Bi-decadal changes in nutrient concentrations and ratios in marine coastal ecosystems: The case of the Arcachon bay, France

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Highlights :

- $[NO_x]$, $[NH_4^+]$ and $[Si(OH)_4]$ increased but $[PO_4^{3-}]$ decreased between 2000 and 2019.
- Seagrass meadow decline directly and indirectly explained through
- - reduced nutrient consumption and sediment stabilization,
- - increased phytoplankton biomass with high P-need.
- Increase in temperature and changes in wind conditions also mattered.

*Colour should be used for all figures in print.

Abstract:

Large amounts of nutrients have been released to the coastal ecosystems during the 20th century. Since then, management policies have been implemented and these amounts decreased in the economically developed countries. We examined the bi-decadal changes in nutrients (nitrate + nitrite, ammonium, orthophosphate and silicic acid) in the Arcachon bay, a semi-enclosed lagoon that hosts one of the largest but declining seagrass meadow in Europe. Seven sites have been sampled for nutrients and biogeochemical parameters during twenty years at low and/or high tide. In addition, continental and climatic data as well as hydro-climatic indices were used. Dynamic linear models were used to assess the bi-decadal changes in nutrient concentrations and ratios, their seasonality, and the bi-decadal changes of their potential drivers. Partial least square path modeling were used to investigate the relationships between potential abiotic drivers and nutrients. During the study period, the concentration of N and Si nutrients increased whereas the concentration of orthophosphate decreased, leading to deep changes in nutrient ratios. Clear relationships between abiotic drivers (local climate, continental inputs and the bay hydrodynamism) and N, P and Si nutrients were highlighted. However, the bi-decadal change in nutrient concentrations and ratios was mainly ascribed to the seagrass meadow decline through direct (less nutrient consumption) and indirect (increase in phytoplankton biomass) processes. Changes in temperature and wind direction may also influenced the nutrients concentrations through processes of remineralisation and flushing time, respectively. This study illustrates (1) the top-down control of seagrass on the nutrients concentrations and stoichiometry, and (2) the competition between primary producers (seagrass *vs* phytoplankton) for their nutrients resource.

1. Introduction

Primary production in coastal ecosystems is mainly controlled by the input and the recycling of nutrients — mainly nitrogen (N), phosphorus (P) and silicon (Si) — and their availability (Bouwman et al., 2013; Nixon et al., 1986). Hence, nutrients availability can indirectly affect all trophic levels through bottom-up effects, and therefore influence ecosystems structure and functioning (Borum and Sand-Jensen, 1996; Bouwman et al., 2013; Nielsen and Richarson, 1996). Nutrients mostly enter coastal ecosystems through river discharge (Seitzinger et al., 2002). While N and P are mostly by-products of human activities (such as agrarian activities that induce the use and release of fertilizers), or urban and industry settlement along the waterways (that release waste-waters; (Galloway et al., 2004, Metson et al., 2017)), Si mostly comes from natural weathering (Tréguer et al 1995).

Anthropogenic activities disturb the three N, P and Si coastal biogeochemical cycles (Lerman et al., 2004) principally due to modifications on the watershed. Intensive agriculture (including fertilizer use and irrigation) and land artificialisation (including urban expansion and power dam creation) are responsible for changes in N, P and Si concentrations in the rivers (Ragueneau et al., 2006; Rosier and Ritchie, 2013) and consequently in the coastal ecosystems. During the past century, the export of nutrients from the continent to the coastal ecosystems has almost doubled (Beusen et al., 2016) due to the human activities (Paerl 2009). During the second half of the twentieth century, the world population increased by 2.5 folds (United Nation, Department of Economic and Social Affairs, Population Division, 2019) and the food and fertilizers productions increased respectively by 3 and more than 4 folds (Roser and Ritchie, 2013). Anthropogenic activities also affect the atmospheric nutrient input to marine ecosystems: the di-nitrogen fixation

along with the dissolved N-deposition from the atmosphere have greatly increased, mainly due to fossil fuel combustion (Bouwman et al., 2013; Seitzinger et al., 2002; Xenopoulos et al., 2017). Such alteration of the biogeochemical cycles (nutrient concentrations and ratios) can increase eutrophication episode rates and magnitudes (Ménesguen and Piriou, 1995; Sinha et al., 2017) that affect the whole ecosystem, from phytoplankton assemblages, sediment and benthic communities, to top trophic levels (Cloern, 2001).

Following the growing concern and knowledge on eutrophication, human societies have implemented management policies to regulate the nutrients export to the coastal ecosystems in the recent decades (i.e. the 1972 US Clean Water Act (33 U.S.C.), the 1991 EU Nitrates Directive (Directive 91/676/EC)). Recent studies in various developed countries pointed out decreasing N and P concentrations in the coastal ecosystems during recent decades, leading to various and numerous impacts. In the Chesapeake bay, the nitrate + nitrite inputs increased by 90% between 1945 and 1980 and then decreased by 5.3% between 1981 and 2012 due to nutrient-management strategies launched in the 1980s (Harding et al., 2016). Due to these N loads reduction, more areas in Chesapeake bay were N-limited or not subjected to apparent nutrient limitation (Zhang et al., 2021). In Moreton bay (Australia), the implementation of a sewage treatment plant helped to reduce the dissolved nitrogen export leading to a decrease of the N:P ratio as well as of the chlorophyll-*a* concentrations (Saeck et al., 2013). The nutrients exported to the San Francisco bay also decreased but it led to an increase of the phytoplankton biomass through cascade effects following the decrease of their predators' population (Cloern et al., 2007). In the Baltic sea, the dissolved Si concentration decreased at the end of the twentieth century and it had been attributed to a decrease in the river Si export (Conley et al., 2002), following the implementation of dams in the watershed (Papush and Danielsson, 2006). Although clear evidences of recovery from eutrophication occurred following large

reduction in nutrients concentrations like in Boston Harbor (Taylor et al., 2020), a lack of response could occur when nutrients concentrations reductions were weaker (Duarte et al., 2008). This highlighted that even though extra human-induced nutrients loads played a key role in coastal ecosystems eutrophication, it was not the only parameter to take into account to reduce eutrophication because the response of ecosystems are non-linear and complex (Cloern et al., 2010), and because ecosystems could change from a state equilibrium to another (Scheffer & Carpenter, 2003, Scheffer et al., 2009) towards the re-oligotrophication process.

Coastal ecosystems and their intrinsic functioning are not only under the direct anthropogenic influence but also under climatic influence. The climatic influence is expressed through a large set of drivers such as precipitations, temperature and wind circulation (Bouwman et al., 2013). For instance, the atmospheric deposition, enhanced by the precipitations, can induce phytoplankton blooms in some ecosystems (Durrieu de Madron et al., 2011). Solar radiation and the associated temperature increase enhance water stratification, which reduces the amount of vertical input from deeper waters (Doney 2006). Also, wind circulation — and tides — can modify hydro- and sediment dynamics (Christiansen et al., 2006) and thus favour benthic nutrient input to the water column in shallow ecosystems.

Within this context of long-term changes in nutrients inputs under anthropogenic and natural drivers, we investigated (i) the bi-decadal (1999 – 2018) inter-annual and seasonal changes in nutrients concentration and ratios, (ii) their spatial variability, and (iii) their drivers at local and large scales in a semi-enclosed and poorly-anthropized ecosystem that also experienced primary producers long-term changes: the Arcachon bay, France.

2. Material and Methods

2.1 Study site

The Arcachon bay is a 180 km² semi-enclosed lagoon located on the South-western coast of France (Figure 1). It faces a semi-diurnal meso- to macro-tidal regime (0.8 to 4.6 m) and has an average depth of 4.6 m and a maximum depth of 20 m in the main channels. The channels run through large intertidal mudflats that account for two third of the total surface area of the bay. Freshwater mainly comes from the Leyre River (75%) with an average flow of 1.3 x 10^6 m^3 per day, from two man-regulated canals (Porge canal and Landes canal) and from several small streams. Freshwater inputs are low compared to ocean water tidal exchange (ca. 400 x 10^6 m^3 in average). In this bay, three main water masses were defined (Bouchet 1968, Robert et al., 1987): (i) the external neritic waters (ENW), directly influenced by the oceanic waters (the highest salinity and the lowest annual salinity and temperature amplitudes), (ii) the intermediate neritic waters (ItNW) and (iii) the inner neritic waters (InNW), particularly influenced by the continental inputs (the lowest salinity and the highest annual salinity and temperature amplitudes).

The watershed of the Arcachon bay has an area of 3500 km². It is mainly covered by forests (ca 80%) and agricultural lands (ca 10%). The urban areas (5%) are mainly located along the bay coastline. The urban effluents are derived since the 1970s and released after treatment in the Atlantic waters outside of the bay (Figure 1). This ecosystem can therefore be considered as poorly anthropized.

The intertidal flats of the bay are colonized by dwarfgrass (Z. noltei), while eelgrass (Z. marina) occupies the shallow subtidal sector around the channel edges. The area colonized

by these two species drastically declined during the past decades (Plus et al., 2010). Between 1989 and 2007, the total area of Z. noltei meadows has decreased by 33% (from 68.5 km^2 to 45.7 km^2) while the area of Z. marina meadows has decreased by 74% (from 3.7 km^2 to 1.0 km^2). Between the 1980s and 1990s, macroalgae proliferations were reported in the bay, *Enteromorpha clathrata* since 1985 and *Monostroma obscurum* since 1989 (Auby et al., 1994; Ménesguen et al., 1997), but these blooms are no longer observed at present. The bay is also an important mariculture site, especially for the oyster *Crassostrea gigas* farming and production of spats (Buestel et al., 2009), and is the main site for the production of Manilla clam *Ruditapes phillipinarum* in France (Caill-Milly et al., 2008).

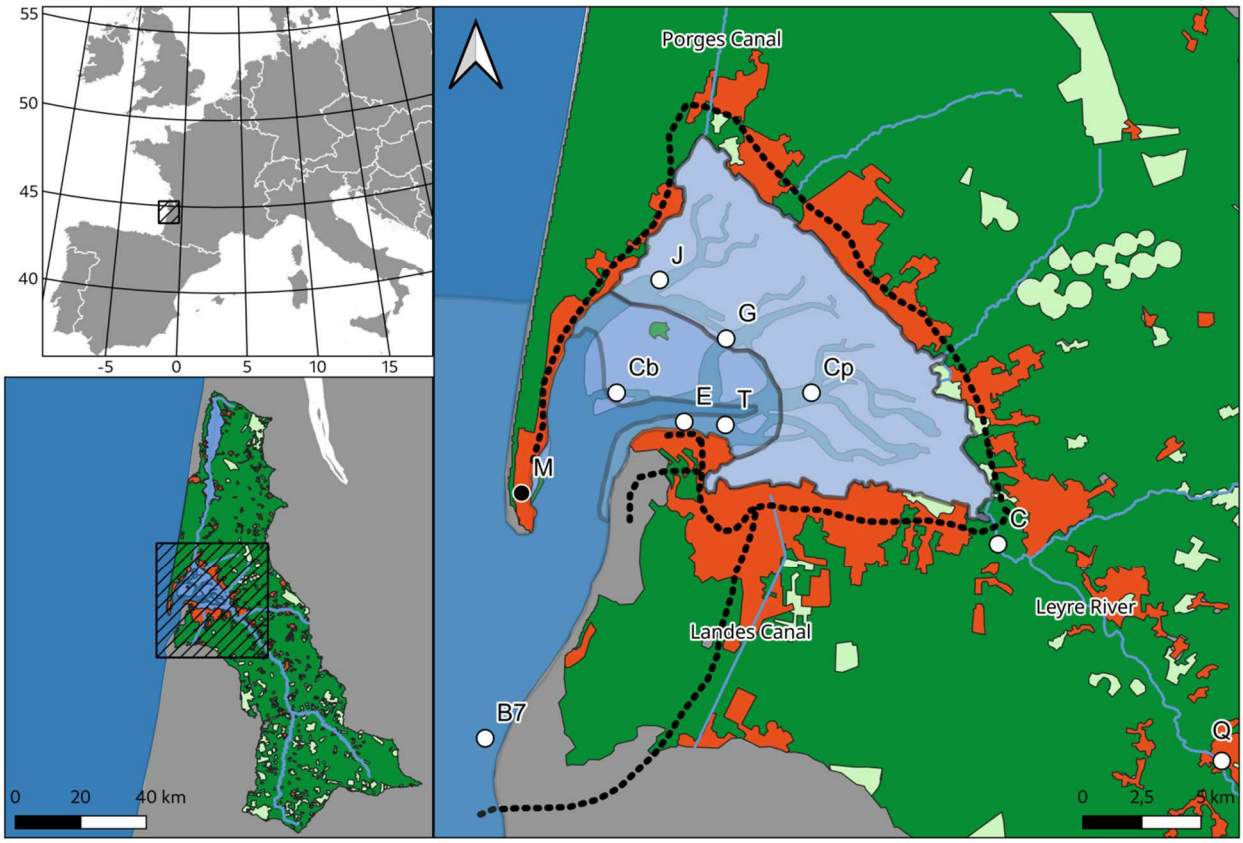

Figure 1 : The Arcachon bay with the location of the sampling sites and water masses. Cp: Comprian; T: Tès; G: Girouasse; E: Eyrac; J: Jacquets; Cb: Courbey and B7: Bouée 7 are the seven coastal sampling sites in the bay, C: site recording the nutrients concentrations in the Leyre river (Lamothe); Q: site recording

the Leyre river discharge (Salles , 2 site on the Leyre river), M: meteorological site (Cap Ferret).

The plain blue lines are the freshwater inputs and the black dotted line represents the main urban effluents tubes. The background colours represent the land use: red for urban lands; light green for agricultural lands; dark green for forestrial lands; gray for land outside the Arcachon bay watershed, light blue for intertidal waterand dark blue for subtidal waters (Corine Land Cover, 2018). The shades delimit the external (western side), intermediate (in the middle) and internal (eastern side) neritic waters (adapted from Bouchet (1968)).

2.2 Data

The present study is based on data sets stored in different databases (Table 1). These data sets gather nutrients concentrations in the Arcachon bay (core parameters of the study) as well as parameters indicators of environmental drivers used as explanatory variables. These latter parameters were selected as proxies of processes potentially linking drivers and nutrients. For instance, salinity can be considered as a proxy of freshwater inputs, riverine nutrients concentrations can be considered as a proxy of nutrient river load, meteorological parameters relate to the climatic influence.

All the data were analysed from March 1999 to December 2018. Data providers are reported in Table 1.

2.2.1 Arcachon bay data

In the bay, two monitoring programs are running: ARCHYD, a local survey that samples seven sites weekly, alternately at high and low tide, some from 1989 and others from 2007; and SOMLIT, a national network that samples, in this bay, three stations bi-monthly at high tide some from 1997 and others from 2005. For the present study six ARCHYD sites (Bouée 7 in the ENW, Courbey and Tès in the ItNW, and Comprian, Girouasse and Jacquets in the InNW) and one SOMLIT site (Eyrac in the ItNW) were selected based on

their sampling duration and monitored parameters. Bouée 7, Comprian and Jacquets are also sites monitored within the REPHY which is another national network. These programs participated to inter-laboratory exercises, both at the local and national scales (Belin et al, 2021; Breton et al., *in prep*).

In the following, low tide and high tide (LT and HT respectively) samplings are differentiated for each site (e.g. Tès LT versus Tès HT). Sites refer to geographic position and stations refer to the combination of a site and a tidal moment.

The nutrients used in this study are: nitrate + nitrite (NO_x), ammonium (NH_4^+), dissolved orthophosphates (PO_4^{3-}) and silicic acid ($Si(OH)_4$). NO_x and NH_4^+ were summed before calculating the Si:N and N:P ratios. Water temperature, salinity, suspended particulate matter (SPM) and chlorophyll-*a* were selected as proxies of potential drivers. In the following, they are referred to as 'biophysical parameters'. For more information regarding these programs, see Cocquempot et al., (2019), Goberville et al., (2010) and Liénart et al., (2017, 2018) for SOMLIT, and Ifremer (2017) for ARCHYD.

2.2.2 Continental data

Three continental variables were collected: two nutrients (NO_x and NH_4^+) and the river discharge (Q). The nutrients were monitored at Lamothe and the discharge at Salles (Figure 1), upstream the dynamic influence of the tide. These data sets were provided by EauFrance and the Adour-Garonne water agency.

2.2.3 Climate data

2.2.3.1 Local-scale climate

Seven meteorological variables were used: four atmospheric circulation variables (the atmospheric pressure at sea-level, the wind intensity and its meridional and zonal components), along with the air temperature, the short wave irradiation and the monthly accumulated mean precipitation. The meteorological variables were obtained from the MeteoFrance forecast weather station located at Cap Ferret. The short wave irradiation was a reconstructed variable provided by MERRA-2 (see Gelaro et al., 2017).

Extra attention is called on the directional components on the wind. As these variables are made from the scalar product between the wind intensity and its direction, they can potentially take values between minus and plus infinity. Winds coming from the North (wind direction strictly over 270° and strictly under 90° based on a wind rose) and wind coming from the South are depicted by negative and positive meridional wind speeds respectively. Winds coming from the East (wind direction strictly over 0° and strictly under 180°) and winds coming from the West are depicted by negative and by positive zonal wind speeds respectively. Winds coming from the exact North/South or East/West have null meridional or zonal speeds respectively. Therefore, increasing negative meridional or zonal speeds depict increasing winds from the North or the East, respectively. Meridional or zonal speeds close to 0 mean null wind intensity along their respective axis.

2.2.3.2 Large-scale climate

Five hydro-climatic indices were used: the Atlantic Multidecadal Oscillation (AMO), the Northern Hemisphere Temperature anomalies (NHT), the East Atlantic Pattern (EAP), the Northern Atlantic Oscillation (NAO) and the Arctic Oscillation (AO). The AMO (Enfield et al.,

2001) represents the changes in the north Atlantic sea surface temperature after removing the human impact whereas the NHT anomalies is an index based on the 1901-2000 north Atlantic temperature average. The NAO (Hurrell 1995; Hurrell & Deser 2009) and the EAP (Barnston & Livezey 1987) are the two most predominant mode of low-frequency variability over the north Atlantic. While the NAO tracks the movements of the Azores high, the EAP values consist of a north-south dipole of pressure anomalies centred on the north Atlantic, from east to west. Finally, the AO is based on atmospheric pressures and is related to the Arctic climate and its southern incursions. The data was provided by the US National Oceanic and Atmospheric Administration (NOAA) National Center for Atmospheric Research (NCAR), Climate Prediction Center (CPC) and National Centers for Environmental Information (NCEI).

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237 *Table 1 : Variables, providers and associated website for the Arcachon bay, the main river, meteorological data and large scale hydro-climatic indices from*

238 *March 1999 to December 2018.*

Type	Variables	Provider	Website
Coastal ecosystem	NO_x, NH_4^+, PO_4^{3-}, $Si(OH)_4$, wT, S, SPM, CHLA	SOMLIT	www.somlit.fr
		ARCHYD	https://wwz.ifremer.fr/surval
			https://doi.org/10.17882/47248
Leyre river	NO_x, NH_4^+, SPM	Eau france	http://www.naiades.eaufrance.fr/
	Q		http://www.hydro.eaufrance.fr/
Meteorological data	aT, Iwind, Vwind, Uwind, MP, P	Meteo-France	https://donneespubliques.meteofrance.fr/?fond=contenu&id_contenu=37
	W	MERRA-2	http://www.soda-pro.com/fr/web-services/meteo-data/merra
Large-scale hydro-climatic indices	AMO	NOAA, NCAR, CPC, NCEI	https://www.esrl.noaa.gov/psd/data/timeseries/AMO/
	AO		https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/monthly.ao.index.b50.current.ascii
	EAP		https://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml
	NAO		https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based
	NHT		https://www.ncdc.noaa.gov/monitoring-references/faq/anomalies.php#anomalies

2.3 Statistical analyses

In order to standardise all the time series, the data was aggregated to the month by applying a median if more than one observation were available for each month. In this study, all the time series have 238 values (238 months from March 1999 to December 2018) based on the available data and the maximum lag in the raw data.

Nutrients, SPM and chlorophyll-*a* concentrations as well as river discharge data were log-transformed prior to any other statistical treatment.

2.3.1 Time series decomposition

Each time series, except the hydro-climatic indices, was decomposed using dynamic linear models (DLMs; West and Harrison, 1997). The DLM approach had already been used succesfully with environmental data series (Hernadez-Farinas et al 2014, Ratmaya et al. 2019). They can be viewed as a dynamic version of linear models: their parameters are allowed to vary with time. The model that has been used here decompose each time series into an inter-annual component and a seasonal component. This model is based on a second-order polynomial that, when appropriate, can produce a quadratic inter-annual component. The time varying seasonal component is based on a trigonometric function with two harmonics that allow the expression of bi-modal patterns (e.g. spring and autumn blooms). As outliers may have strong influence on models, a procedure has been set up to identify and treat them. Data were considered as outliers when their standardized residuals were outside the interval defined by the whiskers of a box-and-whiskers plot applied to a standardized gaussian distribution: in other words, outliers were the 0.35% higher values and the 0.35% lower values. Different models were run following an iterative process where

identified outliers were given a proper observational variance so that they had less weight. This step was repeated until no more outliers were detected. DLMs were applied with the dlm package (Petris, 2010) using the R software (R Development Core Team, 2021).

Residuals of the models are used to assess their validity. The normality of the residuals was checked using a Q-Q plot and tested with the Kolmogorov-Smirnoff test (Kolmogorov, 1933); the residuals independence was checked with plots of estimated auto-correlation function and tested with the Stoffer-Toloi modified test (Stoffer and Toloi 1992); and finally, the homoscedasticity was tested with the Goldfeld-Quandt test (Goldfeld and Quandt, 1965). The models used in the study were those answering to the most of these conditions and with the smaller Akaike Information Criterion (AIC).

2.3.2 Bi-decadal trends

A modified Mann-Kendall test (Yue and Wang, 2004) was applied on the DLMs inter-annual components to assess the significance of the bi-decadal changes (i.e. presence of a positive or negative monotonic linear long-term trend). When a significant trend was detected, the Sen's line (Helsel and Hirsh, 2002) was used to calculate the amplitude of change that occurred between 1999 and 2018. The modified Mann-Kendall was chosen upon the regular Mann-Kendall test in order to remove the serial correlation effect on the test on hydrobiological time series that have autocorrelation.

2.3.3 Nutrient ratios

Nutrient ratios (Si:N, N:P, Si:P) were calculated from the nutrients monthly medians. The value for each month was then compared to the extended Redfield ratio N_{16}:P_1:Si_{16}

(Harrison et al., 1977) in order to calculate the most potentially limiting nutrient. Six combinations were thus possible (from the most to the lesser probably limiting nutrient: P:N:Si, P:Si:N, N:P:Si, N:Si:P, Si:N:P, Si:P:N). One should keep in mind that deviation from the Redfield ratios gives an information on the potential limitation of phytoplankton growth by nutrients but is not a measure of 'real' limitation. The latter also depends on the nutrient concentrations and phytoplankton intrinsic physiology (i.e. Km constants). Thus, none, one or even all the nutrients could (co-)limit phytoplankton growth depending on the difference between their concentrations and the Km constants.

2.3.4 Potential abiotic drivers

The potential abiotic drivers influence was assessed using Partial Least Square Path Modeling (PLS-PM). PLS-PM models were applied using the plspm package (Sanchez, 2013) in the R software (R Development Core Team, 2021). PLS-PM enable to study the links between blocks of variables. The blocks are defined *a priori,* and the links are estimated by ordinary least squares in multiple linear regressions (Sanchez, 2013). PLS-PM are made of two sets of linear equations. The first set define the inner model (measurement model) that determines the links between the latent variables (LV; unobservable variables). The second set define the outer model (structural model) that identifies the links between one LV and its manifest variables (MV; observable variables). The PLS-PM framework consists of building successive models that are assessed, before reaching to the final model. The temporal auto-correlation was taken into account using the Chatfield (1996) modified Box-Jenkins auto-correlation function (Box & Jenkins 1976) coupled with the Chelton formula (Chelton, 1984) to adjust the degrees of freedom in the correlation between the MVs. An auto-correlation correction (AR1) was applied to the linear

309 models of the outer model. Path coefficients are used to estimate the relative influence of a
310 block onto another. Path coefficients are close to multiple linear regression coefficients
311 meaning that they depict standard deviations changes around the mean.

312 A few requirements are needed before reaching the final PLS-PM model. First, the
313 unidimensionality of the loadings is required, (i.e. all the correlations between MVs need to
314 be of the same sign). Therefore when a loading is negative, the opposite of the data is
315 taken. Secondly, it is recommended to keep only MVs with loadings higher than 0.7
316 (Sanchez, 2013). An iterative process was applied here so that after the removal of the
317 weakest MV, a new model was made using the remaining MVs, until all the loadings were
318 over 0.7. This was preferred rather than removing all the loadings that did not meet this
319 requirement, in order to stay as close as possible to the iterative properties of the PLS-PM
320 algorithm.

321 In this study, six blocks of variables were used: the Large scale Climate (AMO, AO, EAP,
322 NAO, NHT), the Local Climate (Iwind, Uwind, Vwind, P, MP, W, aT), the River (Q, NO_x,
323 NH_4^+), the Ecosystem characteristics (S, SPM, wT) and the Nutrients separated into two
324 blocks (NO_x, NH_4^+, $Si(OH)_4$ in the first and PO_4^{3-} in the second). A total of 14 links were
325 considered. The Large scale climate could influence the five other blocks, the Local climate
326 all the other blocks but the large scale climate, the River nutrients could influence the
327 Ecosystem characteristics and the two Nutrients blocks and finaly the Ecosystem
328 characteristics could influence the two Nutrients blocks. Only the significant relationships
329 were considered. As the goal of these models was to point out the drivers influencing the
330 nutrients, if the loading of a nutrient was lower than 0.7 a new block was created with the
331 concerned nutrient instead of removing it.

332 The goodness of fit of the models ranged between 0.49 and 0.74.

3. Results

3.1. Nutrient bi-decadal changes in the bay waters

3.1.1 Overview of the spatial and temporal nutrients changes

In the Arcachon bay, the main freshwater inputs come from the Leyre river at the southeastern end of the bay. Hence, a salinity gradient exists between the Leyre mouth (mean over the studied period: 29.0 ± 4.4 at Comprian) and the channel to the ocean (mean over the studied period: 34.4 ± 0.8 at Bouée 7), at the southwestern side of the bay. Gradients of nutrients are associated to this salinity gradient. Winter concentration of NO_x averaged 42 µM at Comprian LT and 4.8 µM at Bouée 7 HT, with maximum values up to 136 and 13.4 µM respectively. Winter concentration of $Si(OH)_4$ averaged 49 µM at Comprian LT and 4.3 µM at Bouée 7 HT, with maximum values up to 105 and 13.0 µM respectively. The seasonality of these nutrients is large with summer values often lowering to 0.1 µM. The seasonal variations are larger in the InNW than in the ENW by a factor of ca 10. Overall, PO_4^{3-} ranges between 0.02 and 0.96 µM, with higher values usually encountered in winter and autumn in the InNW, and NH_4^+ between ca 0.05 and 17.0 µM, with higher values usually encountered in winter and autumn in the InNW. In the whole data set considered in the present study, mean values of NO_x, NH_4^+, PO_4^{3-} and $Si(OH)_4$ are 7.8, 2.3, 0.11 and 13.7 µM respectively.

3.1.2 Bi-decadal inter-annual variability

In the following, and for convenience, the results are reported for only two contrasted stations: Comprian LT in the InNW (the most influenced by the Leyre river) and Courbey HT in the ItNW (the inner station the most influenced by oceanic inputs). The other figures are available in Supplementary Material. Table 2 presents the changes in nutrients concentration at all the stations when a trend was detected using a modified Mann-Kendall test (p-value < 0.05; Yue and Wang, 2004).

Nutrients concentrations in the Arcachon bay evolved similarly regardless of the different water masses (Figure 2; Supplementary Material A). The NO_x inter-annual components significantly increased (according to the modified Mann-Kendall test (Yue and Wang, 2004)) at all the stations. The NO_x concentrations were multiplied by 3 to 4 folds in the InNW — the strongest absolute change was recorded at Comprian LT — and by 1,5 fold in the ENW (Table 2). The NH_4^+ inter-annual components significantly increased at 6 out of 13 stations (Table 2), either in the ItNW or in the InNW and at high or low tide. The strongest changes occurred in the InNW, where the nutrients were the most concentrated. The strongest NH_4^+ concentration change occurred in the InNW at Jacquets (Supplementary Material A) that is under the direct influence of the Porge canal — the second most important tributary to the bay. The PO_4^{3-} inter-annual components significantly decreased at all the stations but Jacquets LT (no trend). The strongest PO_4^{3-} concentrations decrease occurred in the ENW and the weakest in the InNW. The $Si(OH)_4$ inter-annual components showed similar patterns to NO_x, with a significant increase at all stations of the ItNW and InNW (with the exception of Tès HT) however not in the ENW. The $Si(OH)_4$ concentrations were multiplied by 3 to 4 folds in the InNW (strongest absolute change in Comprian LT), and by 1.5 in the ItNW.

376 *Table 2: Bi-decadal (1999 – 2018) trend changes of all the nutrients at all sites based on the modified Mann-Kendall test (Yue and Wang, 2004). Values are the*
377 *relative (%) and absolute (Δ in µM) change when it was significant (p-value < 0.05). The stations are displayed following a decreasing continental influence, from low*
378 *tide to high tide.*

379

		Inner Neritic Waters						*Intermediate Neritic Waters*					*External Neritic Waters*	
		Comprian LT	Comprian HT	Girouasse LT	Girouasse HT	Jacquets LT	Jacquets HT	Eyrac HT	Tès LT	Tès HT	Courbey LT	Courbey HT	Bouée 7 LT	Bouée 7 HT
NOx (µM)	%	+182	+337	+312	+350	+279	+240	+412	+354	+186	+142	+194	+53	+16
	Δ	+13.7	+4.9	+4.3	+4.2	+2.6	+2.5	+4.7	+8.1	+2.3	+1.6	+2.2	+0.5	+0.1
NH_4^+ (µM)	%	ns	+88	ns	ns	+265	+120	+2	ns	+32	+85	ns	ns	ns
	Δ		+1.4			+2.5	+1	+0.02		+0.4	+0.9			
PO_4^{3-} (µM)	%	-16	-38	-21	-36	ns	-34	-59	-27	-57	-36	-41	-51	-54
	Δ	-0.03	-0.05	-0.02	-0.05		-0.03	-0.10	-0.04	-0.07	-0.04	-0.05	-0.05	-0.05
$Si(OH)_4$ (µM)	%	+94	+65	+49	+49	+100	+64	+70	+63	ns	+55	+32	ns	ns
	Δ	+21.6	+6.1	+6.2	+5.0	+11.7	+4.7	+4.1	+9.40		+4.3	+2.4		

380

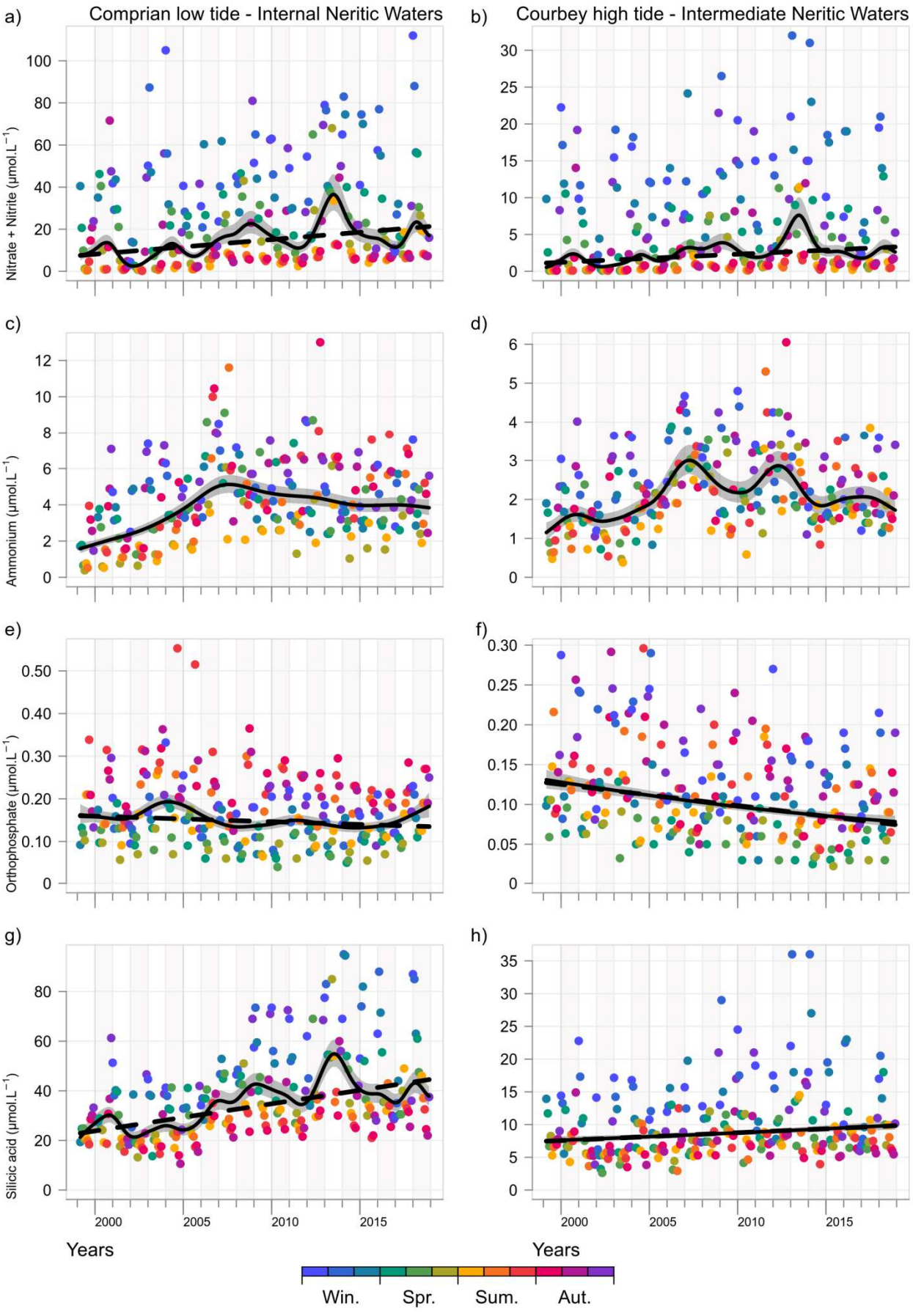
a)
Comprian low tide - Internal Neritic Waters
b)
Courbey high tide - Intermediate Neritic Waters
Nitrate + Nitrite (µmol.L⁻¹)
c)
d)
Ammonium (µmol.L⁻¹)
e)
f)
Orthophosphate (µmol.L⁻¹)
g)
h)
Silicic acid (µmol.L⁻¹)
2000
2005
2010
2015
Years
Years
Win.
Spr.
Sum.
Aut.

Figure 2: Bi-decadal inter-annual component of nitrate + nitrite (a,b), ammonium (c,d), orthophosphate (e,f) and silicic acid (g,h) at two contrasted stations: Comprian low tide (a, c, e, g) and Courbey high tide (b, d, f, h), respectively representative of the inner and intermediate neritic waters in the Arcachon bay. In each panel, the plain black line is the DLM bi-decadal inter-annual component, the gray shadow is its confidence interval at 90%, the dots are the observations for each month coloured in function of the season. The bi-decadal change was estimated with a modified Mann-Kendall test (Yue and Wang, 2004). When the test was significant, the Sen's line was drawn in dashed black.

3.1.3 Bi-decadal seasonality

In addition to the overall concentration increase (NO_x, of NH_4^+, $Si(OH)_4$) or decrease (PO_4^{3-}) across the bay, seasonal patterns were modified during the 20 studied years (Figure 3, Supplementary Material B).

The seasonal component amplitude of NO_x decreased at almost all the stations and was related to both an increase of the minimal (*ca*. summer) values and a decrease of the maximal (ca. winter) values. In the InNW and the ItNW, the occurrence of the seasonal maximum did not change over the time period whereas the occurrence of the seasonal minimum occurred later in summer. It remained stable in the ENW. The seasonal component amplitude of NH_4^+ decreased at most of the stations in relation to the decrease of the maximal values in autumn and winter and to the increase of the minimal values in summer. The occurrence of the seasonal maximum was advanced by a couple of months at most of the stations from winter to autumn, regardless the tide and the water mass (e.g. Figure 3c). The occurrence of the seasonal minimum remained stable at most of the stations, but it was advanced from July to June at Comprian LT (e.g. Figure 3c). The strongest changes occurred in the ItNW and ENW. The seasonal component amplitude of PO_4^{3-} increased at most of the stations except in the InNW where it remained stable (e.g. Figure 3e, f). This increase coincided with an increase of the maximal values in winter and a decrease of the minimal values in summer. The occurrence of the seasonal maximum and minimum were delayed from autumn to winter and from spring to summer, respectively.

401 The seasonal component amplitude of $Si(OH)_4$ either remained quite stable or increased.
402 The increasing amplitude coincided more with an increase of the maximal values in winter
403 than to a decrease of the minimal value. The occurrence of the seasonal maximum
404 remained stable in winter or was delayed from December to January at some stations and
405 the occurrence of the seasonal minimum was often delayed from spring to autumn (see
406 Supplementary Material B).

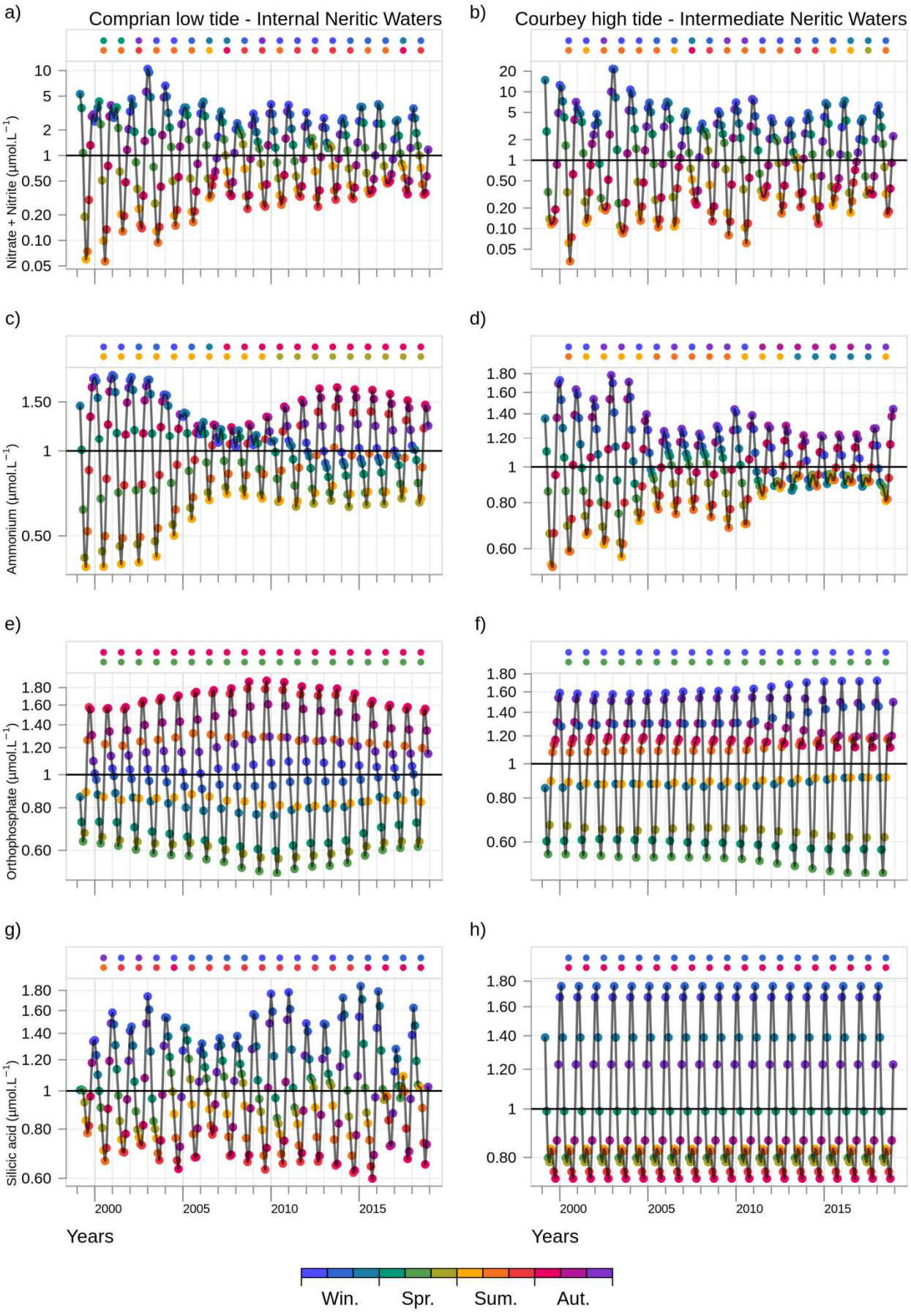
a)
Comprian low tide - Internal Neritic Waters
b)
Courbey high tide - Intermediate Neritic Waters
Nitrate + Nitrite (µmol.L⁻¹)
c)
d)
Ammonium (µmol.L⁻¹)
e)
f)
Orthophosphate (µmol.L⁻¹)
g)
h)
Silicic acid (µmol.L⁻¹)
2000
2005
2010
2015
Years
Win.
Spr.
Sum.
Aut.

Figure 3: Bi-decadal seasonality of nitrate + nitrite (a,b), ammonium (c,d), orthophosphate (e,f) and silicic acid (g,h) at two contrasted stations: Comprian low tide (a, c, e, g) and Courbey high tide (b, d, f, h), respectively representative of the inner and intermediate neritic waters in the Arcachon bay. The dots are the DLM estimations for each month coloured in function of the season. When seasonal values equal to 1 (horizontal black line), the fitted values were equal to the inter-annual component.

The dots at the top of each graph represent the month of maximum (top) and of minimum (bottom) of seasonality for each complete year.

3.1.4 Nutrient ratios

In the Arcachon bay the period of phytoplankton production runs from late February to late October (Glé et al., 2008). Despite large differences in phytoplankton production among the three water masses (Glé et al., 2008), the nutrients ratios evolved similarly over the two decades (Figure 4; Supplementary Material C). At the beginning of the period (ca. 1999-2003), phytoplankton growth was potentially limited by P in early spring but by N from late spring to autumn (Figure 4b). However, over the two decades, the potential N limitation period was shortened from 6-7 month in the early 2000s to 3-4 month in the late 2010s, and even disappeared at Comprian LT (Figure 4a).

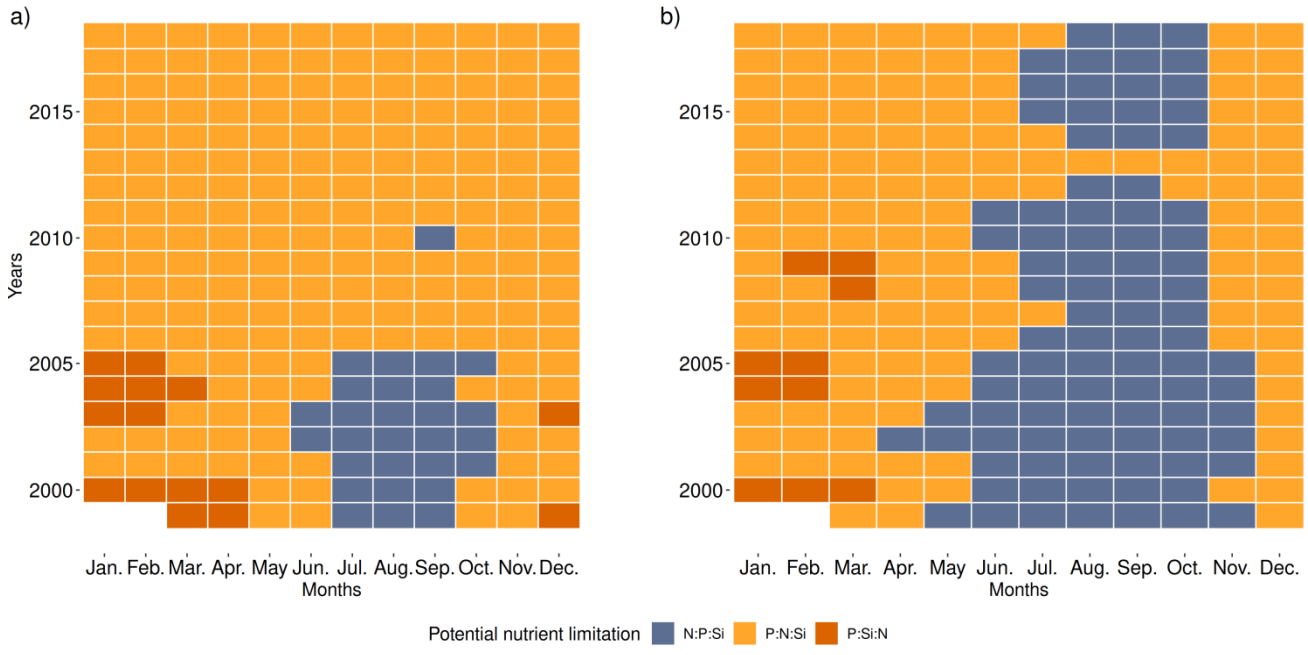

Figure 4: Bi-decadal changes in the potential nutrient-limitation based on the extended Redfield ratio N_{16}:P_1:Si_{16} (Harrison et al., 1977) at two contrasted stations: Comprian low tide (a) and Courbey high tide (b), respectively representative of the inner and intermediate neritic waters in the Arcachon bay. The order of the elements within the ratios indicate the strength of the potential limitation (for instance P:N:Si indicates that N is potentially less limiting than P but more than Si). Note that all the possible combinations were investigated (see section 2.3.3) but that only three were detected.

417

418 3.2 Bi-decadal changes of possible drivers

419 3.2.1. Biophysical parameters of the bay waters

420 Changes in biophysical parameters were observed concomitantly to changes in nutrients
421 concentrations and ratios (Table 3, Figure 5 and 6, Supplementary Material A and B).

422 The water temperature inter-annual components in the Arcachon bay significantly increased
423 at 7 over 13 stations. The increase was more pronounced in the inner and southernmost
424 part of the bay (e.g. at Comprian and Eyrac HT with an increase of more than 0.4 °C over
425 the two decades; Figure 5a, Table 3). The salinity inter-annual components significantly
426 increased at 3 sites at high tide and showed a high inter-annual variability at all the stations.
427 The SPM inter-annual components significantly increased at low tide at the all the InNW
428 sites and at Tès. The chlorophyll-*a* inter-annual components significantly increased at most
429 of the stations, especially at low tide in the InNW and ItNW (Table 3).

430 The seasonal component amplitude of water temperature remained stable such as the
431 occurrence of the seasonal maximum (July or August) and minimum (January or February).
432 The seasonal component amplitude of salinity remained stable even though there was a
433 high variability in the inter-annual maximal and minimal values. The occurrence of the
434 seasonal maximum remained stable in summer and autumn yet for some years the
435 maximum was in winter or spring. The occurrence of the seasonal minimum remained
436 stable in winter and spring. No clear pattern emerged from the seasonal component

amplitude of SPM: it increased (e.g. Courbey HT, Bouée 7 LT), remained stable (e.g. Girouasse LT, Bouée 7 HT) or decreased (e.g. Comprian LT). The seasonal maximum occurred in winter and remained stable at most stations but Comprian LT where it was delayed from winter to summer and Comprian HT where it remained stable in spring. The chlorophyll-*a* seasonal component amplitude remained stable at a majority of stations. The occurrence of the seasonal maximum remained stable in spring or in summer but at Comprian LT where it was delayed from summer to spring. The occurrence of the seasonal minimum remained stable in autumn or winter.

Table 3:Table representing the bi-decadal (1999 – 2018) trend changes of the additional parameters at all stations. Values are the relative (%) and absolute (Δ in µM) change when it was significant (p-value < 0.05). The stations are displayed following a decreasing continental influence, from low tide to high tide.

		Inner Neritic Waters						*Intermediate Neritic Waters*					*External Neritic Waters*	
		Comprian LT	Comprian HT	Girouasse LT	Girouasse HT	Jacquets LT	Jacquets HT	Eyrac HT	Tès LT	Tès HT	Courbey LT	Courbey HT	Bouée 7 LT	Bouée 7 HT
wT (°C)	%	+3	+3	ns	+2	ns	ns	+4	ns	+2	ns	ns	+3	+1
	Δ	+0.52	+0.44		+0.29			+0.56		+0.30			+0.37	+0.10
Sali (psu)	%	ns	ns	ns	+3	ns	ns	ns	ns	+3	ns	+4	ns	ns
	Δ				+0.98					+1.04		+1.17		
SPM ($mg.L^{-1}$)	%	+72	ns	+164	ns	+107	ns	ns	+62	ns	ns	ns	ns	ns
	Δ	+7.17		+9.90		+5.90			+5.13					
CHLA ($\mu g.L^{-1}$)	%	+93	ns	+42	ns	+28	ns	+37	+41	+22	ns	+10	+13	+14
	Δ	+2.22		+0.79		+0.62		+0.53	+0.81	+0.36		+0.13	+0.29	+0.22

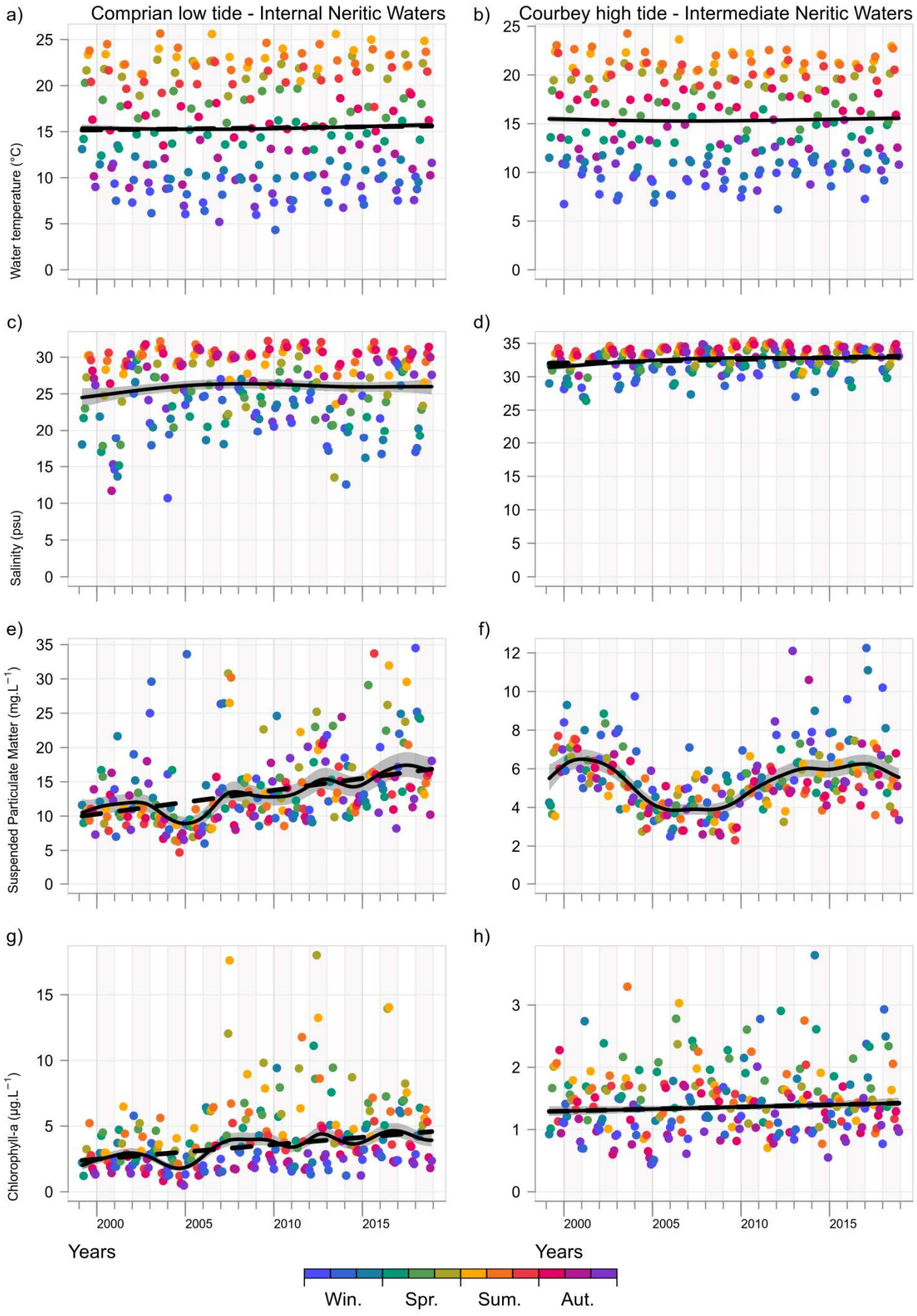

Figure 5: Bi-decadal inter-annual component of water temperature (a,b), salinity (c,d), suspended particulate

matter (e,f) and chlorophyll-a (g,h) at two contrasted stations (Comprian low tide (a, c, e, g) and Courbey high tide (b, d, f, h)) respectively representative of the inner and intermediate neritic waters in the Arcachon bay. In each panel, the plain black line is the DLM bi-decadal inter-annual component, the gray shadow is its confidence interval at 95%, the dots are the observations for each month coloured in function of the season. The bi-decadal changes were estimated with a modified Mann-Kendall test (Yue and Wang, 2004). When the test was significant, the Sen's line was drawn in dashed black.

448

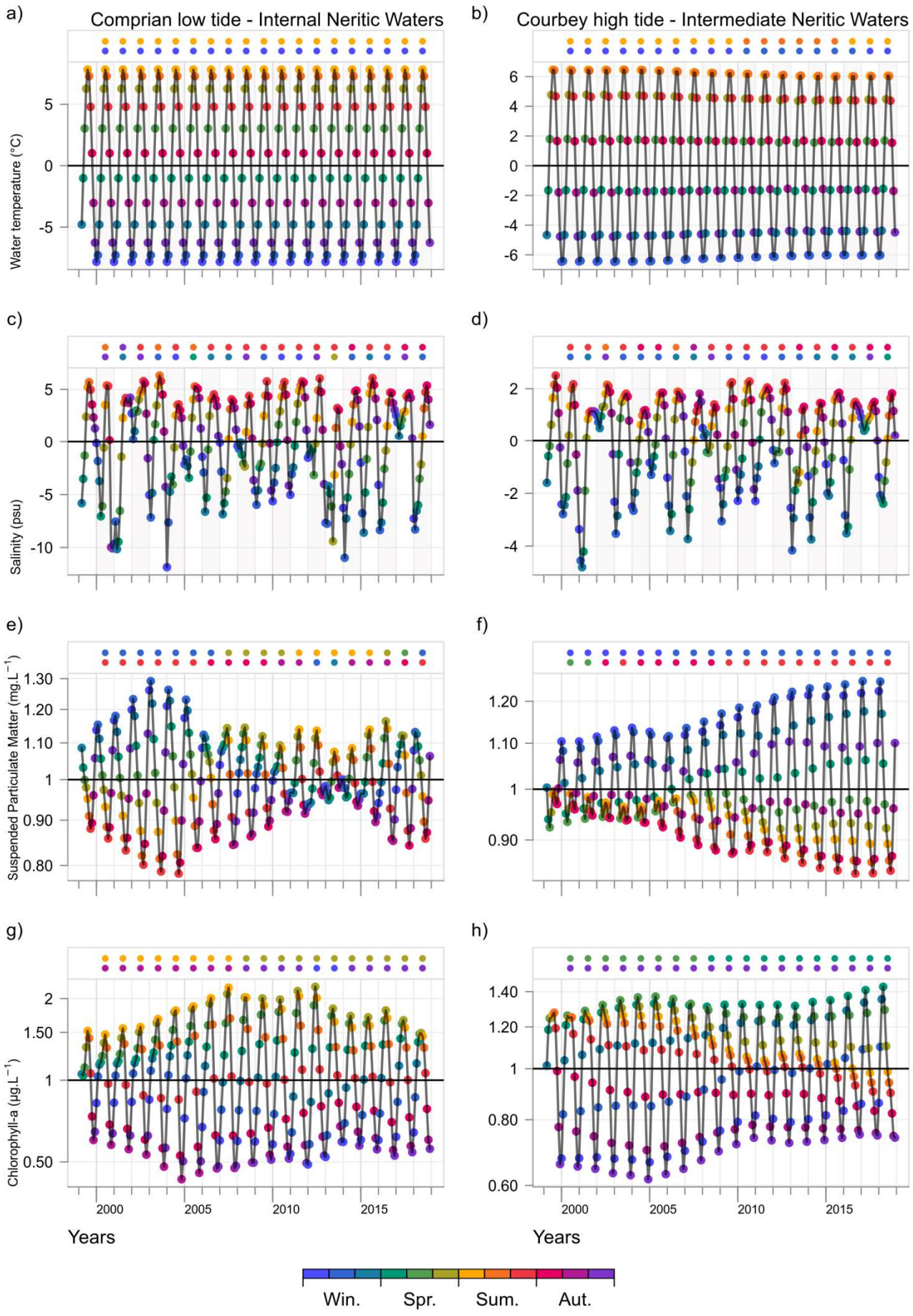

Figure 6: Bi-decadal seasonal components of water temperature (a,b), salinity (c,d), suspended particulate

matter (e,f) and chlorophyll-a (g,h) at two contrasted stations (Comprian low tide (a, c, e, g) and Courbey high tide (b, d, f, h)) respectively representative of the inner and intermediate neritic waters in the Arcachon bay. The dots are the DLM estimations for each month coloured in function of the season. When seasonal values equal to 0 (water temperature and salinity) or to 1 (suspended particulate matter and chlorophyll-a; horizontal black line), the fitted values were equal to the inter-annual component.

The dots at the top of each graph represent the month of maximum (top) and of minimum (bottom) of seasonality for each complete year.

449

450 3.2.2. River parameters

451 The Leyre discharge inter-annual component showed a strong inter-annual variability but
452 no significant increase nor decrease over the two decades (Figure 7a). The NO_x inter-
453 annual component also showed a strong inter-annual variability although less important
454 than the discharge rates (Figure 7c) No significant increase nor decrease were detected.
455 The NH_4^+ inter-annual component showed no significant increase nor decrease although
456 two distinct periods occurred with an increase from 1999 to ca. 2007 and a decrease from
457 2008 to 2018 (Figure 7e). The SPM inter-annual component showed a significant
458 decrease in the Leyre River (Figure 7g).

459 The seasonal component amplitude of the river discharge, the maximal and minimal
460 values as well as their occurrence (seasonal maximum in winter/spring and minimum in
461 autumn) remained stable over the study period although they were characterised by a high
462 year-to-year variability (Figure 7b). The seasonal component amplitude of NO_x was higher
463 in the middle of the period resulting in a slight decrease of the maximal and minimal values
464 at the end of the period. The period of occurrence of the seasonal maximum remained
465 stable in late autumn / early winter, and the occurrence of the seasonal minimum was
466 delayed from summer to autumn (Figure 7d). The seasonal component amplitude of NH_4^+
467 increased and was characterised by both an increase of the maximal and a decrease of
468 the minimal values. Except for the two first years, the occurrence of the seasonal
469 maximum remained stable in winter and the minimum was stable in autumn (Figure 7f).
470 The seasonal component amplitude of SPM increased with both an increase of the

maximal and a decrease of the minimal values but the occurrence of the seasonal maximum and minimum remained stable in spring and autumn, respectively (Figure 7h).

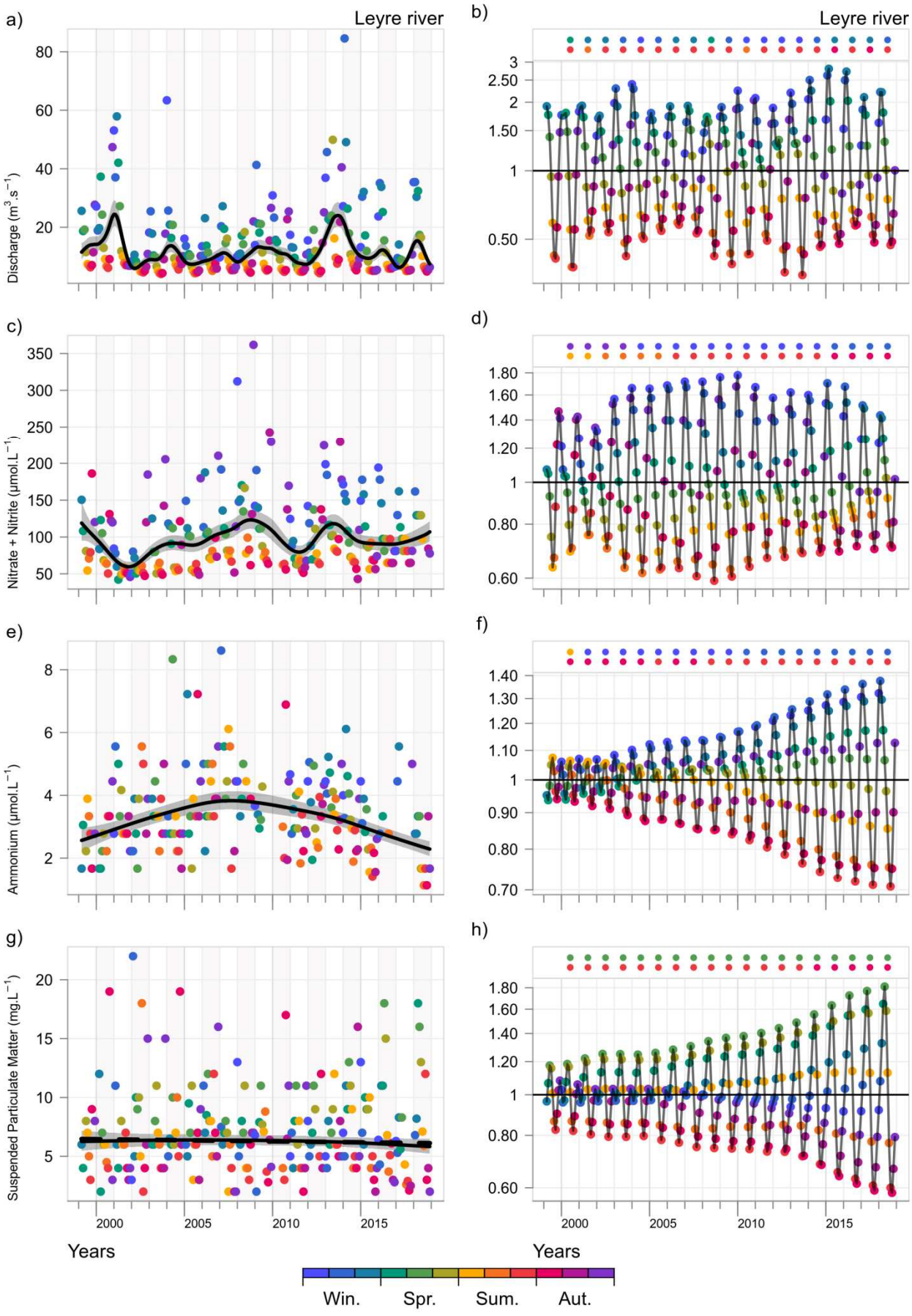

Figure 7: Bi-decadal inter-annual (a, c, e, g) and seasonality (b, d, f, h) components of river discharge (a,b),

nitrate + nitrite (c,d), ammonium (e,f) and suspended particulate matter (g,h) in the Leyre river. In the right hand side panels the plain black line is the DLM bi-decadal inter-annual component, the gray shadow its confidence interval at 90%, the dots are the observations for each month coloured in function of the season. In the left hand side panels the dots are the DLM estimations for each month coloured in function of the season. When seasonal values equal to 1 (horizontal black line), the fitted values were equal to the inter-annual component.

The bi-decadal changes were estimated with a modified Mann-Kendall (Yue and Wang, 2004). When the test was significant, the Sen's line was drawn in dashed black. At the top of each panel.

473

474 3.2.3. Local climate

475 The air temperature, irradiance, atmospheric pressure, and zonal component of the wind
476 did not show any trend whereas the wind intensity, meridional component of the wind and
477 monthly accumulated precipitation significantly decreased (Figure 8a, c, e, g, i, k, m). The
478 air temperature and irradiance seasonal component amplitude, seasonal maximal and
479 minimal values as well as their period of occurrence (seasonal maximum in summer and
480 minimum in winter and seasonal maximum in spring and minimum in autumn, respectively)
481 remained stable over the studied period (Figure 8b, d). The seasonal component
482 amplitude of the atmospheric pressure decreased over the studied period and was
483 characterised by a decrease of the maximal values. The period of occurrence of the
484 minima changed from summer to spring in 2005 whereas the occurrence of the maximum
485 always occurred in winter (Figure 8f). The seasonal component amplitude of the
486 accumulated rain increased over the studied period. It was characterised by both an
487 increase of the maximal and minimal values and the seasonal maximum and minimum
488 occurred in autumn and summer respectively (Figure 8h). The seasonal component
489 amplitude of the wind intensity increased and was characterised by both an increase in
490 maximal and minimal values. The period of occurrence of the seasonal maximum and
491 minimum remained stable in winter and summer respectively (Figure 8j). The seasonal
492 component amplitude of the zonal component of the wind decreased and was
493 characterised by the decrease of the maximal values and the increase of the minimal

494 values. The period of occurrence of the seasonal maximum changed from summer to
495 spring and the seasonal minimum remained in autumn (Figure 8l). The seasonal
496 component amplitude of the meridional component of the wind remained stable, as well as
497 the value and period of occurrence of the seasonal maximum (autumn) and minimum
498 (summer) (Figure 8n).

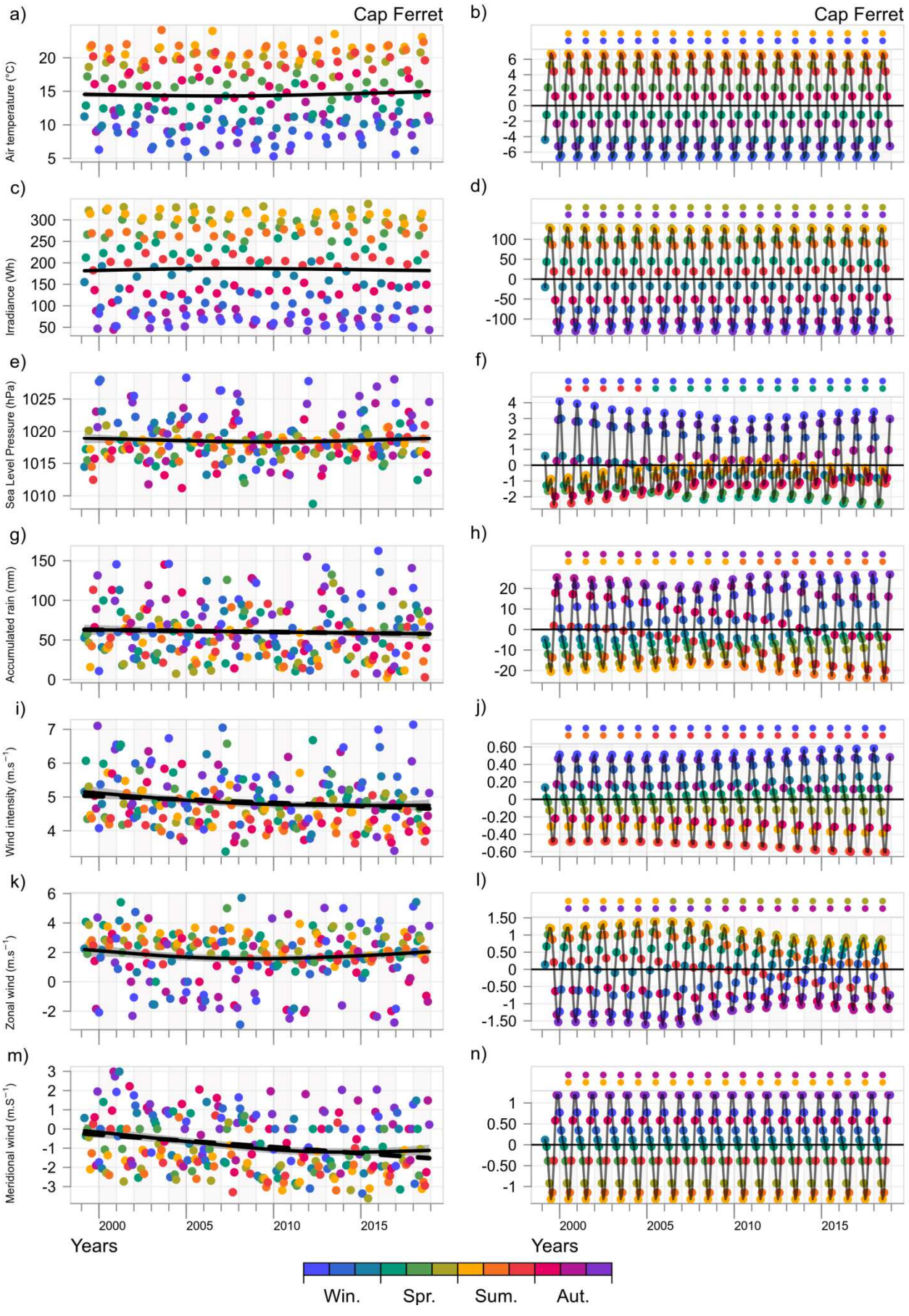

Figure 8: Bi-decadal inter-annual components (a, c, e, g, i, k, m) and seasonality (b, d, f, h, j, l, n) of air

temperature (a,b), irradiance (c,d), sea level pressure (e,f), monthly accumulated rain (g,h), wind intensity (i,j), zonal wind (k,l) and meridional wind (m,n) at Cap Ferret. In the right hand side panels the plain black line is the DLM bi-decadal inter-annual component, the gray shadow its confidence interval at 90%, the dots are the observations for each month coloured in function of the season. In the left hand side panels the dots are the DLM estimations for each month coloured in function of the season. When seasonal values equal to 0 (horizontal black line), the fitted values were equal to the inter-annual component.

The bi-decadal changes were estimated with a modified Mann-Kendall (Yue and Wang, 2004). When the test was significant, the Sen's line was drawn in dashed black. At the top of each panel.

499

500 3.3. Relationships between the nutrients and the abiotic drivers

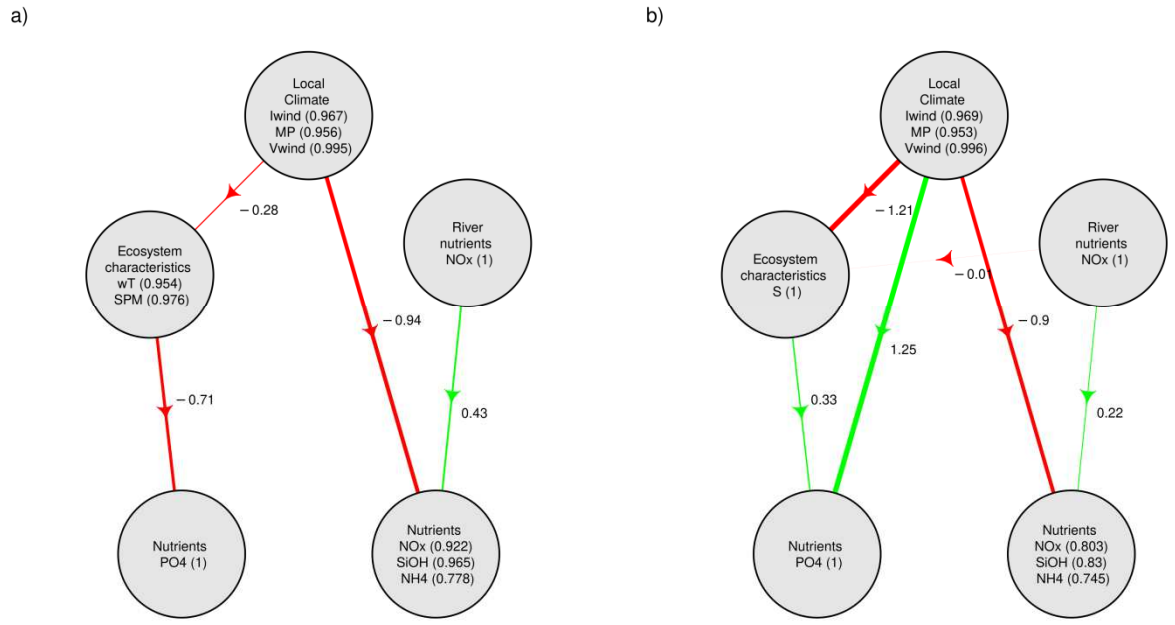

Figure 9: Relative influence of the potential drivers on the nutrients at Comprian LT (a) and Courbey HT (b). In each circle (latent variable; groups) are given and are followed by each manifest variable (parameter) and its loading (= correlation) to the latent variable. Green and red arrows represent positive and negative link respectively, with the associated path coefficient, the width of the arrow represents the strength of the relationship. Goodness of fit are 0.56 (a) and 0.62 (b).

501

502 Among the considered drivers, all groups but the Large scale climate had a significant
503 direct and/or indirect influence on the bi-decadal inter-annual components of one or more
504 nutrients (Figure 9). The Local climate always influenced a block of nutrients and was
505 mostly expressed by wind and precipitations. At most stations, the NO_x, NH_4^+ and $Si(OH)_4$
506 group was more influenced by the River nutrients and the PO_4^{3-} by the Ecosystem

507 characteristics. The river influence on the N- and SI-nutrients was inversely proportional to
508 the distance to the river (stronger in the InNW and at low tide than in the ENW and at high
509 tide; Figure 9a, b). At most of the sites, the Ecosystem characteristics influence on the
510 PO_4^{3-} was expressed by the SPM at low tide and by salinity at high tide (Figure 9a, b).

4. Discussion

In the Arcachon bay, NO_x, NH_4^+ and $Si(OH)_4$ concentrations increased in the beginning of the twenty-first century whereas PO_4^{3-} concentrations decreased. These results were inconsistent with results reported about other economically-developed countries. For example, NO_x and organic phosphorus decreased in the lagoon of Venice (Sfriso et al 2019). In the bay of Seine, NO_x concentrations remained stable since 2007 and NH_4^+ concentration decreased since the 1990s (Romero et al., 2016). Other French ecosystems also exhibited overall decreases of N- and Si-nutrients over the last two decades (Lheureux et al., 2021). During the past decades, nutrients concentrations usually decreased following the implementation of dams and the application of management policies (Ragueneau et al., 2006).

Two categories of processes were investigated in order to explain the changes in nutrients concentrations in the Arcachon Bay: (1) external nutrients inputs from adjacent ecosystems and (2) internal processes occurring within the Arcachon bay.

4.1 Changes in external drivers and consequences to nutrients

a) Leyre river inputs

As in most temperate coastal ecosystems, N- and Si-nutrients in the Arcachon bay mainly come from the rivers (Rimmelin et al., 1998). In this ecosystem, they mainly come from the Leyre River (Canton et al., 2012), as illustrated by the combined nutrients and salinity gradient from the internal to the external neritic waters (section 3.1.1; Table 2). Thus, any increase or decrease of river nutrients concentrations and/or discharge would lead to any subsequent change in nutrients concentrations in the bay as suggested by the results of the PLS-PM (Figure 9).

There was no significant change in the river concentrations nor discharge (Figure 7) during the two past decades. Thus, the bi-decadal increase in NO_x, NH_4^+ and $Si(OH)_4$ concentrations in the bay cannot be explained by changes in river input. The observed relationship between river inputs and the nutrients in the Arcachon bay (section 3.1.1; Figure 9) came from their similar inter-annual variability. In contrast to N- and Si-nutrients, PO_4^{3-} did not mainly come from the Leyre River but from the sediment through remineralisation and tidal pumping (Canton et al., 2012; Deborde et al., 2008; Delgard et al., 2013; Glé et al. 2008; Plus et al., 2015). Thus, the Leyre River hypothesis does not stand for PO_4^{3-} either.

In addition, there was no significant correlation between changes in nutrients concentrations and changes in salinity, which can be considered as a proxy of freshwater inputs. Therefore, the freshwater inputs were not suspected to having influenced the bi-decadal nutrients changes in the bay.

b) <u>External drivers to flushing time</u>

An increase of the flushing time might lead to a decrease in nutrients export to the ocean and thus an increase in nutrients retention and concentrations within the bay. Flushing time is driven by the combination of freshwater inputs, residual currents, geomorphology, and indirectly by wind conditions.

The wind and the river discharge were quantified as being of similar importance on the Arcachon bay flushing time (Plus et al., 2009). In the Arcachon bay, because of its geomorphology (the connection to the ocean is toward a narrow channel oriented along a North-South axis), the meridional component of the wind is of interest. A decrease (or a shift) in the South to North wind component would thus participate in an increase of the flushing time (Plus et al., 2009) and consequently to a decrease of the nutrients retention

559 and concentrations within the bay (Figure 8). In addition, there was a negative relationship
560 between the meridional wind and the N- and Si-nutrients and, when any, positive with
561 PO_4^{3-} (Figure 9).

562 Thus, the wind was suspected to have an influence on the PO_4^{3-} changes in the Arcachon
563 bay although it cannot explain the increase in NO_x, NH_4^+ and $Si(OH)_4$ concentrations over
564 the past two decades.

565

566 *c) Direct urban inputs*

567 Compared to open bays, semi-enclosed bays are highly influenced by anthropogenic
568 activities due to their geomorphological characteristics (Peng et al., 2012). However, the
569 Arcachon bay might not struggle with such influence. Indeed, 151 thousand inhabitants
570 were living in the municipalities surrounding the Arcachon bay in 2019 (INSEE,
571 Populations légales en vigueur à compter du 1er janvier 2019) despite a 1.5-fold increase
572 during the study period. Both the population distribution and its increase were well
573 balanced between the Northern and Southern sides of the Arcachon bay.

574 Since the 1970's, the waste-water effluents are collected all around the bay, treated and
575 poured into the ocean at around 15 km at the South of the bay (Figure 1). As the long
576 shore wave direction is oriented southward (Idier et al., 2013), these effluents were thus
577 not likely to enter the bay. Therefore, urban effluents are not expected to have contributed
578 to the observed changes in nutrient concentrations within the bay due to the coupled
579 management actions were taken prior to the data collection and the regional water
580 circulation.

581

4.2 Changes in internal processes and consequences to nutrients

a) Direct influence of the seagrass decline

As mentioned above, seagrass beds extent drastically declined in Arcachon bay between 1988 and 2007, with a sharp drop between 2005 and 2007, resulting in a decline of C sequestration capacity as seagrass biomass from 25,000 to 16,500 ton $C.y^{-1}$ (Plus et al., 2010; Ribaudo et al., 2016). Since that time, the seagrass beds have declined further and winter biomasses are lower than in the past (Cognat, 2019)

Since these two species contain and take up N, P and Si, the seagrass meadows in the Arcachon bay acts as a sink for nutrients (Wasserman et al., 1992; de Wit et al., 2005; Plus et al., 2015 and references therein). Following the decline of the seagrass beds extent, the *Z.noltei* nutrients consumption and N, P and Si stock capacity decreased.

The decrease in N and P uptake by the seagrass meadow was quantified at ca. 30% between 2005 and 2009 (Plus et al., 2015). Si uptake decrease was not quantified but probably followed the same pattern. The *Z. noltei* loss was particularly strong in the InNW (Plus et al 2010), where the NH_4^+ seasonality changed the most (Figure 3c). The period of occurrence of the NH_4^+ maxima values was advanced from January to October and the minima from early summer to late spring (e.g. Figure 3c), suggesting a modification of the biogeochemical processes in the Arcachon bay.

Clearly, a direct consequence of the decrease in *Z.noltei* biomass is its decrease in nutrient uptake. This can explain the increase in NO_x, NH_4^+ and $Si(OH)_4$ concentrations but not the decrease in PO_4^{3-} concentration in the bay.

b) Indirect influence of the seagrass decline

606 The seagrass meadow plays a role in the sediment stability. Its action on the sediment
607 results in a more active particle trapping and storage (Ward et al., 1984), in a weakened
608 hydrodynamic pressure (Fonseca and Fisher, 1986) and finally in a reduction of particle
609 resuspension and an improvement of the water transparency. A reduction of the sediment
610 stability could enhance the sediment resuspension (Madsen et al., 2001) that
611 consequently enhances the inputs of benthic nutrients stored in the sediment pore water
612 into the water column (Wainright, 1990).

613 In the Arcachon bay, the decrease of the surface covered by *Z. noltei* altered the sediment
614 stability of tidal flats (Ganthy et al., 2011) and overall the sediment dynamics (Cognat,
615 2019). There was an increase in SPM during the study period (Table 3, Figure 5e) which
616 coincided in space with the decline of the seagrass meadow in the InNW (Figure 5e)
617 where a lot a seagrass patches disappeared (Plus et al., 2010). Thus, the decrease of the
618 surface covered by *Z. noltei* had likely increased the advection of benthic nutrients to the
619 water column. In addition, the nutrients flux from the sediment to the water column is
620 higher in bare sediments than in vegetated sediments in the Arcachon bay (Delgard et al.,
621 2013). Consequently, the decrease of the seagrass meadow induced an increase of the
622 nutrients concentrations in the water column through the enhancement of the nutrient flux
623 from the sediment to the water column. Again, this can explain the increase in NO_x, NH_4^+
624 and $Si(OH)_4$ concentrations but not the decrease in PO_4^{3-} concentration in the bay.

625 In oxic conditions like in the Arcachon bay, PO_4^{3-} ion has the property of adsorbing onto
626 the particles (Froelich et al., 1988). Consequently, an increase in SPM concentration could
627 enhance the PO_4^{3-} adsorption and consequently decrease the PO_4^{3-} concentration in the
628 dissolved phase, as seen at Comprian LT, Girouasse LT and Tès LT (Table 2 and 3;
629 Figures 2e, 5e, 9a and Supplementary Material A). However, the capacity of resuspended
630 sediment particles to adsorb water column PO_4^{3-} partly depends on the (under)saturation
631 of the adsorption sites of the particles. In the absence of information regarding the

saturation state of these sites, the influence of resuspended sediment on the PO_4^{3-} concentration in the Arcachon bay cannot be assessed.

c) Complementary physical influence

Water temperature increased significantly at many stations (Table 3). An increase in temperature could increase the remineralisation processes and the benthic flux of nutrients to water column in muddy sediments (Nowicki & Nixon 1985), thus favouring an increase in remineralised-nutrients (NH_4^+, PO_4^{3-}, $Si(OH)_4$) concentrations in the water column. Also, an *in-situ* experiment revealed that an increase in ambient temperature could increase the PO_4^{3-} adsorption to the sediment (Zhang and Huang, 2011). Thus, the increase in water temperature may have contributed to the increase of the concentrations in NH_4^+, PO_4^{3-}, $Si(OH)_4$ and may have concurrently decreased PO_4^{3-} concentration in the Arcachon bay.

d) Biotic compartment: influence of phytoplankton

It was assumed that the seagrass decline has led to an increase in nutrients concentrations in the Arcachon bay. Phytoplankton, as all primary producer, has a tight relationship with nutrients since nutrients are mandatory for their growth. Chlorophyll-*a* concentration increased during the study period (Table 3; Figure 5g, h; Supplementary Material A) suggesting an increase in phytoplankton biomass, increase probably due to the concomitant increase in nutrients concentrations. However, the response of N-nutrients and $Si(OH)_4$ (increase) to the seagrass decrease and to the phytoplankton increase was opposed to the PO_4^{3-} response (decrease). This may be explained by the higher N:P:Si ratios for *Z. noltei* than for phytoplankton: *Z. noltei* N:P ratio and Si:P ratio range between 15 and 35 mol mol^{-1} (Brun et al., 2002; Plus et al., 2006) and between 25 and 80 mol mol^{-1} (Wasserman et al., 1992), respectively, whereas the reference value of phytoplankton N:P:Si ratios is 16:1:16 mol mol^{-1} (Harrison et al., 1977). This indicates that, for a given

need in N and Si, the need in P is higher for the phytoplankton (which is essentially diatom-dominated, Glé et al. 2008) than for *Z. noltei*.

At the beginning of the study period in the Arcachon bay, the phytoplankton was potentially more often limited by N (N:P:Si ratio < 16:1:16) during most of the production period (Figure 4, Supplementary material C). Thus, the increase in N (and Si) availability due to the seagrass decline has led to the increase in phytoplankton biomass. Because the need in P (for a given need in N and Si) is higher for the phytoplankton than for *Z. noltei*, the increase in phytoplankton biomass have favoured the decrease in PO_4^{3-} concentration. Consequently, along the study period, the potential nutrient-limitation has switched from N to P during the phytoplankton production period (Figure 4, Supplementary material C). Depending on the site, the potential P-limitation occurred during most or during all the phytoplankton production period.

To summarize, the increase in NO_x and $Si(OH)_4$ concentrations may have supported the phytoplankton biomass that have concurrently favoured the PO_4^{3-} decrease in the bay.

e) <u>Biotic compartment: influence of fauna</u>

In coastal ecosystems, benthic primary consumers have two main direct and indirect influence on nutrients. First, filter feeders consume phytoplankton as a main trophic resource (Kaspar et al., 1985); thus, they extract organic matter from the water column preventing its export to the ocean, they transform it into benthic biomass and then transfer it to the sediment as faeces and pseudo-faeces (Lindström Swanberg, 1991). Therefore, filter feeders contribute to maintain nutrients within the coastal ecosystems by enhancing the intra-ecosystem organic material recycling into nutrients (Kaspar et al., 1985; Dame and Dunkers 1988), especially in well-mixed shallow systems Del Amo et al. 1997). Second, benthic species can stimulate benthic algal productivity and bioturbation

682 processes, thus enhancing the benthic nutrient release (Lindström Swanberg, 1991).
683 Concerning the pelagic realm, zooplankton also participates to the nutrient
684 remineralisation through organic matter feeding and excretion.

685 In the Arcachon bay, the estimated stock of benthos was around 100 kt. This included
686 around 17 kt of the cultivated oyster *Crassostrea gigas* and 65 kt of wild oysters, in 2009
687 and 2011 respectively (Scourzic et al., 2012); around 2kt of the Manila clam *Ruditapes*
688 *philippinarum* (Sanchez et al., 2018); around 0.4 kt of the cockle *Cerastoderma edule*
689 (calculated from Blanchet (2004) and Ricciardi and Bourget (1998)); around 0.32 kt of the
690 crepidula *Crepidula fornicata* in 2011 (de Montaudouin et al., 2018) and around 15 kt of
691 other species (calculated from Blanchet (2004) and Ricciardi and Bourget (1998)).
692 *Cerastoderma edule* and *Crepidula fornicata* biomasses increased during the study period
693 but they were not considered having an influence on the nutrients regarding their very low
694 biomasses. *Ruditapes philippinarum* biomass remained similar between 2003 and 2018.
695 Although the stock of cultivated oysters decreased between the end of the twentieth
696 century and 2009 (Scourzic et al., 2012), there is unfortunately no information regarding
697 the wild oysters stock changes (H. Blanchet and X. de Montaudouin, pers. com.).

698 Thus, it would be speculative to consider a major influence of these species on the
699 nutrients but one can consider that the oysters being the major compartment, their
700 biomass changes might drive the bivalve species influence on the nutrients. If the wild
701 oysters biomass had increased, it might have induced an increase in the trapping of
702 phytoplankton and its direct remineralisation into nutrients, directly or through the bacterial
703 remineralisation of faeces and pseudo-faeces; and thus it might have contributed to the
704 increase in N- and Si- nutrient concentrations in the Arcachon bay avoiding its flush out of
705 the system through tidal turnover. If the wild oysters biomass had decreased, the inverse
706 processes were expected.

707

4.3 Synthesis of the nutrient changes and perspectives

Upon these hypotheses, it appeared that nutrients changes in the Arcachon bay principally resulted from internal processes, and that most of them were linked. The seagrass meadow decline was at the centre of our explanation as it was involved in most of the processes (Figure 10).

First, less nutrients were consumed by seagrasses, leaving more available nutrients in the water column. These newly available nutrients supported an increase of the phytoplankton biomass that participated in the change in nutrient ratios: the higher phytoplankton need in P than the *Z. noltei* (for a given need in N and Si) shifted the main potential limitation of phytoplankton production from N to P. This phytoplankton biomass increase triggered the P depletion when NO_x, NH_4^+ and $Si(OH)_4$ increased.

Second, the decrease of surface covered by the seagrass meadows increased bare sediment surface, leading to a rise of both sediments and nutrients fluxes from the bed to the water column. However, the impacts of resulting higher SPM concentrations on PO_4^{3-} concentrations (through sorption processes) could not be assessed yet.

Finally, despite the increase in water temperature that probably might have had a synergistic effect on the enhancement of remineralisation, the observed wind direction changes, through their influence on the flushing time, could have contributed to the decrease in PO_4^{3-} concentrations.

Many studies described the (pluri-)decadal bottom-up control of nutrient concentration on primary producers and even on higher trophic levels (Carpenter and Kitchell, 1993; Derolez et al., 2019, 2020; Sand-Jensen et al., 2017). The present study illustrates on the one hand the top-down control of primary producers on the nutrients concentrations and stoichiometry, and on the other hand the competition between primary producers through their resource in nutrient. Specifically, the study highlights the major role of the seagrass

meadow on the bi-decadal changes in nutrients concentrations and ratios, and indirectly on phytoplankton biomass, in the Arcachon bay. The potential nutrient limitation of the phytoplankton growth changed during the studied period due to more available nutrients but different relative uptake needs between phytoplankton and *Zostera*. Other studies found that changes in phytoplankton specific and functional diversity were related to changes in sediment resuspension — as microphytobenthos is related to sediment dynamics (Lucas et al., 2000) — or to climatic and climate-driven physical factors (David et al. ,2012; Hernández-Fariñas et al. ,2014).

Thus, the seagrass meadow might not have had a direct and/or indirect influence only on the phytoplankton biomass but also on its community structure. It would therefore be interesting to study the long-term changes in nutrient ratios, which seem to be important in the ecosystems functioning changes, in relation to phytoplankton community changes. It would also be interesting to put into perspective the patent influence of local processes in the Arcachon bay functioning by including it in a multi-ecosystemic study. Indeed, some studies revealed the influence of large-scale climate onto physico-biogeochemical parameters (including nutrients; Goberville et al. (2010), Lheureux et al. (2021)) and onto phytoplankton communities (David et al. (2012), Hernández-Fariñas et al. (2014)). One question would be: at multi-ecosystem scale, do changes in nutrient concentrations and ratios in coastal ecosystems mainly respond to changes in local or in large-scale drivers?

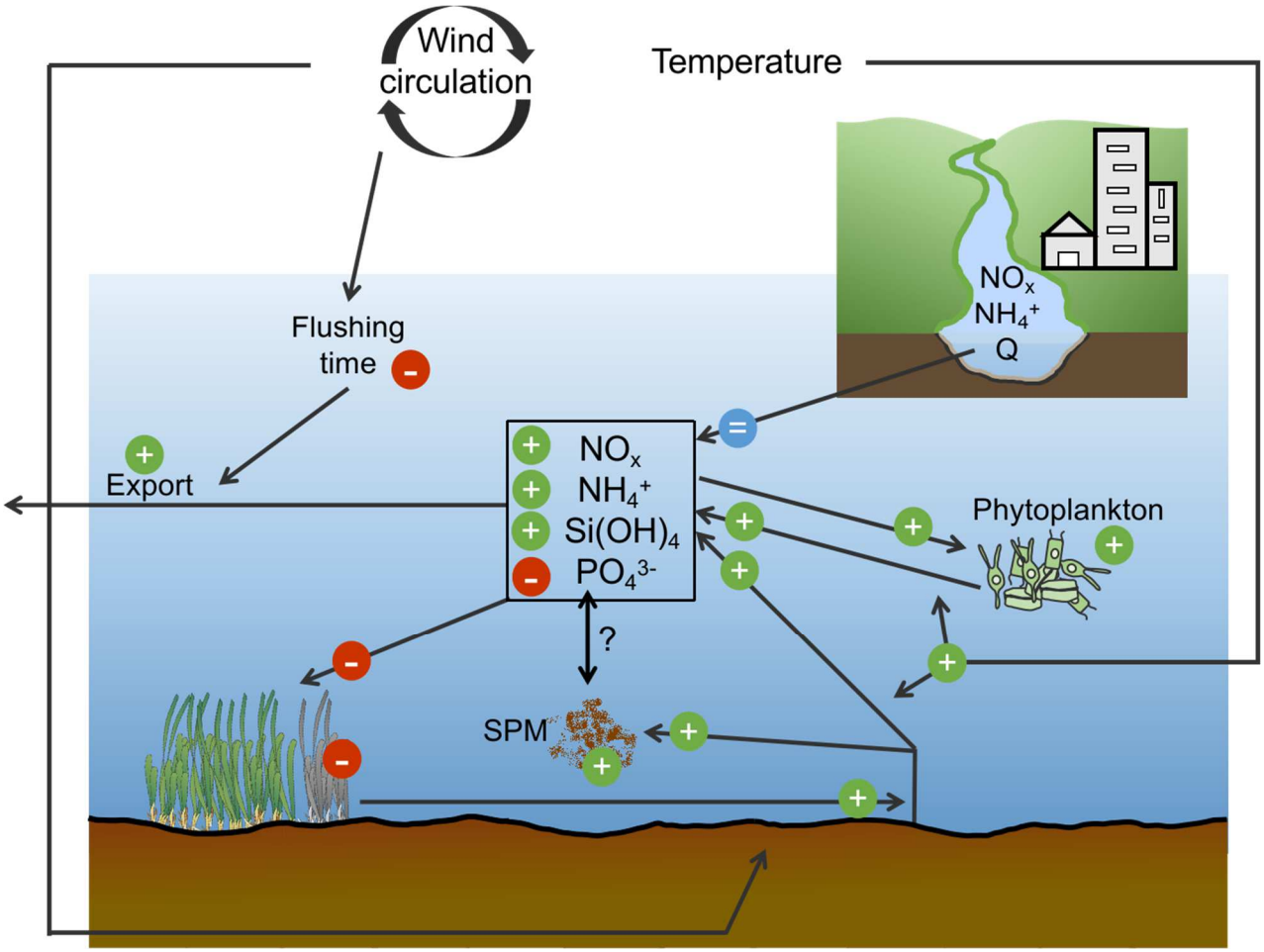

Figure 10: Global scheme summarizing the changes between 1999 and 2018 in the Arcachon bay. NO_x: Nitrate + Nitrite; NH_4^+: Ammonium; PO_4^{3-}: Orthophosphate; $Si(OH)_4$: Silicic acid; Q: River flow; SPM: Suspended Particulate Matter. "+" stands for an increase (concentration, consumption, biomass or flux), "-" stands for a decrease (concentration, consumption, biomass or flux) and "=" stands for no change (concentration, biomass, consumption or flux; either knows or not known so considered not changing).

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CRediT author statement

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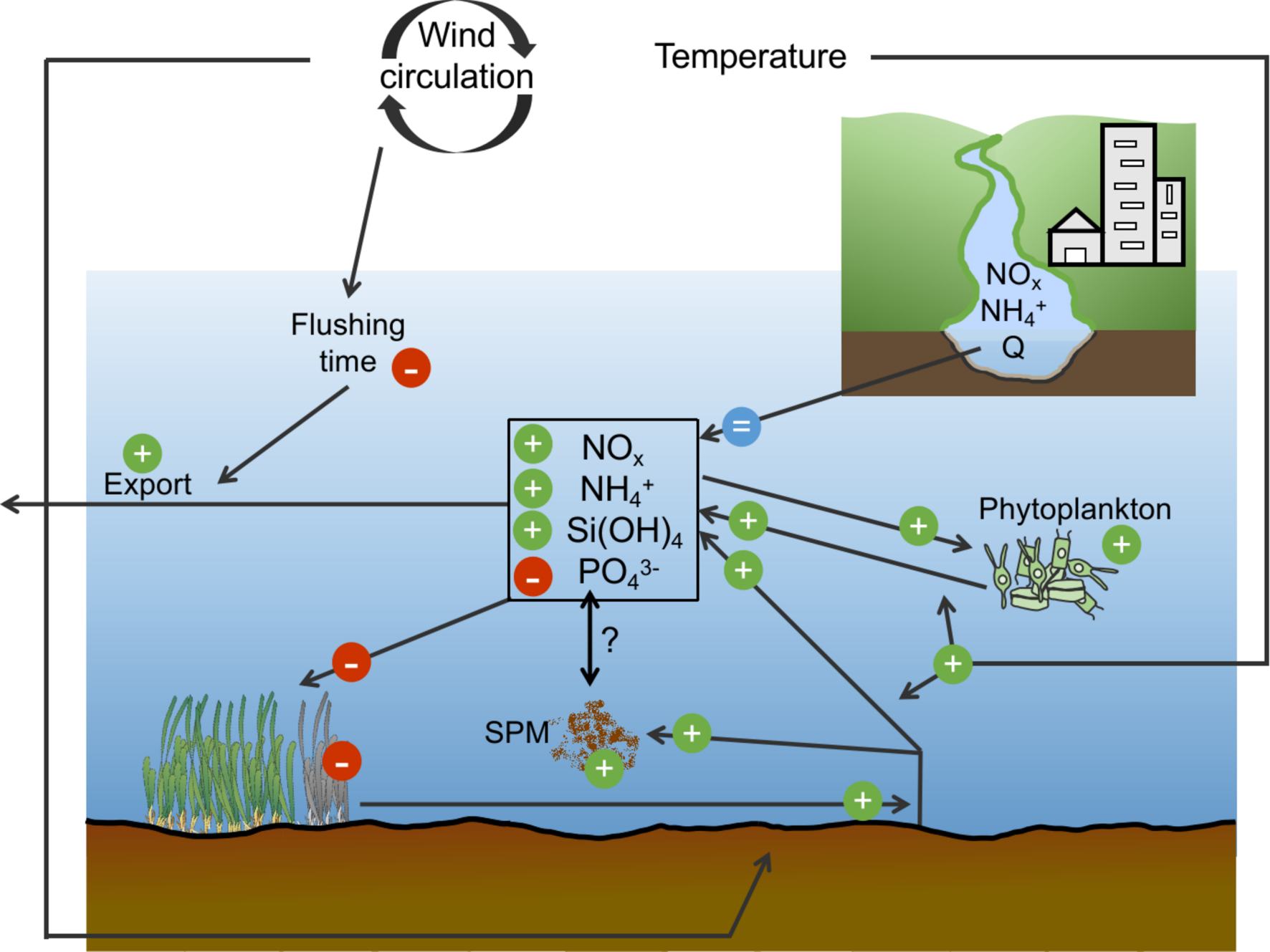
Wind
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