at which they affect exchanges between the benthic and pelagic zones varies in accordance with the respective physical and biological environmental conditions, the "ecological context" (Queirós *et al.*, 2011).

Most biologically important processes are dependent on both solute and particle B/P exchanges and interactions. One example of this is the cycling of OM , which benthic heterotrophs mediate. Most OM in the marine environment originates from primary producers such as phytoplankton, seaweeds, and other macrophytes, which require light and nutrients in solution to grow, the latter being especially important during times and in locations of nutrient depletion (e.g. Davis *et al.*, 2019). During phytoplankton growth cycles, both dissolved OM (DOM) and particulate OM (POM) specimens are produced and introduced to the environment surrounding the plankton (Biddanda and Benner, 1997). Each of these OM compounds may be utilized differently, as detailed in the previous sections of this review. While POM may be consumed by secondary producers and then exported towards the benthos, either passively through incorporation in faecal pellets and marine snow floccules or actively through the vertical migration of the consumers, DOM may stay in suspension. Depending on the hydrological circumstances, the DOM may be fully utilized and degraded by the microbial community within the water column (Mari *et al.*, 2007). Throughout this process, DOM and POM are in constant interaction through a variety of pathways, which are complex enough to warrant entire review papers by themselves (e.g. Mecozzi *et al.*, 2008; He *et al.*, 2016). Once the OM reaches the sea floor, however, it is utilized by macro- and micro-fauna and/or mineralized by the benthic microbial community (Gooday and Turley, 1990). Both pathways are linked and require an oxidizing environment to function, which is where B/P exchange of dissolved O_2 plays an important role (Snelgrove *et al.*, 2018). These and other links exist within the OM cycling process, which highlights the connectivity between solute and particle B/P exchange pathways of C, O_2, nutrients, and many more . Due to the complexity of the marine system and associated observation or experimentation, there are still many questions in want of an answer, offering a guiding direction for future research.

Future direction

Historically, the exchange of particles and solutes, which were seen as two separate pools of resources, was studied one-dimensionally and often in isolation from other ecosystem processes. This review highlights the shortcomings of this treatment of solutes and particles as separate entities instead of inseparably interwoven parts of the same exchange pathways (see e.g. Kristensen *et al.*, 2012). It should be noted that in some fields, such as diagenetic research, the assumption of an integrated solute/particle framework has been the status-quo for decades (Berner, 1980), but this has not been the case in many fields and, especially, in benthic ecology. These differences in approach could in many instances be attributable to a lack of interdisciplinary collaborations that require bridging in future work. A separate consideration of solutes and particles may be necessary in the exploration of specific transport mechanisms, but as B/P processes are typically affected by many types of exchanges simultaneously, such one-dimensional studies can only ever represent basic foundational elements on which a higher understanding is built. Rediscovering the ecological complexity and applying it in areas other than diagenetic research will thus lead to a better holistic understanding and predictive ability, regarding both drivers and consequences of B/P exchanges. The insight that observations at the ecosystem level are too complex to be approached in the way most empirical ecological studies have done in the past is nothing new (Lawton, 1999), and a change in perspective has already been suggested (Thrush *et al.*, 2009). Detailed guidelines have been suggested to aid scientists in their study design to allow the extrapolation of empirical study results to broader temporal and spatial scales (Hewitt *et al.*, 2007). This includes advice such as consideration of contextual natural history to estimate expectable heterogeneity, integration of correlative and manipulative study elements, inclusion of iterative measurements between integrative studies, use of continuous explanatory variables during the analysis stage, and finally, the integration of *in situ* data and model outputs (Hewitt *et al.*, 2007). Time series data have been assessed as one of the most useful tools to provide broad scale temporal context to ecosystem processes (Thrush *et al.*, 1996) such as B/P exchange. Our review highlights that, although the awareness of a need for ecosystem-level approaches clearly exists, and individual B/P exchange processes are often well-studied, not all pathways have been explored equally well in the past and the multidimensional, transdisciplinary approach is still not used as the foundation of B/P exchange research, at large. Some gaps, such as the lack of objective rank-ability of the respective relative importance of drivers of solute and particle B/P exchanges, require exactly the kind of temporal and spatial ecological context described in the previous paragraph. Information on individual driver processes cannot be balanced or compared with one another without coherent scale and contextual information. Furthermore, while some studies hint at parts of different exchange pathways across the sediment–water interface (e.g. Berner, 1980; Glud, 2008; Aller, 2014), there is generally a distinct lack of information regarding the exchanges themselves, and their importance in the greater ecosystem context, as noted in recent work (e.g. Middelburg, 2017). The consequence of this shift in perception is that when dissecting any B/P exchange pathway into its individual processes, it becomes apparent that often not all processes involved are well known well enough to allow for the accurate quantification of the entire pathway. Thus, even when consideration of the environmental spatial and temporal context permits a classification of drivers of exchange by relative importance, not all may be known in enough detail to be of use.

Examples of parameters into which more research should be invested are, for example the effects of biological and anthropogenic actions of the diffusion of solutes other than O_2, *in situ* observations of interactions of boundary layer dynamics with physical drivers of B/P exchange, potential seasonal dominance of biological drivers of B/P exchange over physical ones, lateral particulate matter transport, and residence times within the nepheloid layer.

Embracing the ecosystem as a whole, regardless of the discipline in which individual pieces of research were undertaken, is a vital step towards improved benthic–pelagic understanding (Widdows *et al.*, 2000; Kristensen, 2001; Griffiths *et al.*, 2017) and an in-depth understanding of individual drivers and processes is key to this. However, to integrate studies from various fields as is often necessary when investigating ecosystem-level pathways, such as B/P exchanges, some caution must be exercised. Middelburg (2017) summarizes the different approaches of various disciplines well on the example of organic carbon cycling by pointing out areas of disagreement *versus* overlap, and accumulating elements from each discipline to form a complete picture of current knowledge on the topic.

Collaborative research efforts must move past multidisciplinary approaches in which individuals or teams from different disciplines independently research the same environment, only to later collate their findings, to truly transdisciplinary working practices that take elements of the various disciplines into account from the start. The ideal next step in gaining a deeper understanding of B/P exchange in coastal marine ecosystems will be to fully acknowledge the complexity and interdependencies of the processes involved in individual pathways. This will lead towards a more precise measure of real-life ecosystem-scaled processes, such as elemental cycling, gas exchange, quantification and subsequent mitigation of anthropogenic influences, and much more. Measuring this complexity in real systems will doubtlessly be a challenge, but it could also be the stepping stone to a deeper understanding of the marine environment at local and global scales, providing us with the means to better study, conserve, and protect it. With ongoing environmental change, be it anthropogenic or natural, we will thus be able to make more accurate assessments of the state of the marine ecosystem functioning and take appropriate actions to conserve it.

Funding

This work was supported by the Natural Environmental Research Council (grant number NE/L002531/1).

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Handling editor: Joanna Norkko