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Decadal patterns and trends in benthic-pelagic exchange processes

--Manuscript Draft--

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	Charlie E. L. Thompson
	Ana M. Queirós
	Steve Widdicombe
Abstract:	In marine environments, the exchange of particles and solutes between the seafloor and overlying water column, known as benthic-pelagic (B/P) coupling is an important component in many biological and biogeochemical cycles. Key processes and drivers involved in this exchange display strongly seasonal variability, especially in temperate coastal environments. The magnitude and timings of these seasonal patterns however are not identical year-on-year, and the influence of this inter-annual variability on the rate and direction of B/P exchange, as well as the influence of longer term, multi-year trends, are less well understood. In this current study, multi-year temporal patterns of benthic-pelagic solute and particle exchange were investigated on the examples of particulate organic carbon and dissolved inorganic nitrogen time series data, to assess connections between inter- and multi-annual processes and characterize their nature and what drives them. To this end, a decadal (2009-2018) time-series dataset that combines biological, physical, meteorological and chemical measurements from the Western Channel Observatory, Plymouth, UK was analyzed in combination with supplementary data from several environmental monitoring agencies. Time-series decomposition using seasonal decomposition with locally estimated scatterplot smoothing revealed that the main causes of inter-annual variability were extreme outlier events, some of which were influential enough to cause multi-annual trends. Stochastic meteorological and biological extremes, such as exceptional storms and phytoplankton blooms explained a large proportion of outlier events in the time series. Global-scale climatic fluctuations, such as North Atlantic Oscillation (NAO) and Southern Oscillation Index were reflected in benthic-pelagic exchange trends when they co-occurred in an additive manner (e.g. positive NAO and El Niño). The importance of multi-parameter long-term observatories, such as the Western Channel Observatory, is highlighted, and the use of transdisciplinary time-series datasets to identify individual events which have large ecosystem-level impacts is demonstrated. In order to identify and monitor long-term effects, such as climate trends or decadal global ocean cycles, multi-decadal sustained observations are of vital importance.
Suggested Reviewers:	Karl Attard, Dr karl.attard@biology.sdu.dk
	Mari Joensuu mari.joensuu@helsinki.fi
	Allejandro Gallego a.gallego@marlab.ac.uk
Opposed Reviewers:	
Response to Reviewers:	1. In abstract, you could clarify what kind of benthic-pelagic solute and particle fluxes you refer to (line 33). Response: Now Lines 33-37, added more detail. New sentence: “In this current study, multi-year temporal patterns of benthic-pelagic solute and particle exchange were

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2. Line 44, there's "in" twice (...reflected in in benthic...)
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5. Figure I: it would be good to have a north arrow and a scale to see the distance between different stations.
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Saskia Rühl

Helmholtz Zentrum Geesthacht

Max-Planck-Straße 1

21502 Geesthacht

Germany

01. December 2020

Dr E. Hofmann

Editor

Journal of Marine Systems

Dear Dr Hofmann,

I'm pleased to submit our original research paper titled "Decadal patterns and trends in benthic/ pelagic exchange processes" to be considered for publication in the *Progress in Oceanography*. The manuscript is authored by myself (SR), as well as Prof Steve Widdicombe (SW), Dr Ana M. Queirós (AQ) and Dr Charlie Thomson (CT).

We believe that this manuscript suits the scope of your journal as it is a multidisciplinary approach to studying inter-annual and multi-annual patterns in the interactions and exchanges between benthic and pelagic environments. By taking biogeochemical, biological, meteorological and oceanographic processes into account this study provides a comprehensive interpretation of ecosystem level processes. In a temperate environment, the drivers of benthic/pelagic solute and particle exchange are known to follow intra-annual seasonal patterns. This paper analyses how inter-annual variation and multi-annual trends can cause deviations from typical patterns. Through analysing a decadal dataset comprising of benthic and pelagic multidisciplinary observations, we were able to identify what the main causes of inter and/or multiannual variation are.

Based on the results outlined in our manuscript, the main sources of B/P exchange processes of unusual magnitude or timing are extreme weather events such as storms, unusually long or intense instances of pelagic primary productivity and the additive co-occurrence of global scale climate processes such as the North Atlantic Oscillation and El Niño. We determined that in strongly seasonal temperate environments such as the one in this instance, medium to long-term temporal patterns are best identified through within-season analyses. Though this analysis of a decadal time series revealed multi-year trends, a longer temporal record would make the identification of even more long-term trends such as climate change driven processes possible.

The methods used in this paper are transferrable to any environment, though we ascertain throughout our analysis that the comprehensive nature of the long-term data set available for this location facilitated particularly clear and in-depth results. Based on this, and the need to identify more long-term multi-decadal trends, it is recommended to sustain multidisciplinary long term observatories.

Credit author statement:

SR: Conceptualization, Data curation, Formal analysis, Investigation, Methodology and Writing – Original Draft preparation; **SW**, **CT** and **AQ:** Funding acquisition, Conceptualization, Methodology, Writing - Review and Editing

Our manuscript is an original work and is not being submitted to or published by any other journal. No part of it is under consideration for another publication and none of the authors have conflicts of interest to disclose concerning this publication. All authors have approved of this manuscript at the time of submission. The funding body financially supporting the study was not directly involved in the study design, data collection, or write-up process.

We would like to suggest the following researchers as potential reviewers:

1) Dr Karl Attard (karl.attard@biology.sdu.dk)
2) Dr Mari Joensuu (mari.joensuu@helsinki.fi)
3) Dr Allejandro Gallego (a.gallego@marlab.ac.uk)

Thank you for your consideration, we look forward to hearing from you.

Sincerely

Saskia Rühl

Postdoctoral researcher, Helmholtz Zentrum Geesthacht

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Highlights:

- Benthic-Pelagic exchange depends on a variety of drivers (biological, chemical, etc.)
- The influence of these drivers is temporally variable
- On a decadal timescale biological and meteorological extremes have the biggest impact
- Extreme events in a single year can have effects that last multiple years

Decadal patterns and trends in benthic-pelagic exchange processes

Authors:

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Stephen Widdicombe – swi@pml.ac.uk

Keywords: Benthic-pelagic exchange; Extreme event; Particle; Solute; Time-series;

Abstract

In marine environments, the exchange of particles and solutes between the seafloor and overlying water column, known as benthic-pelagic (B/P) coupling is an important component in many biological and biogeochemical cycles. Key processes and drivers involved in this exchange display strongly seasonal variability, especially in temperate coastal environments. The magnitude and timings of these seasonal patterns however are not identical year-on-year, and the influence of this inter-annual variability on the rate and direction of B/P exchange, as well as the influence of longer term, multi-year trends, are less well understood. In this current study, multi-year temporal patterns of benthic-pelagic solute and particle exchange were investigated on the examples of particulate organic carbon and dissolved inorganic nitrogen time series data, to assess connections between inter- and multi-annual processes and characterize their nature and what drives them. To this end, a decadal (2009-2018) time-series dataset that combines biological, physical, meteorological and chemical measurements from the Western Channel Observatory, Plymouth, UK was analyzed in combination with supplementary data from several environmental monitoring agencies. Time-series decomposition using seasonal decomposition with locally estimated scatterplot smoothing revealed that the main causes of inter-annual variability were extreme outlier events, some of which were influential enough to cause multi-annual trends. Stochastic meteorological and biological extremes, such as exceptional storms and phytoplankton blooms explained a large proportion of outlier events in the time series. Global-scale climatic fluctuations, such as North Atlantic Oscillation (NAO) and Southern Oscillation Index were reflected in benthic-pelagic exchange trends when they co-occurred in an additive manner (*e.g.* positive NAO and El Niño). The importance of multi-parameter long-term observatories, such as the Western Channel Observatory, is highlighted, and the use of transdisciplinary time-series datasets to identify individual events which have large ecosystem-level impacts is demonstrated. In order to

identify and monitor long-term effects, such as climate trends or decadal global ocean cycles, multi-decadal sustained observations are of vital importance.

1. Introduction

The coastal marine system is often studied as a series of compartmentalised environments, including the seafloor (benthic) and water column (pelagic). These environments are often considered separately in single-parameter studies despite being known to be strongly connected. Benthic-pelagic (B/P) exchanges, wherein dissolved and particulate matter are in a process of constant flux, are a good example of the inter-connectedness of the marine environment. B/P exchange pathways are controlled a range of direct drivers, which can overlap. For dissolved matter (DM), the main drivers include biological mixing and bioirrigation, advective flux, physical resuspension and diffusion. Particulate matter (PM) flux, on the other hand, is largely shaped by the interplay of particle sinking and deposition, and resuspension. Each of these direct drivers is in turn affected by a number of physical, meteorological, biological and chemical secondary drivers, as reviewed by Rühl *et al.* (2020a).

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). Seasonal variability strongly influences B/P coupling processes, such as biologically driven exchanges, especially in temperate coastal environments (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 these factors 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, we assessed such a dataset. A ten year time series was collated, including data gathered as part of various programmes undertaken at Western Channel Observatory, a benthic-pelagic long-term monitoring station offshore of Plymouth, UK (WCO; 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.

2. Methods

2.1 Study site

The study uses data from Station L4 (hereafter L4), the main station of the Western Channel Observatory (WCO; Smyth *et al.*, 2015). L4 is situated in the English Channel 11 nm off the coast of Plymouth, UK (50.25°N; 4.22°W, Figure 1). The site is characterized by a combination of the coastal influence of the Tamar estuary, and water column thermal stratification typical of UK continental shelf during summer months (Smyth et al. 2015). Flow conditions at L4 are dynamic with strong tidal and riverine influences (Smyth *et al.*, 2015) as well as wave propagation impacts during high wave events (Joseph, 2019). Tidal mixing can redistribute nutrients to supply pelagic phytoplankton communities (Caddy & Bakun 1994) and carry PM horizontally (Groen 1967) as well as vertically (*e.g*. Weeks *et al*., 1993). Upwelling processes induced by wind can bring nutrients from bottom layers to the euphotic zone, sustaining phytoplankton blooms (McGillicuddy *et al.*, 2007). L4 experiences regular seasonal nutrient depletion in surface waters (Smyth *et al.*, 2010), and organic matter inputs from a variety of seasonally variable sources (Queirós *et al.*, 2019). The seabed is composed of sandy mud (Queirós *et al.*, 2015). 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 OSPAR (OSPAR, 2020).

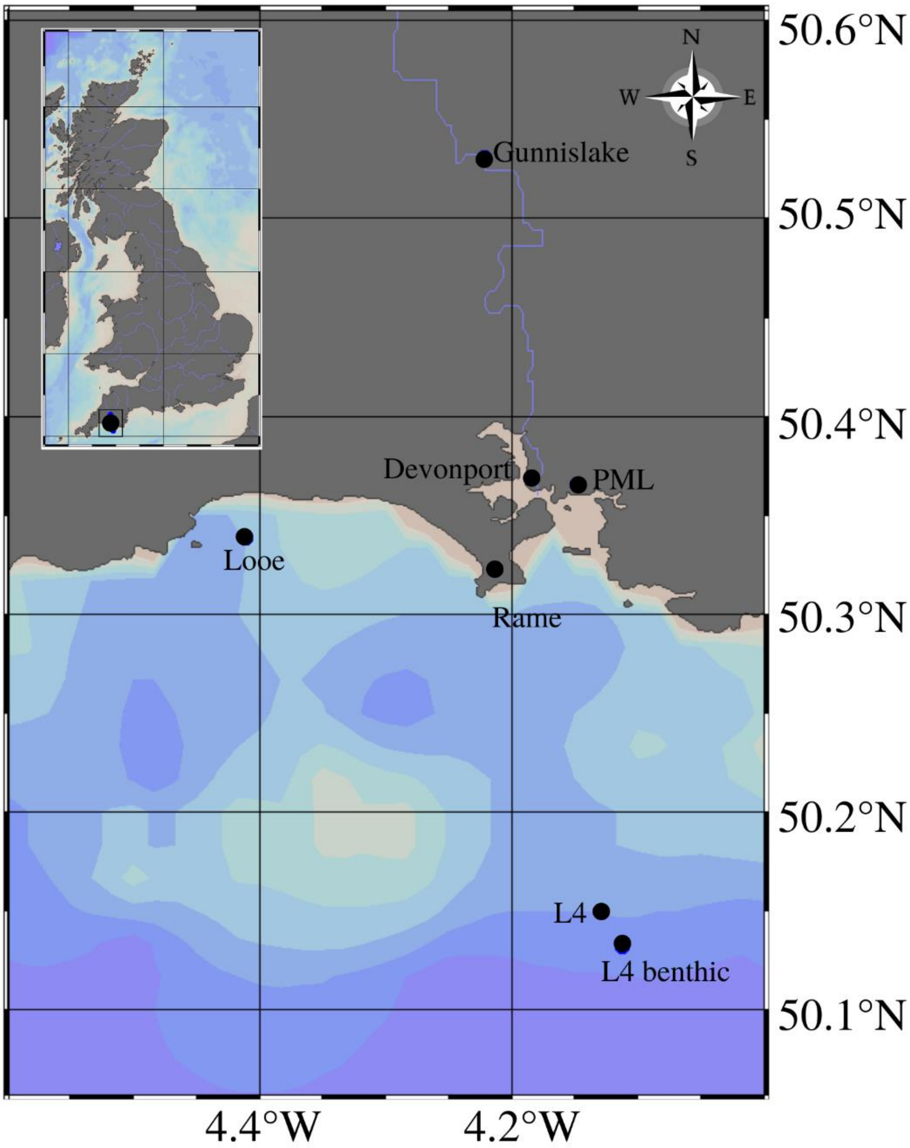

Figure 1: Location of sampling stations including the pelagic and benthic L4 sites, Rame Head MET station, Looe wave buoy, PML MET station, Devonport tidal gauge and Gunnislake river flow gauge, as marked by the black dot relative to Plymouth Sound, and its location relative to the UK in a broader geographical 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 (see Figure 1) and connectivity between the two sites is well documented (T Smyth *et al.*, 2015; Tait *et al.*, 2015; Zhang *et al.*, 2015; Navarro-Barranco *et al.*, 2017; Queirós *et al.*, 2019).

2.2. Datasets

In this study, data of a variety of benthic and pelagic variables (see Table I) at L4 from 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 that 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 1), the National River Flow Archive (NRFA, 2019; see Gunnislake marker in Figure 1), the Permanent Service for Mean Sea Level (PSMSL, 2019; see Devonport marker in Figure 1), and the Looe Wave buoy (NNRCMP, 2019; see Looe marker in Figure 1). 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 I.

Table I: 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); acronym key: Western Channel Observatory (WCO), Meteorological station (MET station), National River Flow Archive (NRFA), Permanent Service for Mean Sea Level (PSMSL), Wave peak period (T_{peak}), Wave period (T_z)

Variable	**Temporal availability of data**	**Data source**	**Sampling location**	**Water depth**	**Sampling frequency**
Particulate Organic Carbon (POC)	2009-2013	WCO	L4	10 m	Monthly
Total Particulate Carbon (TPC)	2009-2013	WCO	L4	10 m	Monthly
Total Particulate Nitrogen (TPN)	2009-2013	WCO	L4	10 m	Monthly
Particulate Organic Nitrogen (PON)	2009-2013	WCO	L4	10 m	Monthly
Coloured dissolved organic matter (CDOM)	2009-2013	WCO	L4	10 m	Monthly
Suspended particulate matter (SPM)	2009-2013	WCO	L4	10 m	Monthly
Oxygen (O_2)	2009-2017	WCO	L4	50 m	Weekly
Phytoplankton abundance and biomass	2009-2018	WCO	L4	10 m	Weekly
Zooplankton abundance	2009-2016	WCO	L4	10 m	Weekly
Meroplankton abundance	2009-2018	WCO	L4	10 m	Weekly
Copepod abundance	2009-2018	WCO	L4	10m	Weekly
Benthic macrofauna abundance and biomass	2009-2018	WCO	L4	54+ m (sediment)	Monthly
Fluorescence	2010-2016	WCO	L4	50 m	Weekly
Chlorophyll a	2010-2016	WCO	L4	10 m	Weekly
Rainfall	2011-2013	MET station	Rame Head / PML	N/A	
Max wave height, T_{peak} and T_z	2009-2018	Looe buoy	Looe (50.203°N / 4.246°W)	Sea surface	Every half hour
Water temperature	2010-2016	WCO	L4	50 m	Weekly
Salinity	2010-2018	WCO	L4	50 m	Weekly
Sediment grain size	2009-2012	WCO	L4	54+ m (sediment)	Sporadic
River flow	2009-2016	NRFA	Gunnislake (50.531°N / 4.222W)	N/A	Daily

Tidal flow	2009-2018	PSMSL	Devonport (50.221°N / 4.111°W)	N/A	Monthly
Nitrate	2012-2018	WCO	L4	50 m	Weekly
Nitrate/Nitrite ratio	2012-2018	WCO	L4	50 m	Weekly
Ammonia	2012-2018	WCO	L4	50 m	Weekly
Silicate	2012-2018	WCO	L4	50 m	Weekly
Phosphate	2012-2018	WCO	L4	50 m	Weekly
BP_c (calculated)	2009-2018	WCO; Queirós *et al*. 2013; Solan *et al*. 2004	L4	54+ m (sediment)	Monthly
BIP_c (calculated)	2009-2018	WCO; Queirós *et al*. 2013; Renz *et al*. 2018; Bruggeman 2019	L4	54+ m (sediment)	Monthly

Data on community bioturbation potential (BPc) were calculated from WCO macrofauna abundance and biomass inventories, using mobility and sediment reworking indices and methods from Queiros *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 Queiros *et al.* (2013) and the Marine Ecosystems Research Project Trait Explorer (Bruggeman, 2019).

2.2 Data analyses

Different subsets of the overall data set listed in Table I were assessed, as contributors to individual drivers of B/P exchange and overall exchange processes (see Appendix A). Data variables were included in driver group subsets by separating and grouping factors identified as influencing the respective exchange processes in Rühl *et al.* (2020a). When individual variables were analysed, data were not normalized but when the overall data set, or variable subsets, were analysed in combination n to determine patterns in B/P drivers and processes, the data were normalized 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 (see Table I) and PM and DM exchange driver and process sub-sets (see Appendix A based on Rühl *et al.*, 2020a), 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 C), 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,). 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).

We 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 A), 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 (Table I) 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-DA, ropls package; Thévenot *et al.*, 2015) were carried out. Within the OPLS-DA, 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 characterization 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" (see Table II), based on distinct intra-annual variability between these periods at this location, determined in Rühl *et al.* (2020b). The winter period was defined as December to February (Table II), 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 (defined by their ≥0.25 year return period (Dhoop & Mason, 2018), based on the long-term records (NNRCMP, 2019). During this period, physically driven upward fluxes were found to be dominant (Rühl *et al*., 2020b). The pre-bloom season includes March and April (Table II) as a period during which the conditions needed for the phytoplankton bloom to occur are established. This was the most stable period, with the least amount of on-going B/P exchanges. During the bloom season (May to June), there is typically a net downward flux of PM, and a net upward flux of DM (Rühl *et al*., 2020b). July to September were defined as the post-bloom season (Table II), during which thermal water column stratification and nutrient depletion prevail (net B/P exchange conditions similar to the bloom period, but lessening in intensity (Rühl *et al*., 2020b)). Autumn was assigned to the months of October and November as the period following this, a transition period between post-bloom and winter conditions during which biological processes are superseded by physical processes, with some overlap between the two along the way (Rühl *et al*., 2020b).

Table II: splitting of the year into five phenological/meteorological periods

Period	**Months included**
Winter	December – February
Pre-bloom	March – April
Bloom	May – June
Post-bloom	July – September
Autumn	October - November

ANOSIM, OPLS-DA 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 (see Table I) 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. Results

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 III. Many datasets exhibited strong seasonal patterns, with low impact scores for the trend and outlier components (Table III). Where strong trend contributions were quantified, their pattern appeared to indicate inter-annual variability or multi-annual cycles, rather than long-term trends.

Table III: Interquartile ranges (IQR) for each of the time series components; higher percentages indicate higher importance of that component, as marked in bold; acronym key: Wave peak period (T_{peak}), Wave period (T_z), Suspended Particulate Matter (SPM), Coloured Dissolved Organic Matter (CDOM), Total Particulate Carbon (TPC), Total Particulate Nitrogen (TPN), Total Organic Carbon (TOC), Total Organic Nitrogen (TON), Oxygen (O_2)

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 biomass	35.75	**42.28**	13.00	19.85
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 IV and Figure 2).

Table IV: 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

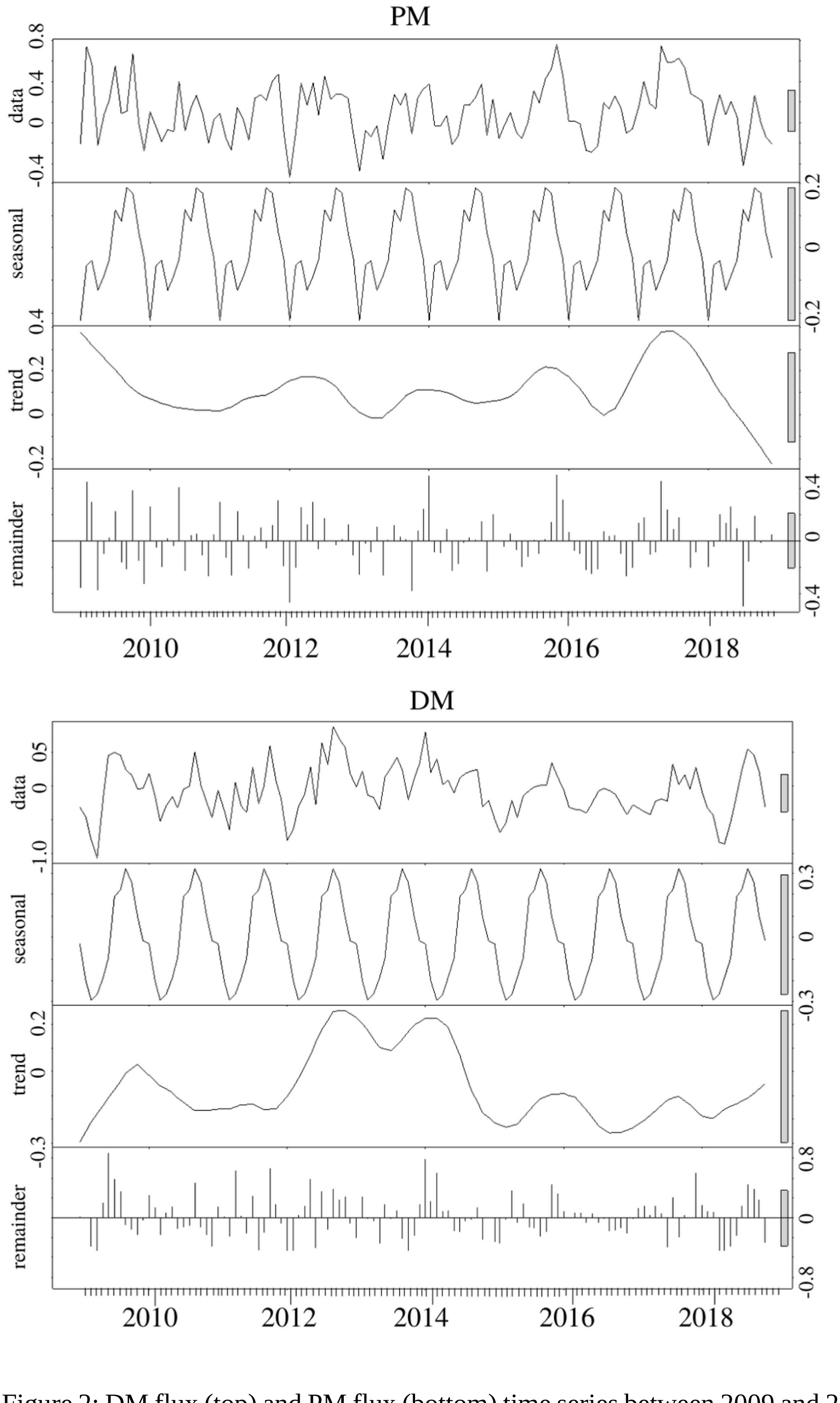

Figure 2: DM flux (top) and PM flux (bottom) time series between 2009 and 2018; Within each of the two plot groups, the original data is displayed on top (data) followed by the seasonal component (seasonal), trend line (trend) and outliers from the norm (remainder); The grey bars on the right of each 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 2, top). 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, Figure 1). The large peak in the overall PM trend between 2017 and 2018 (Figure 2, top) is present in the PM deposition data set as well, but not in the PM resuspension data (Appendix B, Figure 2). This indicates that the processes of deposition likely drive this effect in the overall PM trend. Likewise, the apparent bi-annual cycle in the trend component of DM exchange (Figure 2, bottom) is overshadowed by a double peak (2012-2014) which is also apparent in similar trends in diffusion, bioirrigation and biological mixing (Appendix B, Figures 3-4). This double peak is also present in the trend analysis of nutrient availability throughout the water column (Appendix B, Figures 5-6), river flow and rain fall (Appendix B, Figure 7), as well on that of wave height and T_z in the same period (Appendix B, 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 2) are also apparent in outlier events in either PM resuspension or deposition (see assignment of all outlier peaks >0.2 in Figure 3). 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 3.

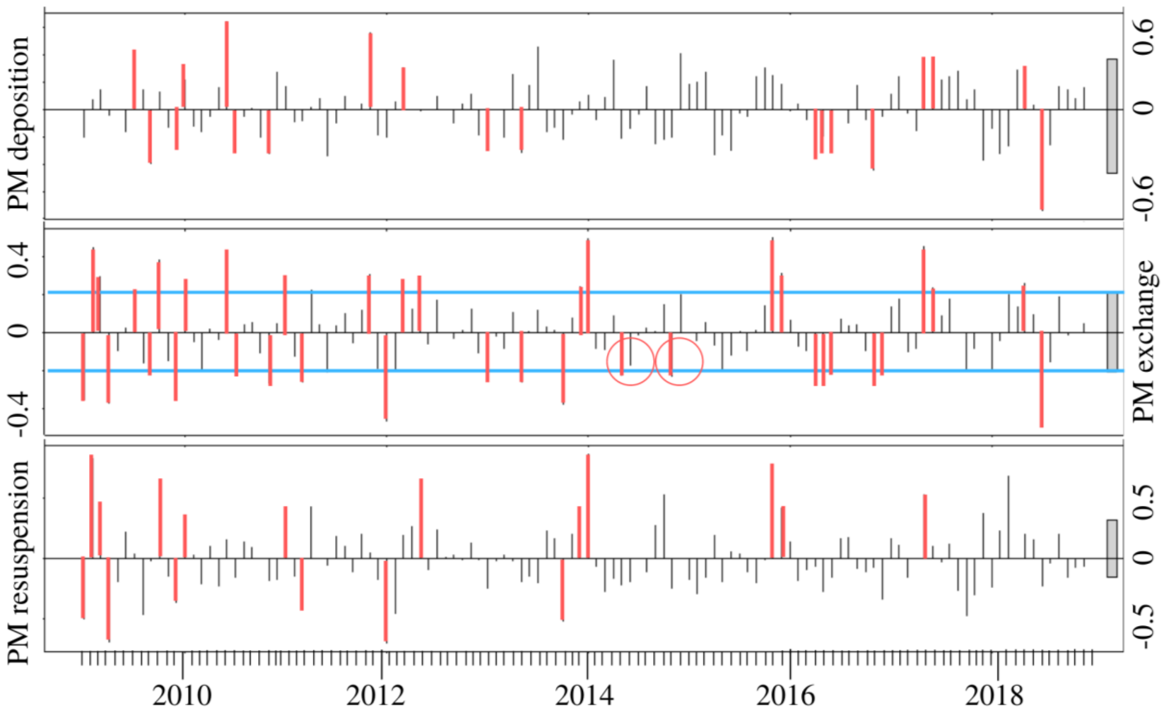

Figure 3: Outlier component of PM deposition (top), PM exchange (middle) and PM resuspension (bottom) time series data sets; outliers above 0.2 and below -0.2 in the overall PM exchange outliers which are likely to be linked also to peaks in deposition outliers or resuspension outliers are indicated 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, 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 2013/2014 winter storms (Masselin*k et al*., 2016a), 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, Figures 7 and 9). These conditions 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 4). 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 4).

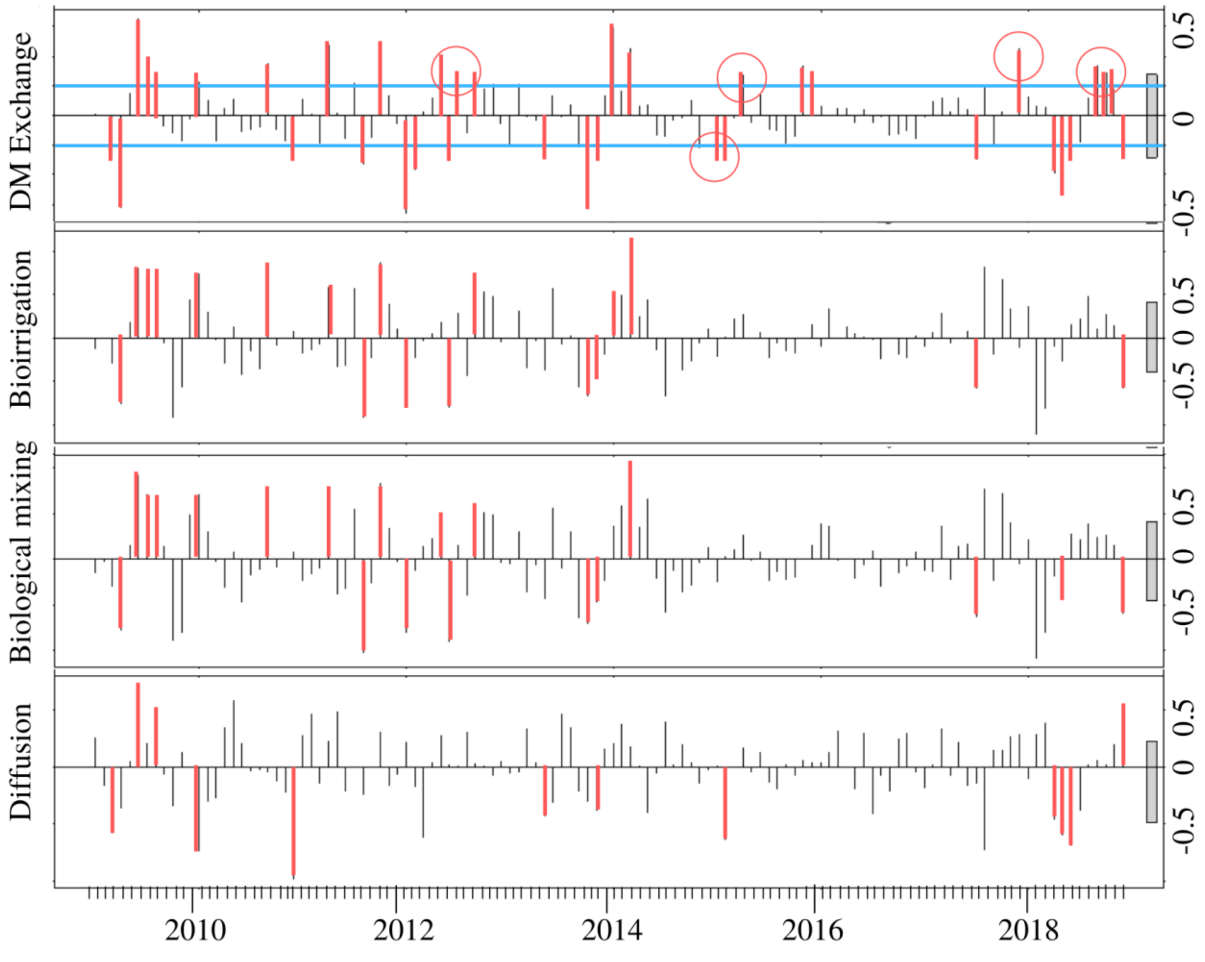

Figure 4: Outlier components of DM exchange, bioirrigation-driven DM exchange, biological mixing-driven DM exchange and diffusion-driven DM exchange time series data sets (top to

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 after Dhoop & 2018; see STL decompositions of wave height and duration in Appendix B, 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, 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, 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, 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, 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).

3.2 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), which could be confirmed despite the low R value of this particular test based on the known seasonal variability in B/P exchanges at this location described in Rühl *et al.* (2020b). 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 C 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 D, 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.

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

Within-period testing using two-way crossed ANOSIMs indicated that there were distinct inter-annual differences within the overall normalized 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 C and D 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 C and D 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 D, 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 V).

Table V: 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, 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 (≥0.25 year return period based on Dhoop & Mason, 2018; 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, 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, 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 periods trends in 2017 are also apparent in the trend component of phytoplankton bloom parameters (see Appendix B, Figure 1), as well as similar trends detected in general zooplankton abundance, in particular that of copepods (see Appendix B, 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 5) 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 rainfall which led to outliers in the form of high salinity and low river flow at that time, may be connected (see Appendix B, 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.

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. Our 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); biostabilizer 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.

Temperate coastal locations such as the area containing station L4 are shaped by a variety of small-scale processes (*e.g.* tidal cycles and seasonality), that are not addressed in this study but are well represented in the existing literature (*e.g*. Karl *et al*., 1996; Highfield *et al*., 2010; Tarran *et al.*, 2015; Rühl *et al.*, 2020b). In contrast, this study shows more long-term temporal patterns than that, such as the effects of biological extremes such as phytoplankton blooms of unusual magnitude, their duration or intra-annual timing. It shows that extreme events can for example change the relative importance of biological and physical drivers of B/P exchange. 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 downward 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*., 2016b). 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 our case, we found strong biannual cycles, 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, Doney and Steinberg, 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 scrutinized.

Published information of time-series collections and studies of B/P exchange at other locations corresponds well with the findings of this study. Cai *et al.* (2012) for example, links climatic oscillations to localized meteorological extremes in Australia, and outlines a trend of increasing frequency of extreme events based on past data. Vantrepotte and Mélin (2011) decompose a global time series record of chlorophyll a from 1997 to 2007 into seasonal, outlier and trend components and detect large inter-annual variability in primary production in subtropical domains as well as the Northeast Atlantic and South of Australia. Also on Chlorophyll, López *et al.* (2017) found turbidity to be one of the main drivers of temporal inter-annual variability. Extreme periods of climatic and biological variability, lasting multiple years, identified in the North Pacific have been shown to cause long-term shifts in biological communities (McKinnell & Dagg, 2010; DFO, 2020). Rodil *et al.* (2020) showed strong biologically driven B/P coupling in the Baltic, with seasonal variability over the course of a year. The latter study site would be an interesting target for a more long-term study.

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 analyzed 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 inter-annual B/P exchange variability, may be affected by climate change. Changes in pH and the increased frequency and wider 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 contextualize 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 trends 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 analyzed, 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 we analyzed, 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 of datasets (high frequency and low frequency), 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, Turley and Allen, 1990). Guided by the underlying temporal structure of the WCO sampling, we then have a sufficiently strong temporal frame onto which all datasets can be aligned and thus used to provide greater insights about the ecosystem analyzed. 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.

5. Conclusions

We determined that 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. In the mean-time, the integration of a variety of data sets, including modelling, in-situ and satellite data, should be promoted in order to gain the most holistic impression possible.

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Appendices:

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

Process → ------------------------- **Driving variables ↓**	PM Resuspen-sion	PM Deposi-tion	Absolute PM flux	Diffusion-driven DM exchange	Phys. Resuspen-sion driven DM exchange	Advection-driven DM exchange	Biological mixing driven DM exchange	Bioirriga-tion-driven DM exchange	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				✔	✔	✔	✔	✔	✔

Appendix B

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

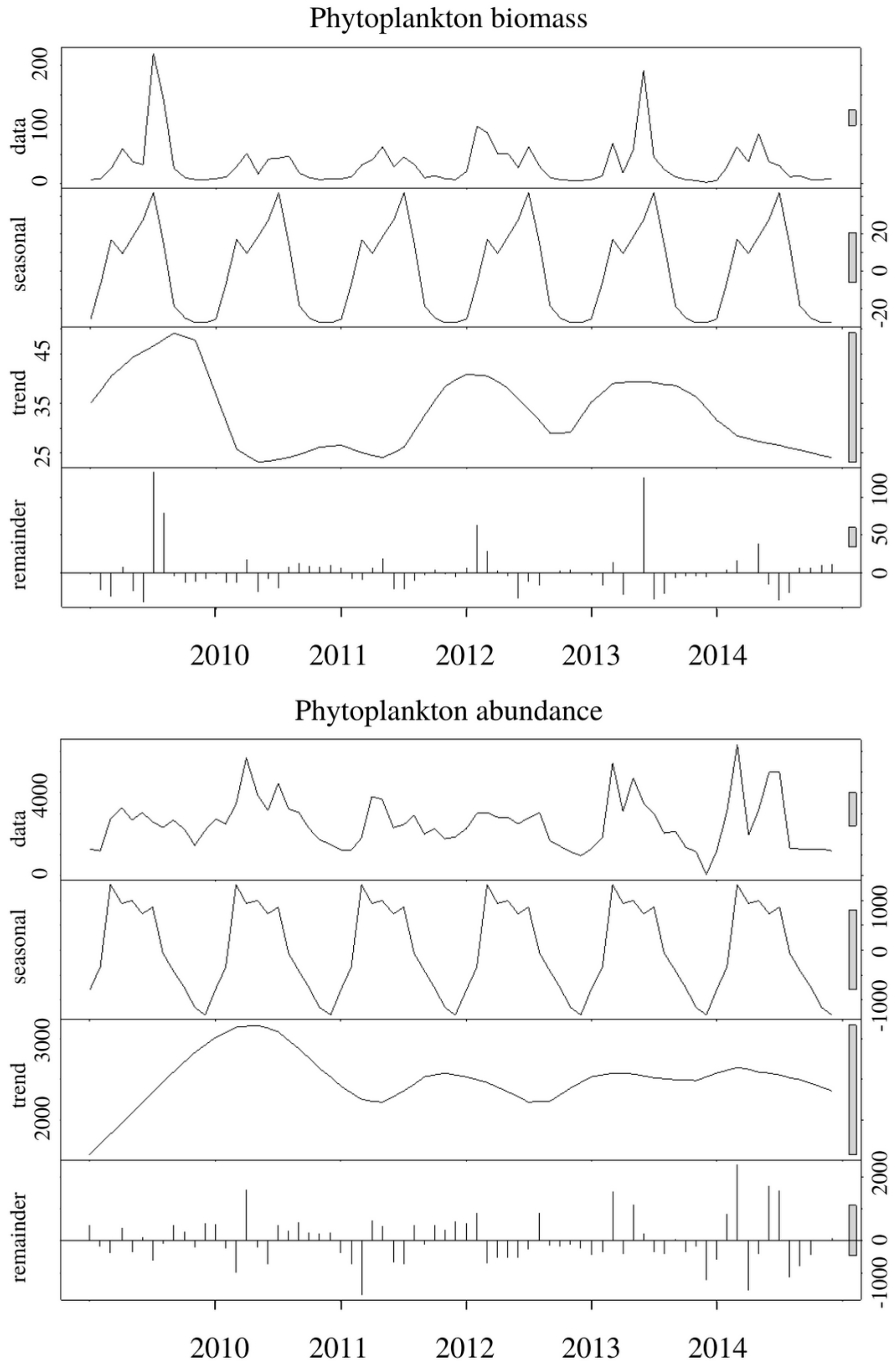


Figure 2: STL decomposition of PM deposition and resuspension

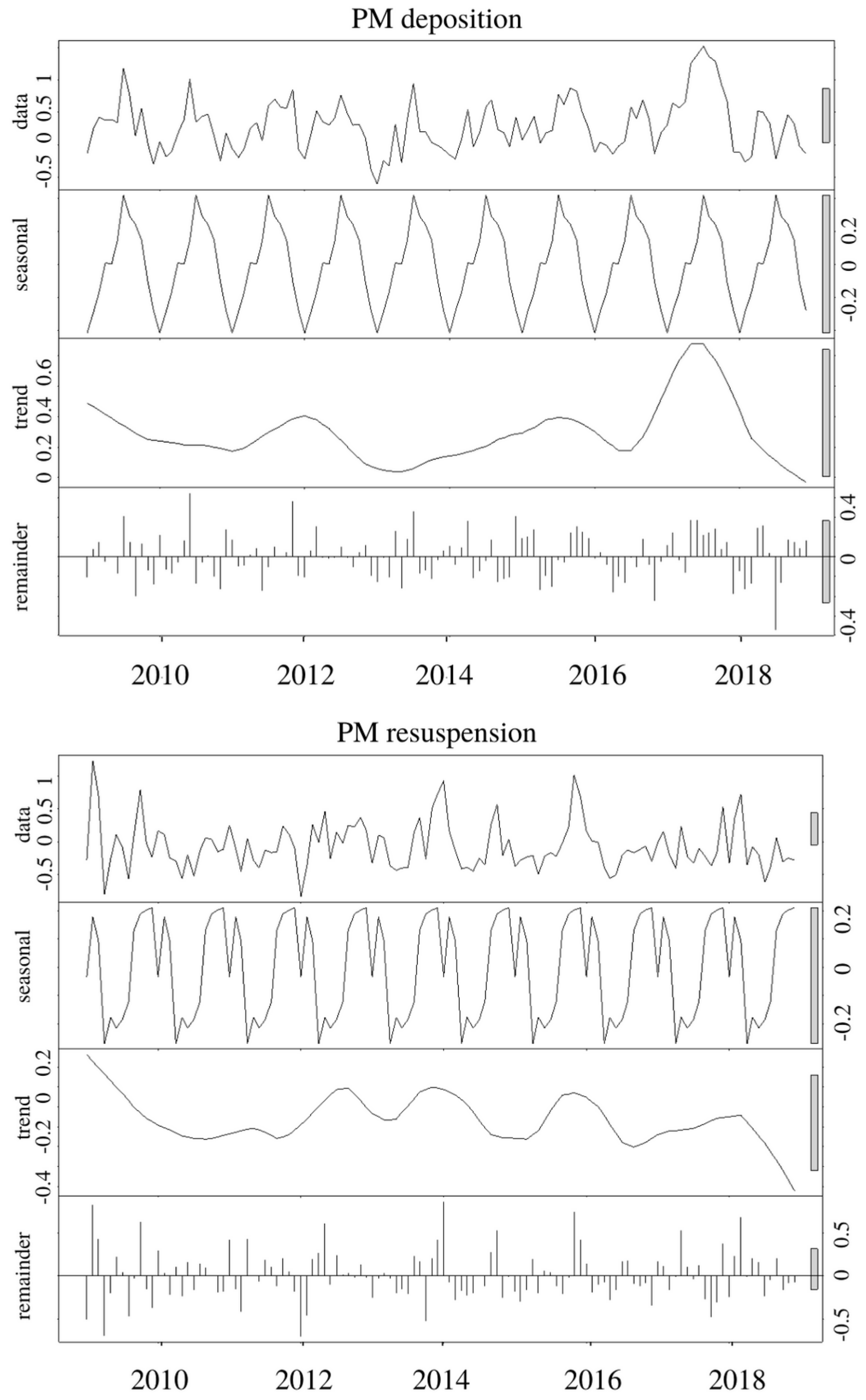


Figure 3: STL decomposition of DM exchange through bioirrigation and biological mixing

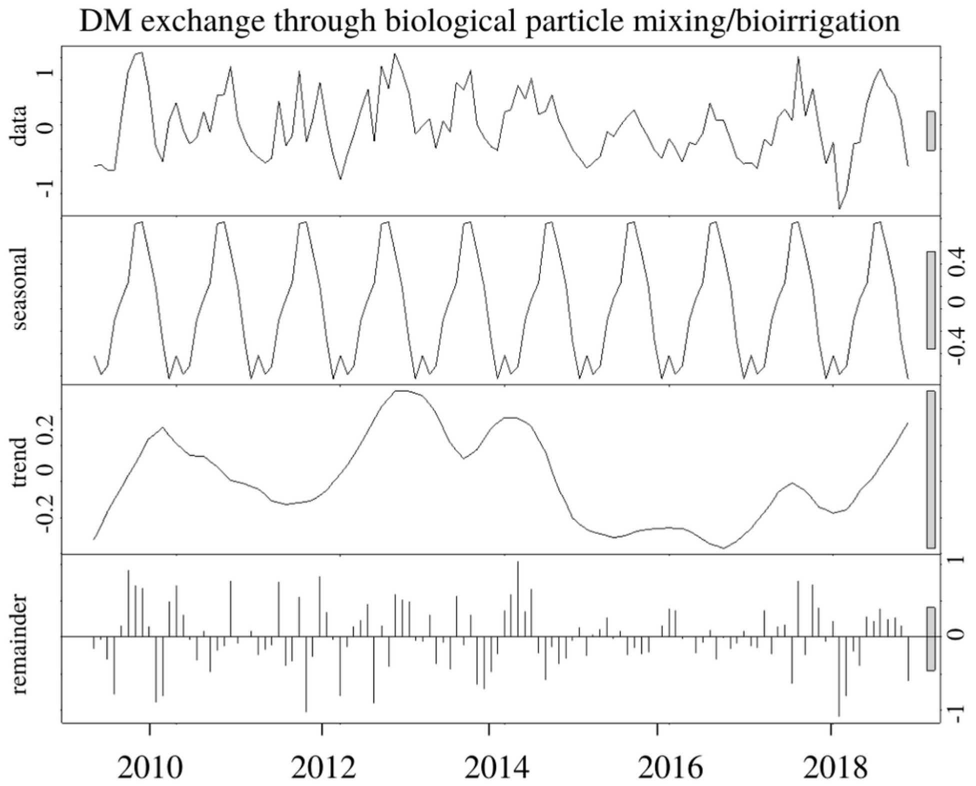


Figure 4: STL decomposition of DM exchange through physical resuspension / advection and diffusion

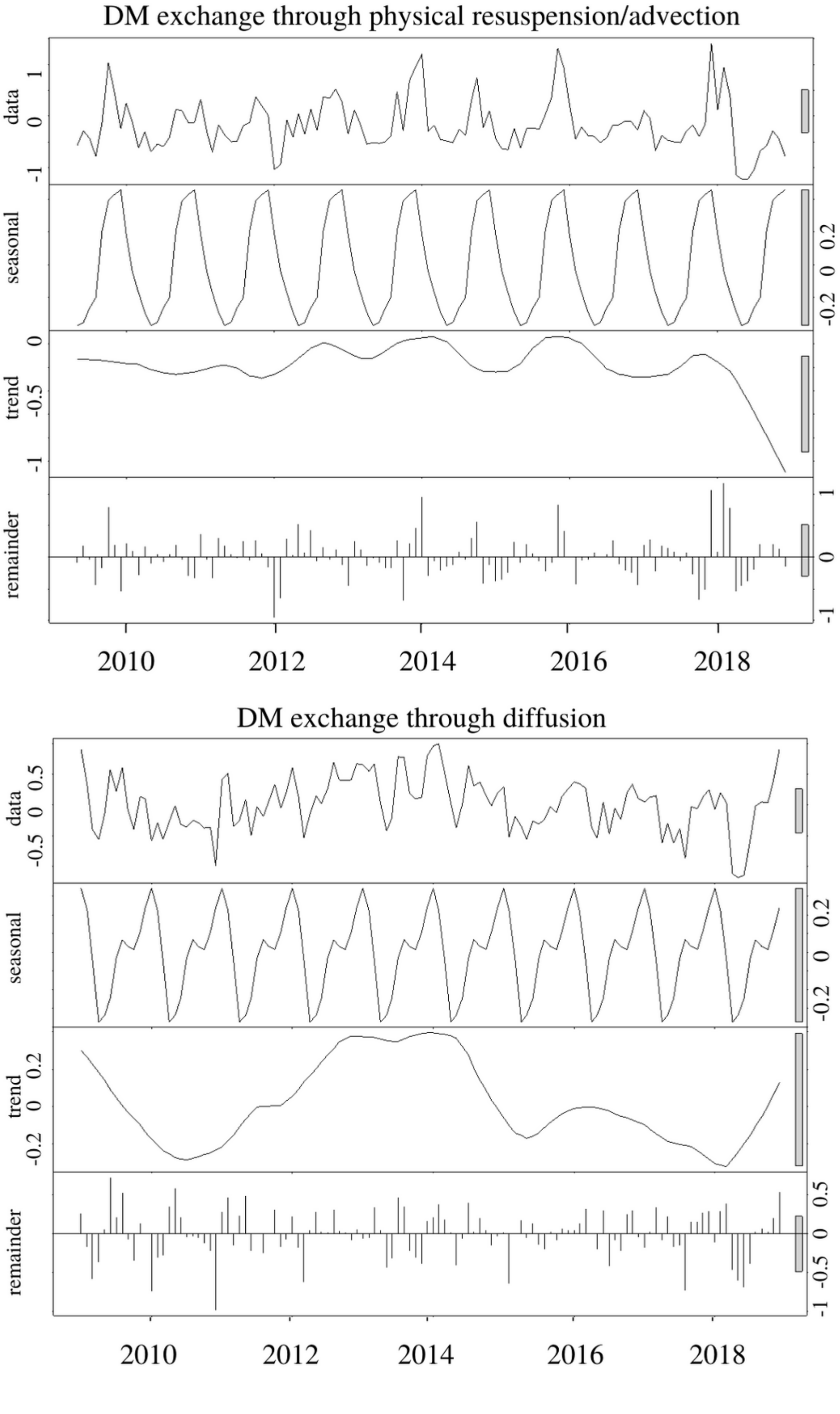


Figure 5: STL decomposition of Ammonia and Silicate concentration

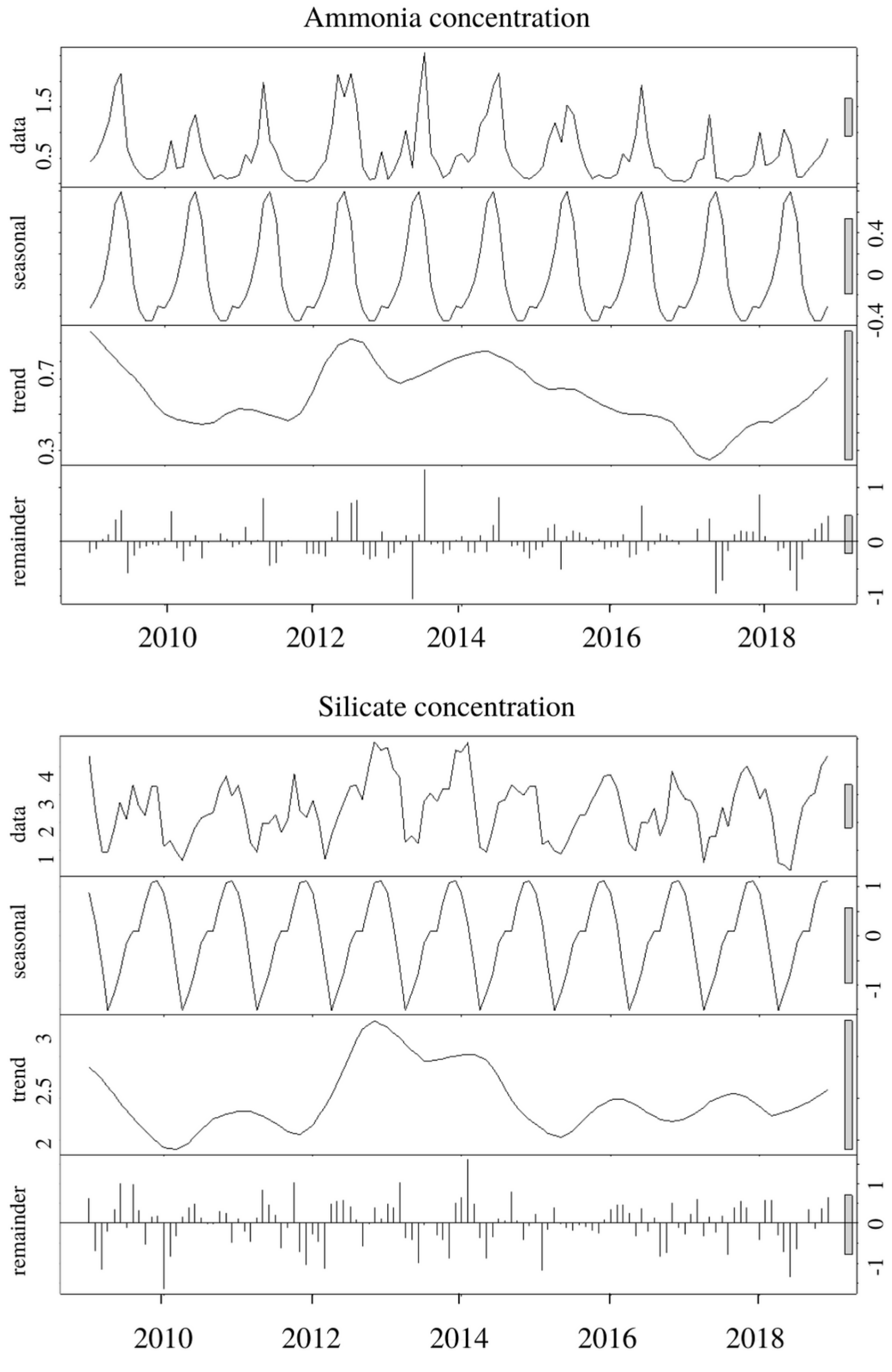


Figure 6: STL decomposition of Nitrite and Phosphate concentration

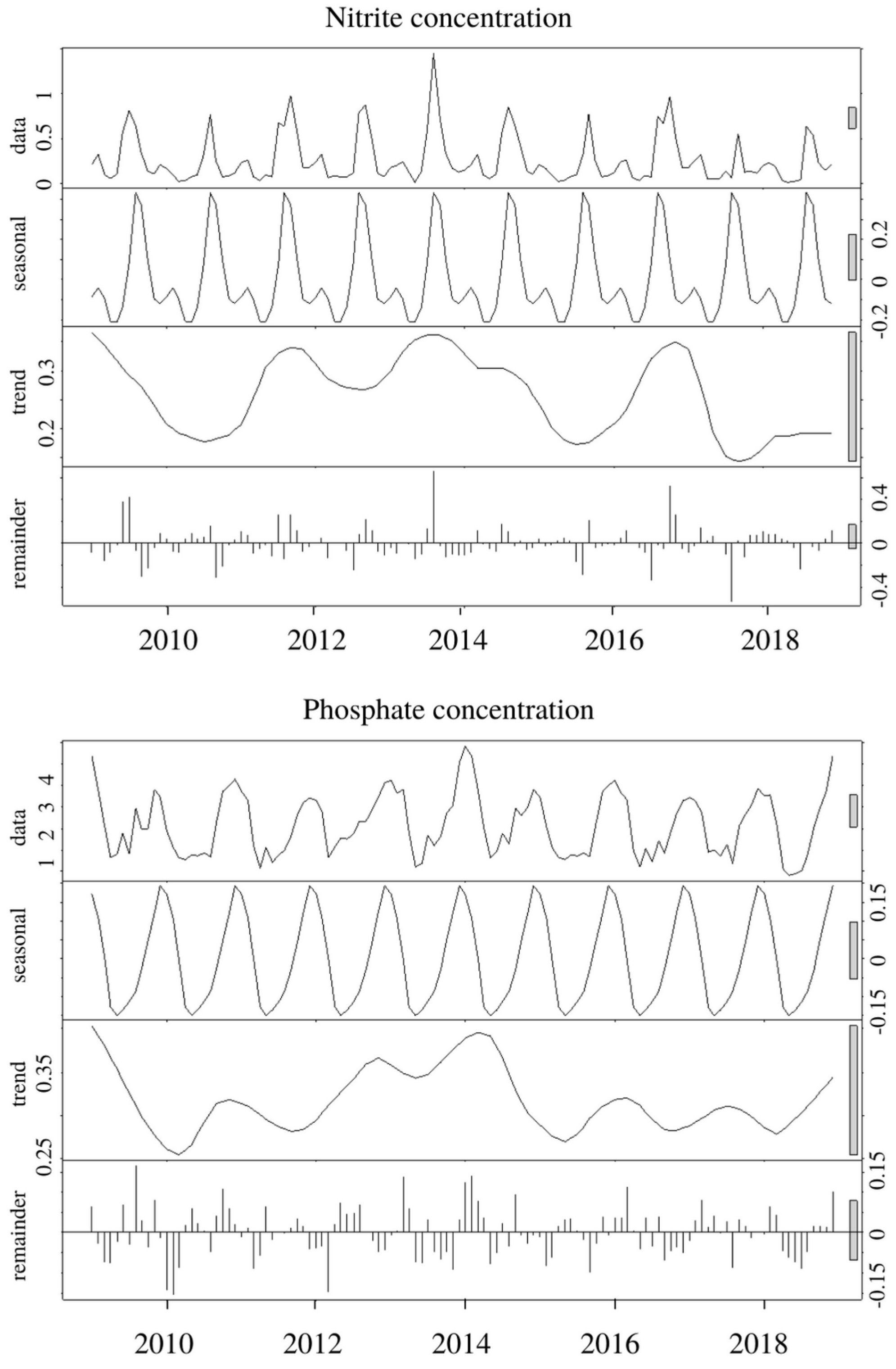


Figure 7: STL decomposition of rain fall and river flow

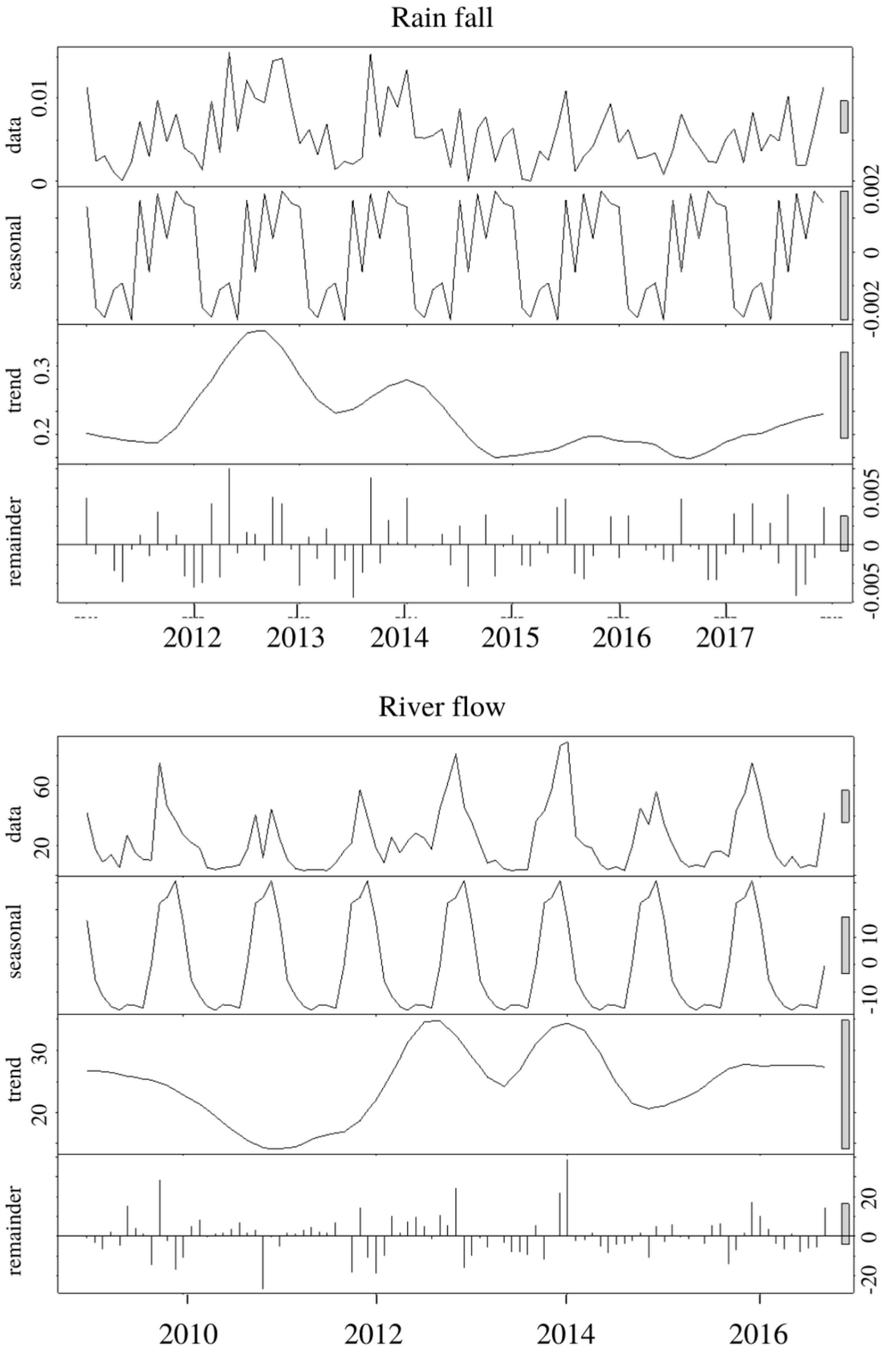


Figure 8: STL decomposition of wave height and Wave period (T_z)

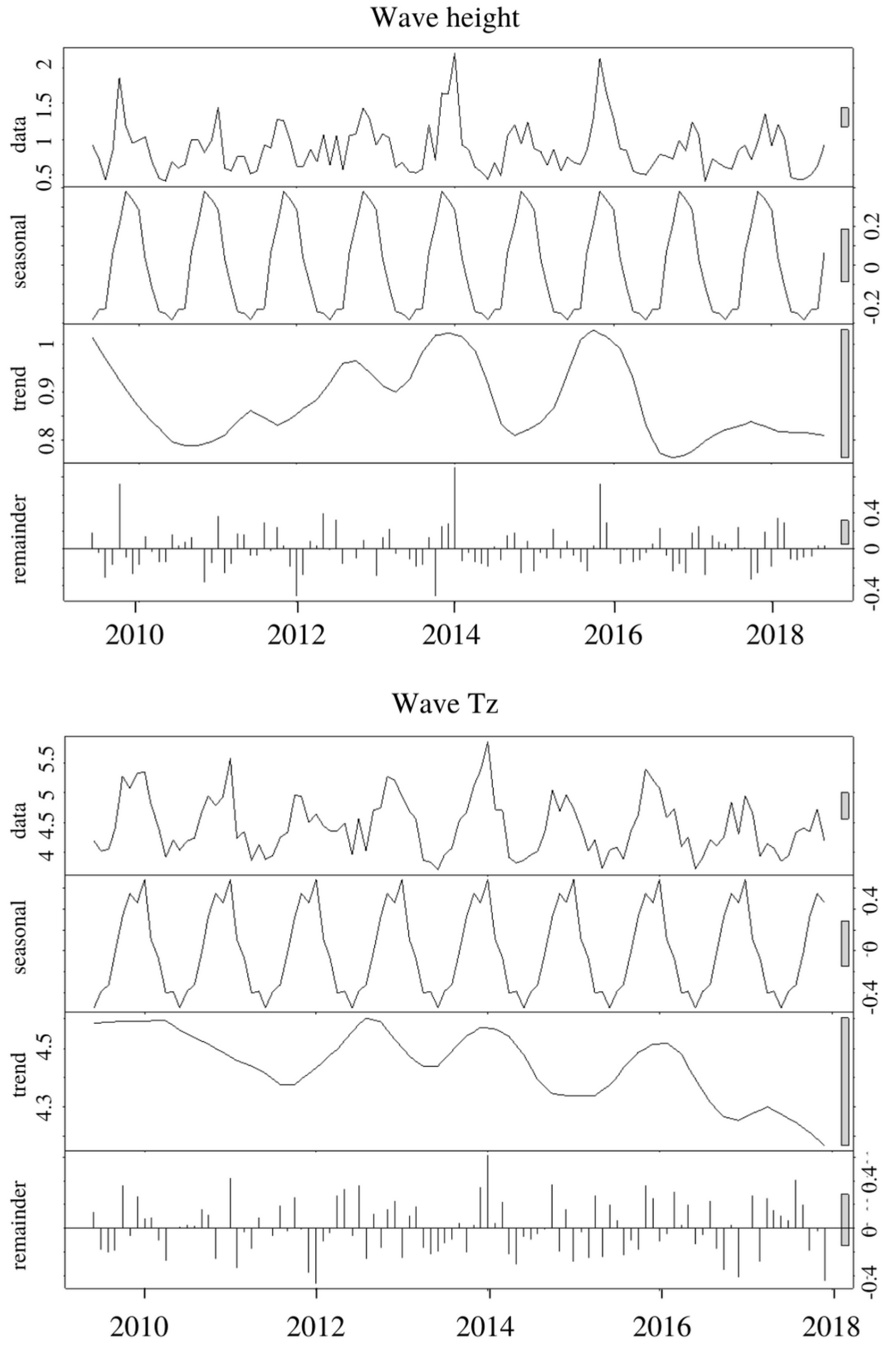


Figure 9: STL decomposition of POC concentration and tidal flow

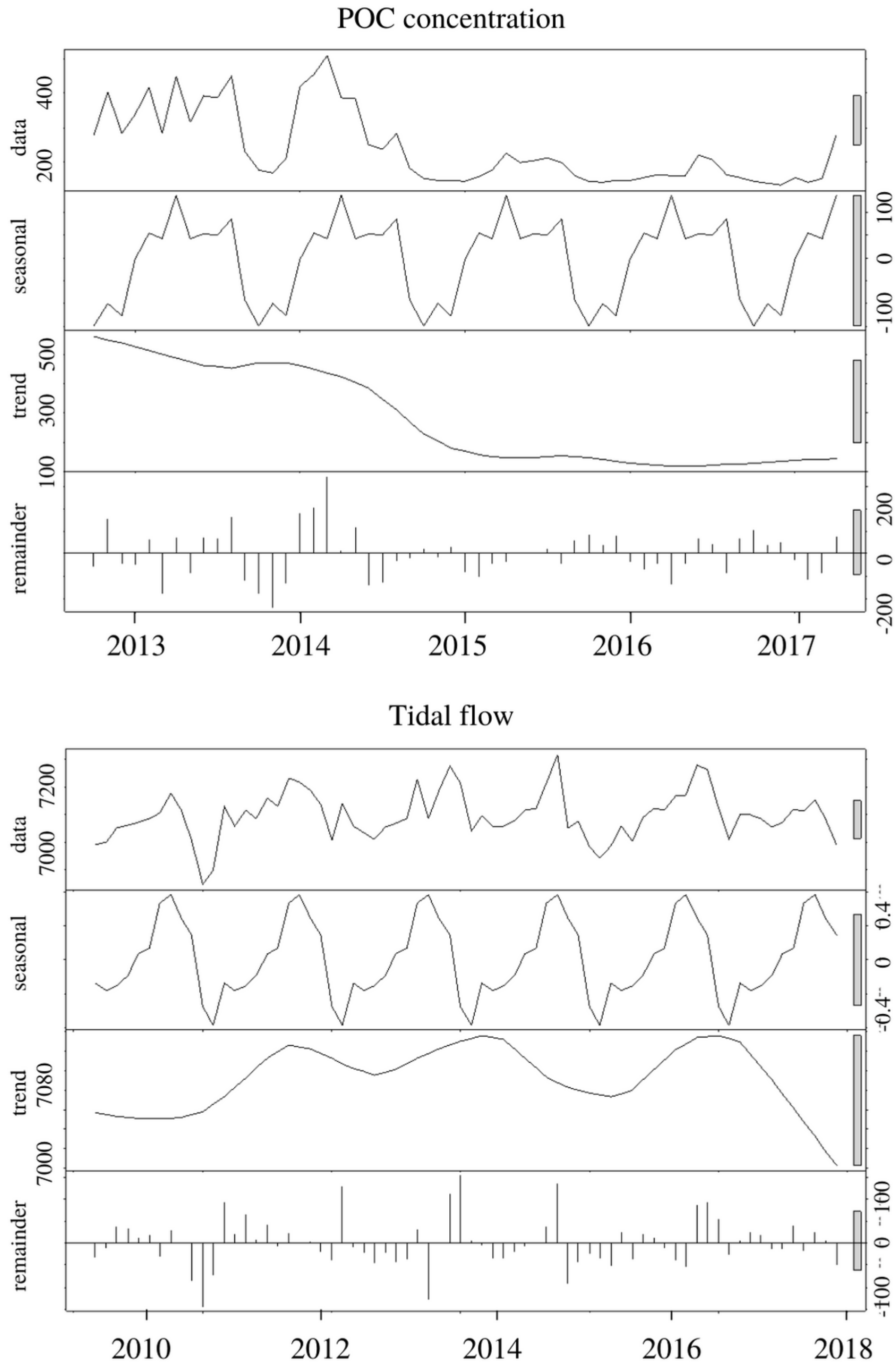


Figure 10: STL decomposition of within-season DM B/P exchanges

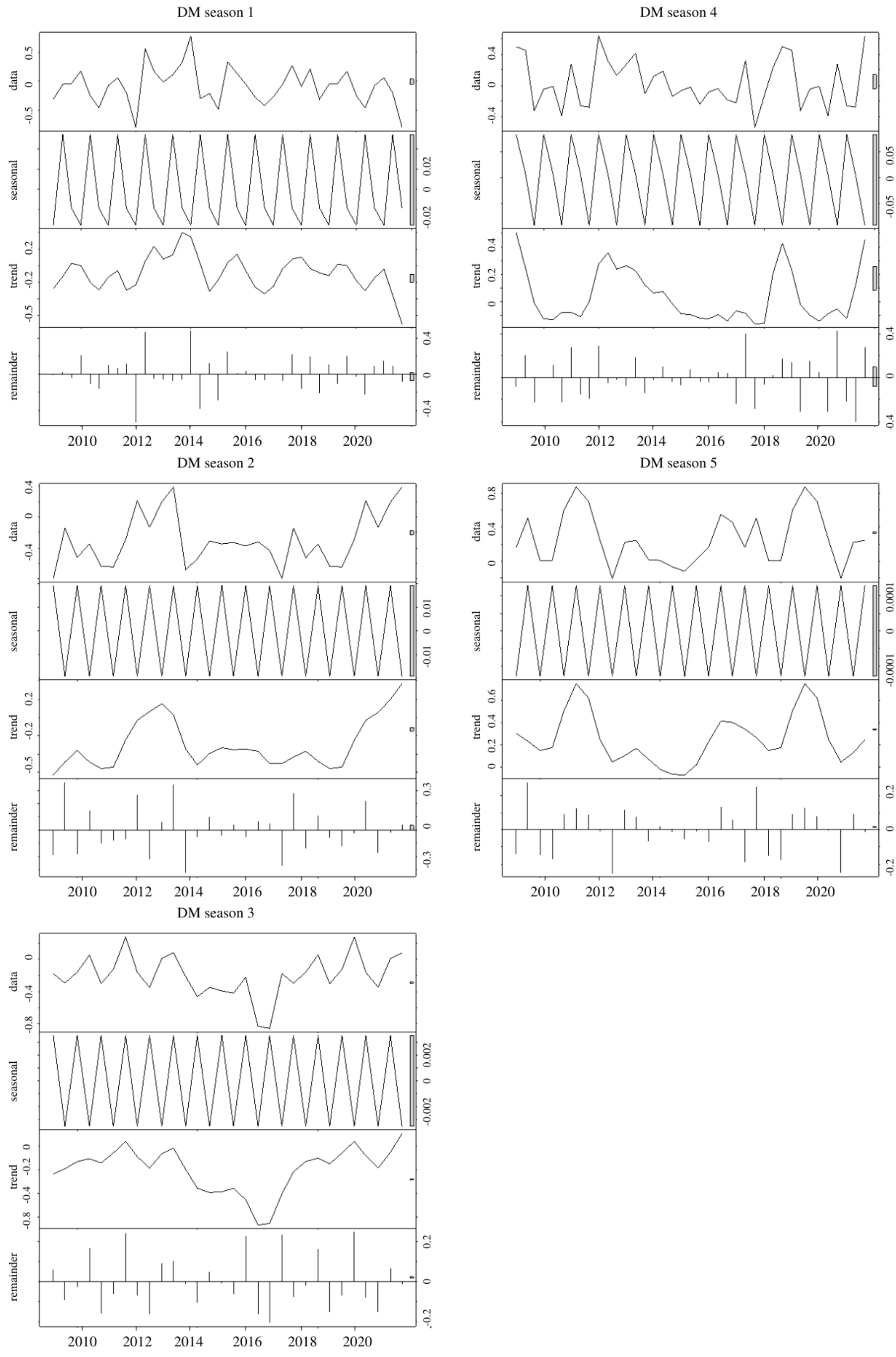


Figure 11: STL decomposition of within-season PM B/P exchanges

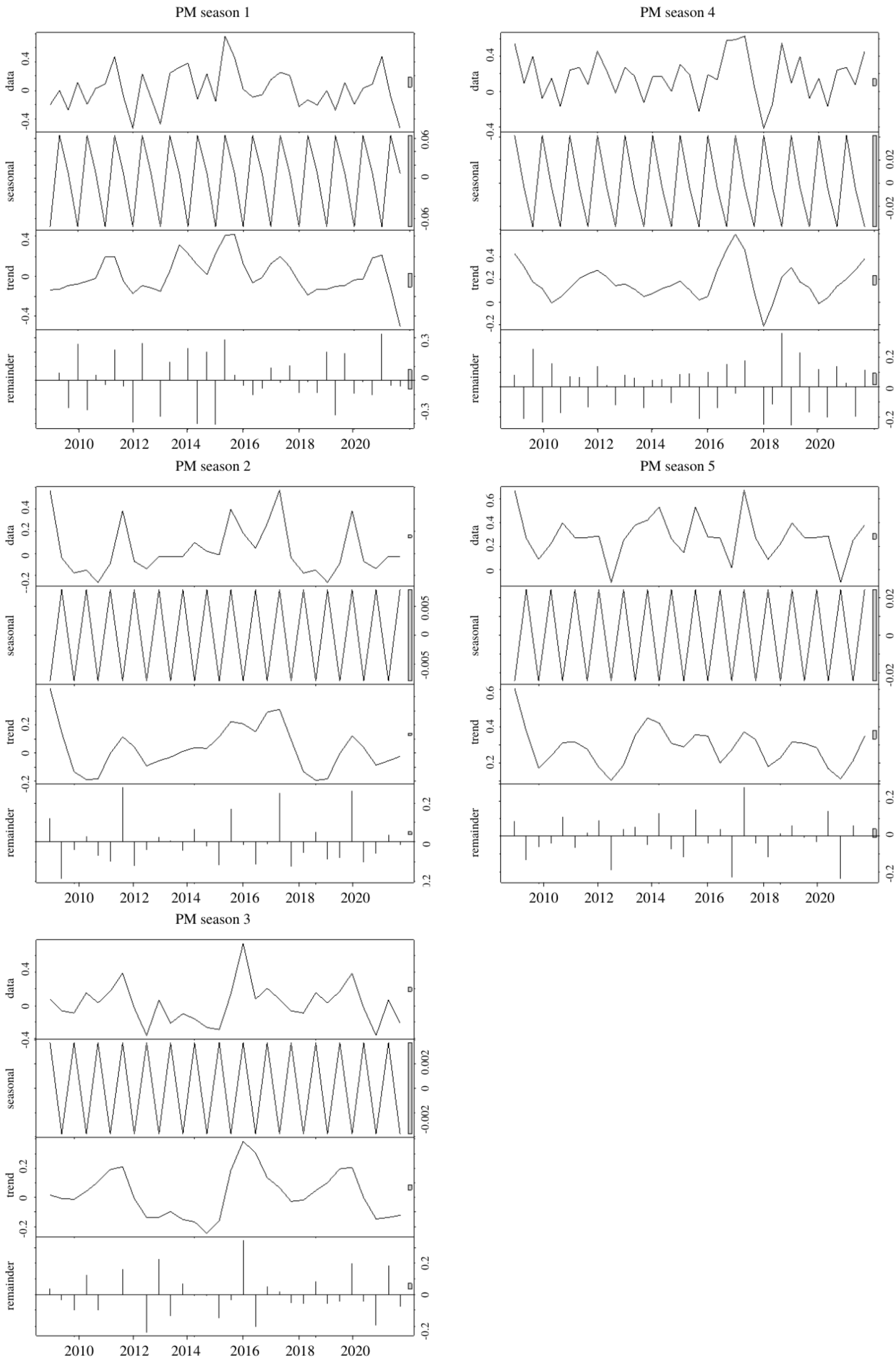


Figure 13: STL decomposition of SPM and salinity

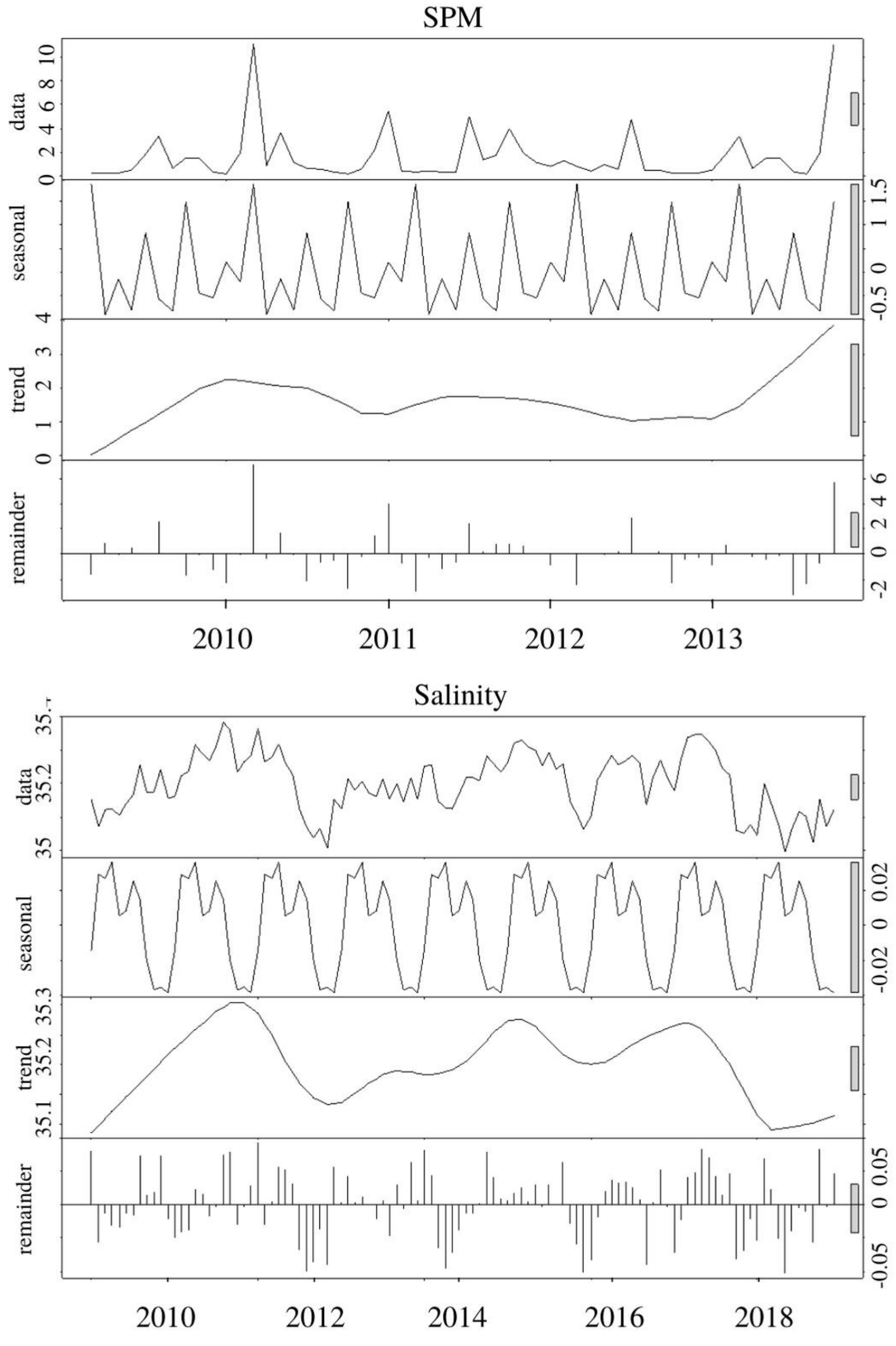
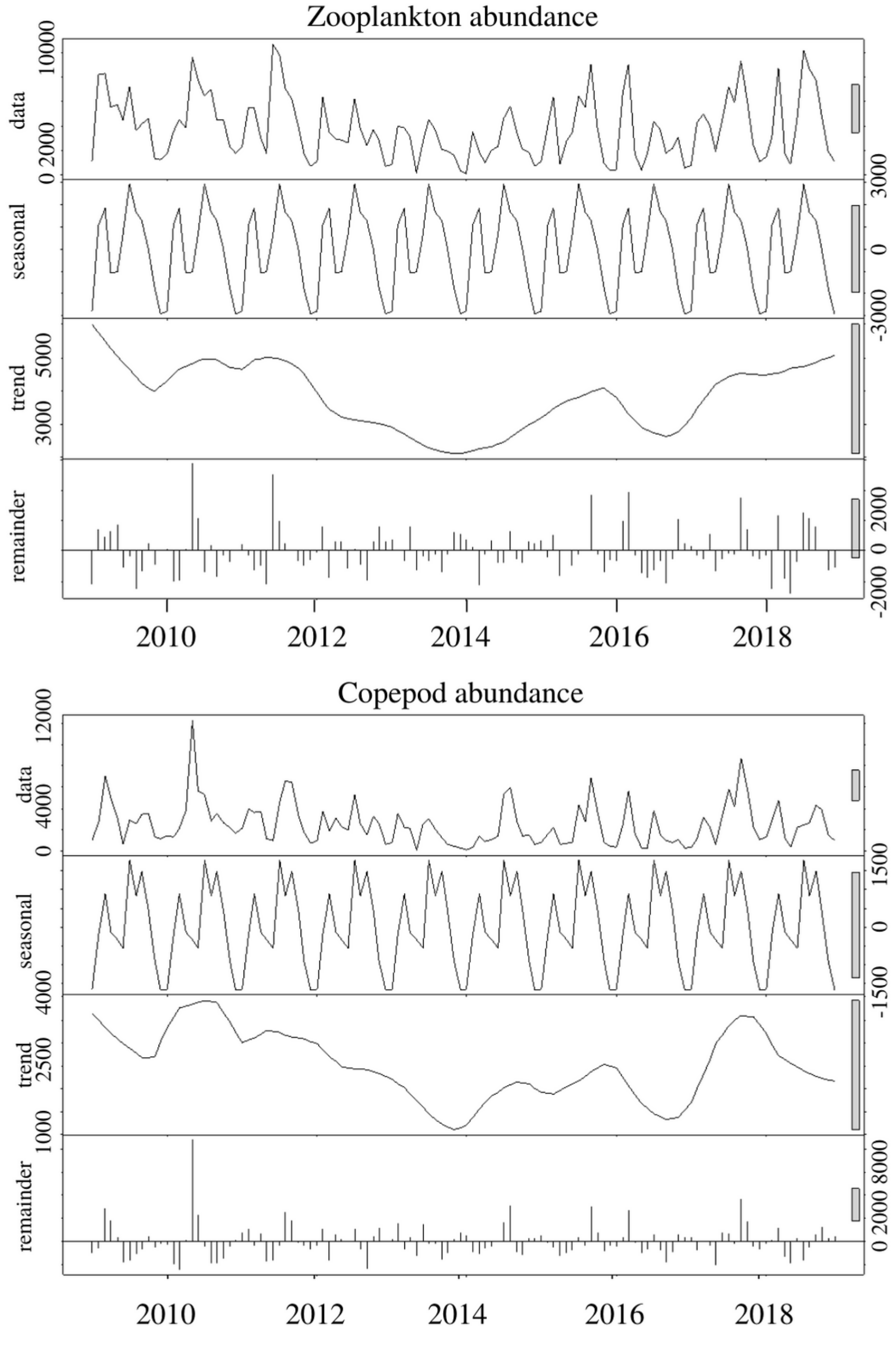


Figure 14: STL decomposition of zooplankton and copepod abundance



Appendix C: Orthogonal Partial Least Squares (OPLS) analyses results; R2X = R^2 value of the primary OPLS training component, R2Y = R^2 value of the secondary OPLS training component, Q2Y = Q^2 value of the OPLS validation component, pR2Y = significance of the R^2 component, pQ2Y = significance of the Q^2 component

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

Appendix D: Factors that contributed significantly to Orthogonal Partial Least Squares (OPLS) model fits, as identified by Variable Influence on Projection (VIP) values > 1

Model	Variable	VIP
Model 1: Entire data set all periods	PAR at 50 m	2.523
	Wave height	1.063
	T_{peak}	1.748
	T_z	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 period 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 period 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 period 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 period 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 period 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 period 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 period 2	[Nitrate]	1.025
	Nitrate/Nitrite ratio	1.426
	[Silicate]	1.058
	[Phosphate]	1.281
	[O_2]	1.675
Model 9: DM diffusion period 3	[Ammonia]	1.252
	[Silicate]	1.702
	[O_2]	1.683
Model 10: DM diffusion period 4	[Nitrate]	1.407
	Nitrate/Nitrite ratio	1.460
	[Silicate]	1.552
	[Phosphate]	1.432
Model 11: DM diffusion period 5	Nitrate/Nitrite ratio	1.087
	[O_2]	2.034
Model 12: PM deposition period 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 period 2	Copepod abundance	1.010
	River flow	1.467
	Fluorescence	2.498
	Temperature	2.211
	CDOM	1.876

Model 14: PM deposition period 3	Copepod abundance	1.955
	Fluorescence	1.572
	PAR	1.661
	Tidal flow	1.887
	Zooplankton abundance	2.054
Model 15: PM deposition period 4	Fluorescence	1.011
	PAR	1.647
	Temperature	1.119
	Tidal flow	1.656
	[POC]	2.260
	[PON]	2.270
Model 16: PM deposition period 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

Figure 1

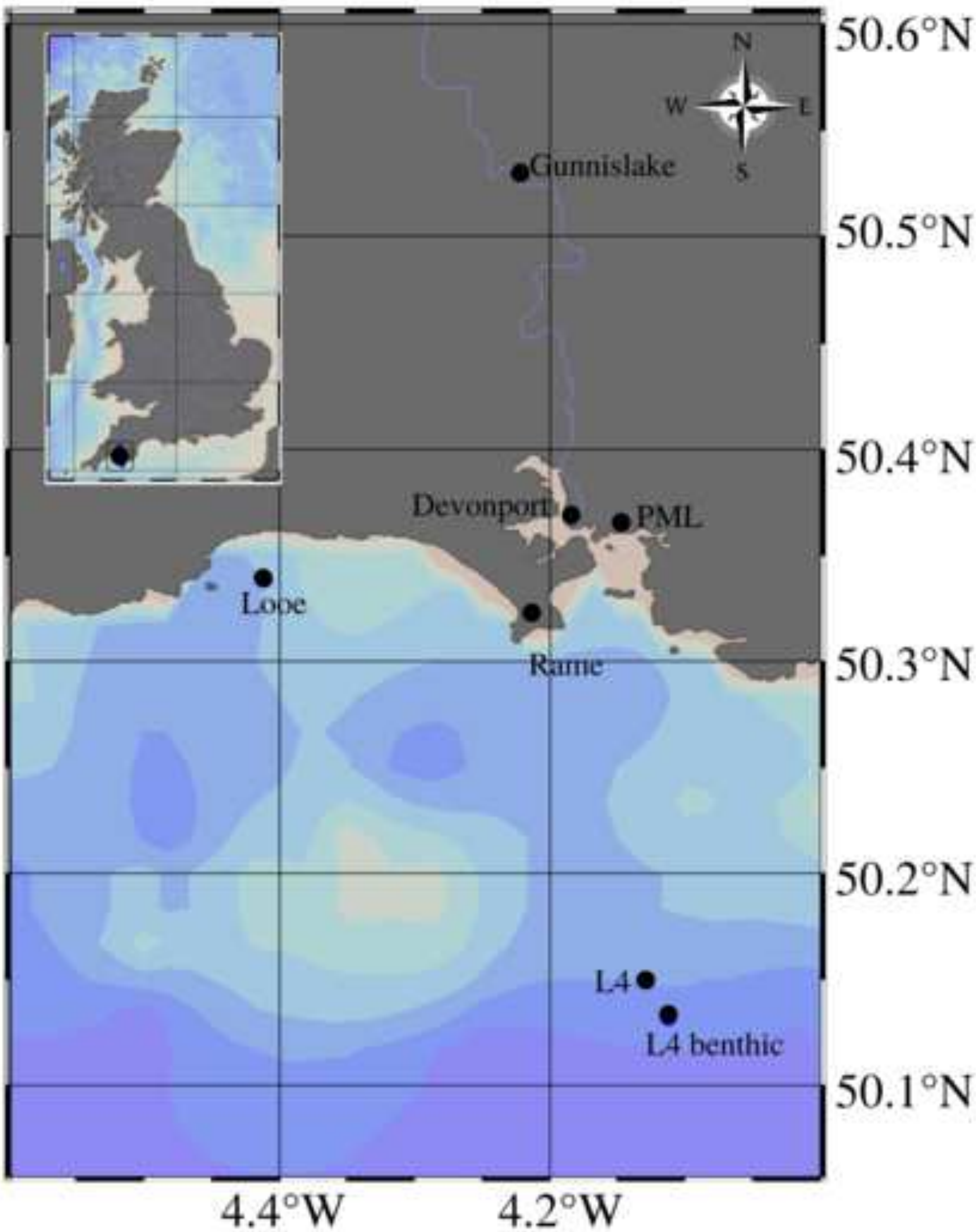

50.6°N
50.5°N
50.4°N
50.3°N
50.2°N
50.1°N
4.4°W
4.2°W
N
W
E
S
Gunnislake
Devonport
PML
Looe
Rame
L4
L4 benthic

Figure 2

Click here to access/download;Figure;Figure2.png

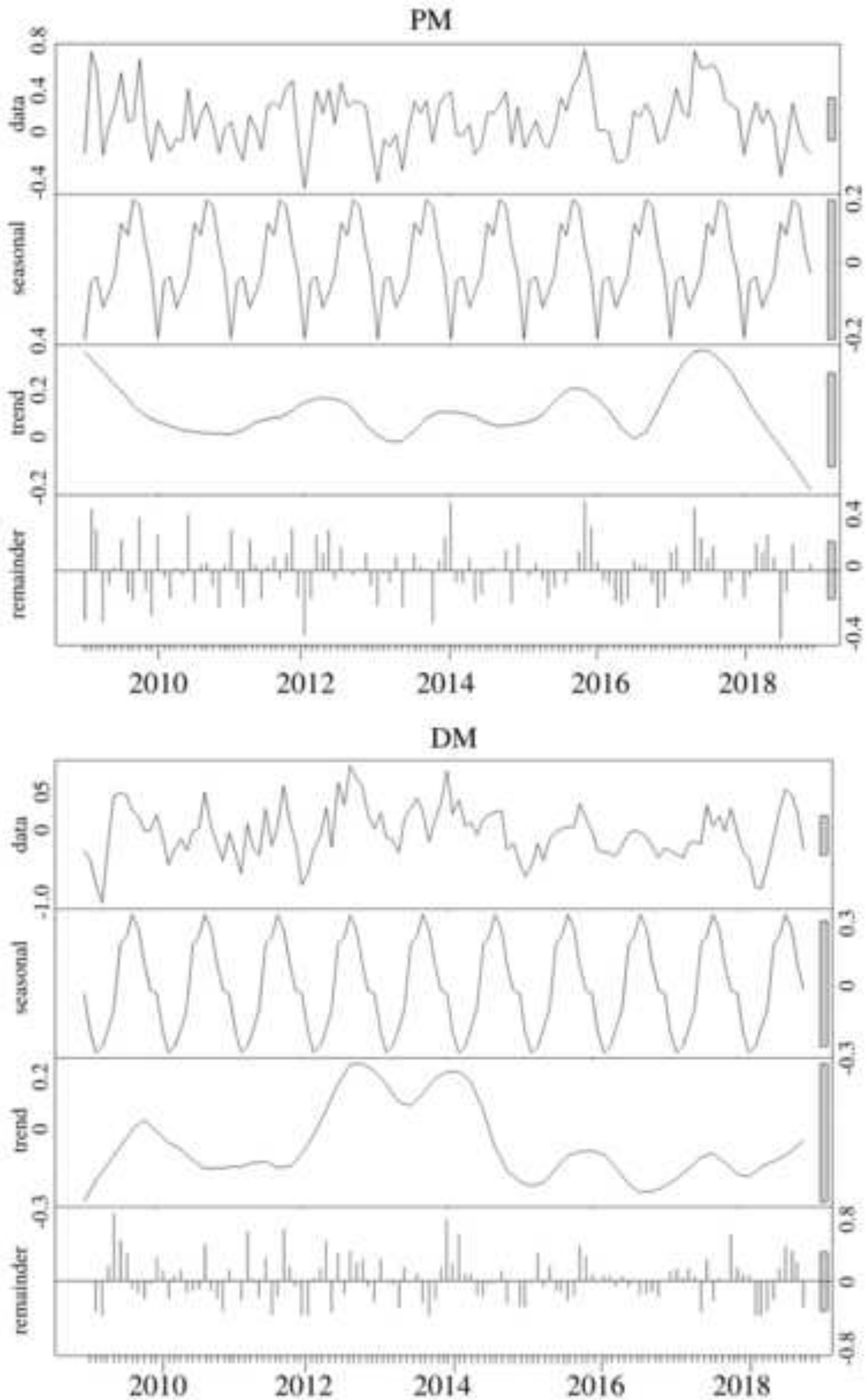


Figure 3

Click here to access/download;Figure;Figure3.png

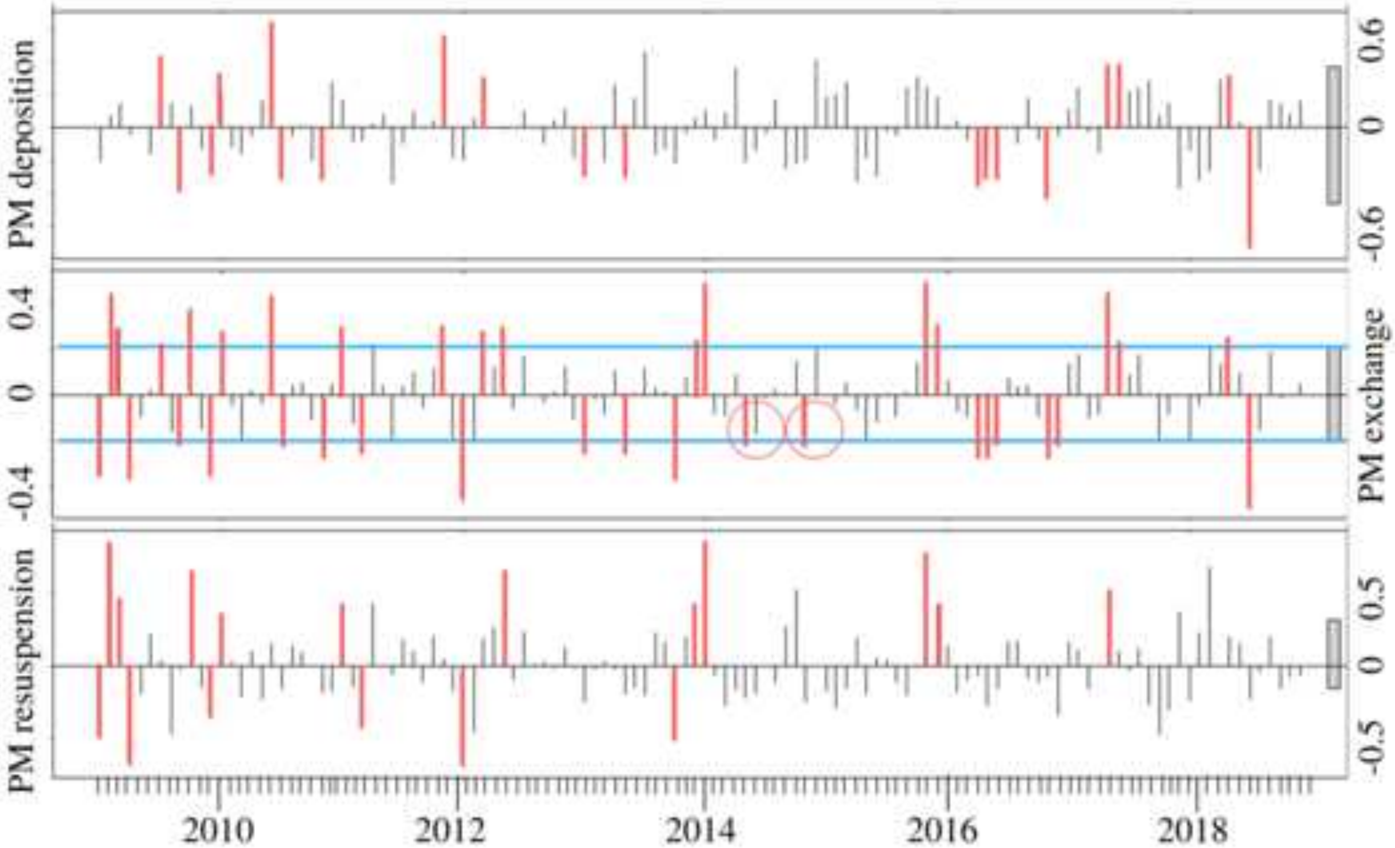
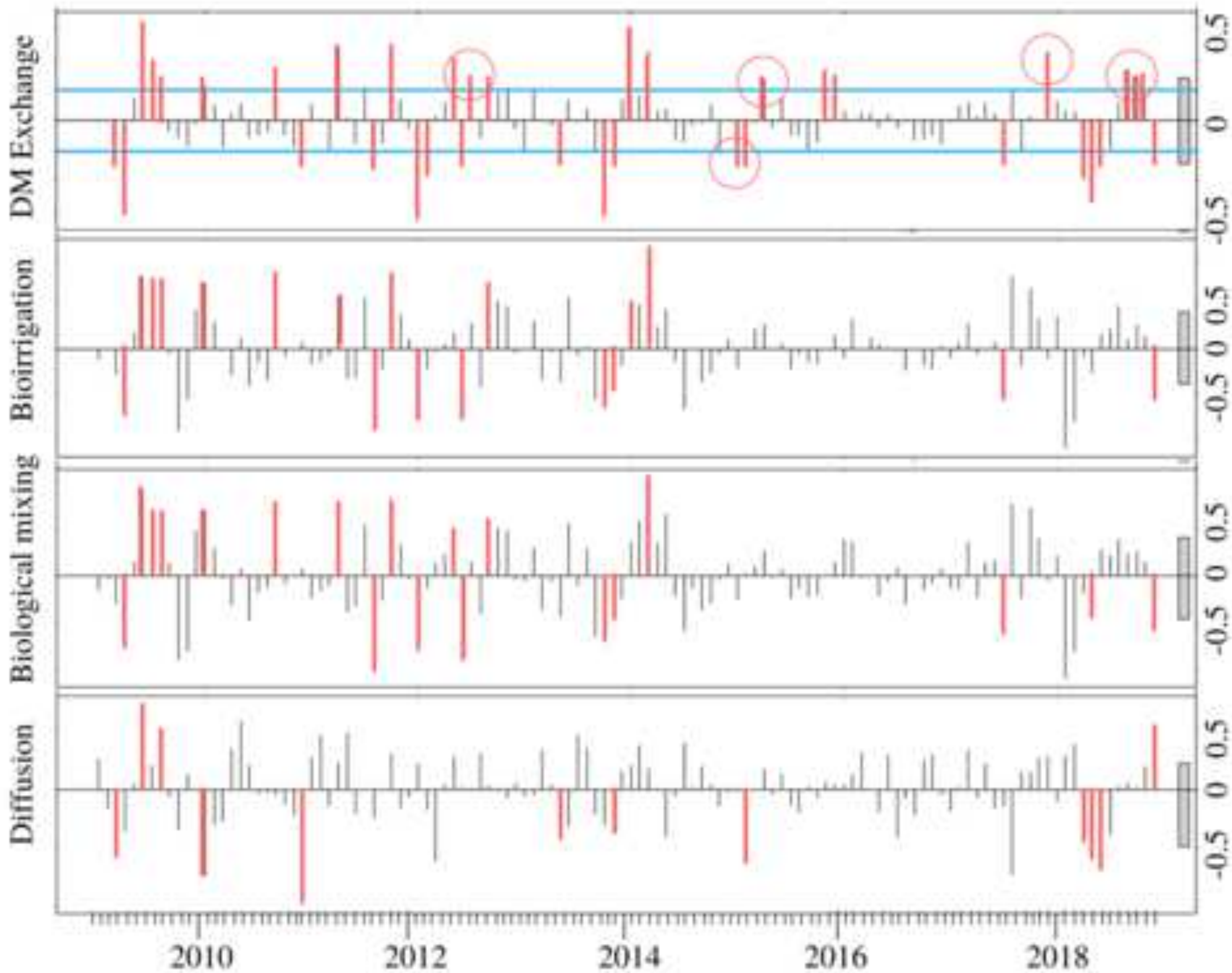


Figure 4


DM Exchange
Bioirrigation
Biological mixing
Diffusion
0.5
0
-0.5
2010
2012
2014
2016
2018