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Trajectories of nutrients concentrations and ratios in the French coastal ecosystems: 20 years of changes in relation with large-scale and local drivers

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* Colors should be used for all figures.

Keywords: nutrients concentrations, long-term changes, global change, ecosystem trajectories, multi-ecosystem

Highlights

- Most ecosystems showed overall decreasing nutrients concentrations
- Both climatic changes and human activities drove nutrients concentrations
- Ecological ecosystem trajectories are useful tools to study ecosystems changes
- Ecosystems had similar trajectories based on their continental influence
- Ecosystems internal functioning had a non-negligible importance on trajectories

Abstract

Along with their important diversity, coastal ecosystems receive various amounts of nutrients, principally arising from the continent and from the related human activities (mainly industrial and agricultural activities). During the 20th century, nutrients loads have increased following the increase of both the global population and need of services. Alongside, climate change including temperature increase or atmospheric circulation change has occurred. These processes, Ecosystem state changes are hard to monitor and predict. To study the long-term changes of nutrients concentrations in coastal ecosystems, eleven French coastal ecosystems were studied over 20 years as they encompass large climatic and land pressures, representative of temperate ecosystems, over a rather small geographical area. Both univariate (time series decomposition) and multivariate (relationships between ecosystems and drivers) statistical analyses were used to determine ecosystem trajectories as well as typologies of ecosystem trajectories. It appeared that most of the French coastal ecosystems exhibited trajectories toward a decrease in nutrients concentrations. Differences in trajectories mainly depended on continental and human influences, as well as on climatic regimes. One single ecosystem exhibited very different trajectories, the Arcachon Bay with an increase in nutrients

60 concentrations. Ecosystem trajectories based on ordination techniques were proven to be
61 useful tools to monitor ecosystem changes. This study highlighted the importance of local
62 environments and the need to couple uni- and multi-ecosystem studies. Although the
63 studied ecosystems were influenced by both local and large-scale climate, by
64 anthropogenic activities loads, and that their trajectories were mostly similar based on
65 their continental influence, non-negligible variations resulted from their internal
66 functioning.

67

68 Graphical abstract

69

1. Introduction

External inputs from the lithosphere, anthroposphere and atmosphere as well as the recycling of nitrogen (N), phosphorus (P) and silicon (Si) by the biosphere are among the main factors controlling the primary production in the hydrosphere and particularly in the marine temperate coastal ecosystems (Bouwman et al. 2013; Nixon et al. 1986). In these ecosystems, nutrients mainly come from rivers and other continental run-off (Seitzinger et al. 2002). Other processes participate in the input of nutrients such as vertical advection from deep water, benthic advection in shallow ecosystems, organic matter remineralisation or atmospheric deposition. Indubitably, nutrients are influenced by a set of marine biogeochemical processes — e.g., recycling, consumption, tidal pumping — and drivers — e.g. climate, human activities (Deborde et al. 2008; Bouwman et al. 2013). In most coastal areas, N and P mainly come from anthropogenic activities on land — e.g., urban expansion, industrial effluents or intensive agriculture — that considerably alter their natural cycles (Galloway et al. 2004, Metson et al. 2017). Si principally comes from natural weathering (Tréguer et al. 1995) but its cycle can be altered by modifications on lands like the creation of dams (Papush and Danielsson, 2006). The export of nutrients from the continent to the coastal ecosystems has almost doubled at the global scale between 1901 and 2000 (Beusen et al. 2016), in response to human activities (Paerl 2009).

Temperate coastal ecosystems are very diversified (as seen in Duarte et al. 2008) and this diversity is expressed at different scales. Coastal ecosystems are characterised by different geomorphologies defining their intrinsic characteristics. Geomorphology shapes their shoreline, influences their internal processes (Adame et al. 2010) and thus affects

exchanges with contiguous ecosystems. Coastal ecosystems are also characterised by their “trophic status” (from oligo- to eutrophic): they experience various levels of nutrient concentrations and phytoplankton biomass. Moreover, coastal ecosystems struggle with different tidal regimes or continental influences and are under different anthropogenic pressures and climatic conditions. Such diversity in coastal ecosystems characteristics may drive the multiplicity of nutrients origins, dynamics as well as their concentrations and ratios. For instance, among the well-studied ecosystems, Chesapeake Bay (USA) is a mesotrophic bay facing a macro-tidal regime (in its meso- and polyhaline zones). It experiences important freshwater discharges: $86 \text{ km}^3.\text{yr}^{-1}$, (Yang et al. 2015) with 96 000 tons of dissolved inorganic nitrogen per year (Feng et al 2015) coming from its large watershed ($166\,000 \text{ km}^2$). In contrast, Venice Lagoon (Italy) is a mesotrophic semi-enclosed bay facing a micro-tidal regime with only few freshwater discharges $-1 \text{ km}^3.\text{yr}^{-1}$ and 4 000 tons of dissolved inorganic nitrogen per year (Solidoro et al. 2010) from its small watershed (1840 km^2). Both ecosystems have similar nutrients concentrations (Facca et al. 2011, Harding et al. 2019) but with different watershed surface areas and supplying origins: nutrients are mainly brought by the rivers all along the watershed in Chesapeake Bay *versus* run-off through highly industrialised urban lands in the vicinity of the bay in the Venice lagoon (Pastres et al. 2004, Sfriso et al. 1992).

In addition to the natural geomorphology and to the nutrient supply origins, the climatic pressures applied to coastal ecosystems play a role on nutrients concentrations in several ways and at different scales (Bouwman et al. 2013). Temperature has effects on benthic fluxes and remineralisation — through its influence onto the biological compartment — as well as on nutrient vertical fluxes — i.e., through the stratification (Doney 2006).

Precipitations influence not only continental inputs of nutrients but also the atmospheric deposition (Durrieu de Madron et al. 2011). Winds and tides influence currents and thus the horizontal nutrients advection as well as the hydro- and sediment dynamics (Christiansen et al. 2006). Moreover, light availability might favour specific phytoplankton, macroalgae or angiosperms taxa and thus might influence nutrients uptake, and therefore modify nutrients concentrations and ratios (Litchman et al. 2007).

Anthropogenic pressures can be different depending on the human activities and on the nature of the ecosystems (Borja et al. 2010). In addition to the increasing direct anthropogenic pressures on the coast due to both the growing agricultural and industrial activities to fulfil humans needs, the increasing population and human modifications made on the watersheds directly impact and modify the coastal ecosystems. For instance, some major Asian deltas have been losing their geomorphological features due to a reduced load of sediments from the rivers following the implementation of dams (Mimura, 2006). Another example of rather unexpected human-induced change in coastal nutrient concentrations is that management policies implemented to reduce N and P loads in the Rhine and Meuse Rivers had induced an increase of Si concentrations in the coastal North Sea (Prins et al. 2012). It was shown that the retention of Si in the rivers decreased with decreasing eutrophication resulting in increased continent to ocean Si fluxes.

Within a restricted geographical area, French coastal ecosystems display a wide range of characteristics such as a high range of salinity, low to high continental influence, micro- to megatidal regime in estuaries, semi-enclosed bays, open littorals, etc. Within this context, the objective was to examine how nutrients concentrations and their respective ratios in different, although contiguous, coastal ecosystems responded to global change during the

142 past two decades by investigating (i) the overall ecosystems characteristics based on
143 nutrients concentrations and ratios in relation with their potential drivers and (ii) by
144 establishing a typology of ecosystems according to their temporal trajectories of the
145 nutrients concentrations and ratios.

146

2. Material and methods

2.1. Ecosystems

Eleven contrasted French coastal ecosystems were considered. The diversity of these ecosystems (Figure 1; Table 1) relies on their geomorphologies (estuary to open systems), tidal regime (micro- to mega-tidal), trophic status (oligo- to eu-trophic as stated in Liénart et al. 2017, 2018) and continental influences (annual salinity mean from 3 to 38) including river flow (from 1 to 1650 m³.s⁻¹) and watershed area (470 to 127535 km²). Seven of the eleven ecosystems are represented by more than one sampling stations, enabling to point out potential continent-ocean gradients within ecosystems. In addition, the climatic conditions of these ecosystems are different: annual air temperature averages range from 11 to 16°C and annual monthly precipitation from 50 to 83 mm.

2.2. Stations and data

The coastal parameters were retrieved from two French monitoring programs: the SOMLIT and the REPHY (including regional sub-programs ARCHYD and SRN) (red dots on Figure 1) at twenty-nine stations located in the eleven coastal ecosystems. These two monitoring programs produce sub-surface data (although one station was sampled at 5m depth for 6 years) for more than twenty years, at a weekly to monthly frequency. The two programs participated to annual inter-laboratory exercises at the national scale (Belin et al, 2021; Breton et al. in prep). For more information regarding these programs, see Cocquempot et al. (2019), Goberville et al. (2010), Liénart et al. (2017, 2018) and Lheureux et al. (2021) for SOMLIT, and Belin et al. (2021) for REPHY. The data retrieved

for this study run from January 2000 to December 2019. Different databases were used for gathering data regarding nutrients — the core parameters — and parameters arising from the lithosphere and atmosphere potentially forcing coastal ecosystems such as parameters indicative of hydrological, continental and climate drivers (Table 1).

Continental variables were provided by EauFrance and the French water agencies (blue and green dots on Figure 1). The meteorological variables were obtained from MERRA-2 for the local scale (see Gelaro et al. 2017) and by the National Centers for Environmental Protection and the National Center for Atmospheric Research (NCEP/NCAR) for the regional scale. The hydro-climatic teleconnection indices were 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).

2.2.1. Core parameters: nutrient concentrations and ratios

Four nutrients (nitrate + nitrite (NO_x), ammonium (NH_4^+), orthophosphate (PO_4^{3-}), and silicic acid ($\text{Si}(\text{OH})_4$) concentrations and their corresponding ratios (N:P, Si:N, Si:P) were used.

2.2.2. Environmental drivers

2.2.2.1. Local bio-physical data

Three bio-physical parameters (water temperature, salinity, chlorophyll-a) were also considered. Instead of using raw salinity measures, salinity was standardised according the 3 French facades. Each observation was divided by the facade percentile 97.5 (North Sea / English Channel = 35.40, Atlantic Ocean = 35.29, Mediterranean Sea = 38.36).

Hence, this salinity index (i.e., standardised salinity) can be used as a proxy of marine *versus* continental water body influence. It varies between 0 (freshwater) and 1 (marine water).

2.2.2.2. Continental data

Four continental variables were collected (three nutrient concentrations (NO_x , NH_4^+ and PO_4^{3-}) and the river flows). The nutrient concentrations and the river flows were monitored upstream the dynamic influence of the tide, when any. When more than one river influenced a given ecosystem, river flows were weighted by the distance between the river mouth and the station while associated nutrients concentrations were weighted by the river flow and the distance between the river mouth and the station (see Liénart et al. 2018).

2.2.2.3. Local-scale climate data

Seven meteorological variables were used: four atmospheric circulation variables (the atmospheric pressure, the wind intensity and its meridional and zonal components — see Lheureux et al. (2022) for more details on the components positive or negative values meaning), along with the air temperature, the short-wave irradiation and the monthly accumulated precipitation.

2.2.2.4. Large-scale climate

The same parameters but the short-wave irradiation were collected at regional scale (30°N to 60°N and 15°W to 15°E). Datasets were derived from reanalysis procedures and improved statistical methods had been applied to produce stable monthly reconstruction

212 on a $2.5^{\circ} \times 2.5^{\circ}$ spatial grid, but on a $1^{\circ} \times 1^{\circ}$ spatial grid for SST (see Betts et al. (1996),
213 Kalnay et al. (1996) and Kistler et al. (2001) for further details on the methodology).
214 Empirical orthogonal functions (EOF) were applied on each of these parameters to extract
215 the temporal changes (the two first principal components) and the spatial extent of the
216 changes (eigenvalues) over the geographical window. The extracted temporal
217 components originating from two gridded climate data providers were correlated
218 (Pearson's $\rho > 0.940$, raw data not shown) regardless of the data sets (NOAA *vs*
219 Copernicus) or the data spatial resolution ($> 1^{\circ} \times > 1^{\circ}$ *vs* $\leq 1^{\circ} \times \leq 1^{\circ}$).

220 Five hydro-climatic teleconnection indices were used: the AO) and the Arctic Oscillation
221 (AO). The AMO (Enfield et al. 2001) represents the Atlantic Multidecadal Oscillation
222 (AMO), the Northern Hemisphere Temperature anomalies (NHT), the East Atlantic
223 Pattern (EAP), the Northern Atlantic Oscillation (NAO) in the north Atlantic Ocean
224 surface temperature after removing the human impact whereas the NHT anomalies is an
225 index based on the 1901-2000 north Atlantic temperature average. The NAO (Hurrell
226 1995; Hurrell & Deser 2009) and the EAP (Barnston & Livezey 1987) are the two most
227 predominant mode of low-frequency variability over the north Atlantic. While the NAO
228 tracks the movements of the Azores high, the EAP values consist of a north-south dipole
229 of pressure anomalies centred on the north Atlantic, from east to west. Finally, the AO is
230 based on atmospheric pressures and is related to the Arctic climate and its southern
231 incursions (Higgins et al. 2000).

232 **2.3. Statistical analyses**

233 **2.3.1. Step 1: Data pre-treatment**

234 All the time series were reduced to one data per month by applying a median if more than
235 one observation were available for each month. Nutrients (concentrations and ratios),
236 chlorophyll-a and river flow data were log-transformed before any other statistical
237 analysis. More details regarding the whole statistical pathway can be found in
238 Supplementary material A.

239 To only consider the year-to-year changes, the interannual component was extracted for
240 each time series, except for the large-scale hydro-climatic indices, using dynamic linear
241 models (DLM, West and Harrison, 1997). DLMs have already been used in ecological
242 studies dealing with nutrients, phytoplankton and climate data (Hernández-Fariñas et al
243 2014, Ratmaya et al. 2019, Lheureux et al. 2022).

244 To detect monotonic significant changes across the whole time period (20 years),
245 modified Mann-Kendall tests (Hamed and Rao, 1998) were performed on each time series.
246 Additionally, three modified Mann-Kendall were performed on three 10-year drifting
247 windows: 2000-2009, 2005-2014, 2010-2019 on each time series. Using the sign of the
248 associated Sen-Theil slopes, it was possible to detect trend inversions (inversion of sign)
249 or trends that occurred during a specific span along the 20-year studied period.

250 **2.3.2. Step 2: Co-inertia analysis (COIA)**

251 Between-Group COInertia Analysis (BGCOIA, Franquet et al. 1995) and Within-Group
252 COInertia Analysis (WGCOIA, Franquet and Chessel 1994) are traditionally used to study
253 the changes in species-environment relationships (Thioulouse et al. 2018) by analysing

series of pairs of tables. In this study, they were used to study changes in nutrients concentrations and ratios *versus* drivers relationships. The COIA was used to reveal the main co-structures — i.e., common structures to the nutrients and to the drivers data sets — by combining the two separate PCAs (Principal Component Analysis) into a single analysis (Thioulouse et al. 2018).

2.3.3. Step 3: Overall characteristics of the nutrients concentrations and ratios in the ecosystems (BGCOIA)

The BCA allowed to focus on the ecosystems overall nutrients concentrations and ratios along the French coast by pointing out the different responses of each station to the environmental drivers. The BCA was computed so that each station is a group. This final BGCOIA analysis enabled to point out the overall characteristics and co-structures at each station, hence for each ecosystem.

2.3.4. Step.4: Bi-decadal changes of the nutrients concentration and ratios per stations (WGCOIA)

The WCA focussed on the remaining co-structure in the data sets at each station, hence for each ecosystem (i.e., temporal changes). An extra standardisation by station was applied on the results of the two PCAs and the two tables of group averages were subtracted by the corresponding DLMs inter-annual components. Thus, the analysis enabled to focus on the long-term responses of nutrients to drivers during the two past decades for each station and compare them.

2.3.5. Step.5: Typology of stations according to the bi-decadal response of nutrients concentrations and ratios to the drivers

An Euclidean distance matrix was computed for each month, so a total of 240 distance matrices (240 dates) were computed, each giving the Euclidean distances between each station at a given month. The « station x station » couples were then ranked based on their distance before being summed over the months to constitute a global distance matrix. A fuzzy partitioning coupled to a silhouette analysis were then computed on this global distance matrix to find out the relevant number of clusters and the percentage of chance of each station to belong to each identified cluster (Borcard et al, 2011).

2.3.6. Softwares

DLMs (package “dlm” (Petrus, 2010)), BGCIOA and WGCIOA (package “ade4” (Bougeard and Dray, 2018; Chessel et al. 2004; Dray and Dufour, 2007; Dray et al. 2007; Thioulouse et al. 2018)), fuzzy partitioning (package “cluster” (Maechler et al. 2021)) and associated figures (packages “ggplot2”(Wickham, 2016), “ggrepel” (Slowikowski 2021), “rnatuarearth” (South, 2017), “rnatuarearthhires”, (South, 2021), “rgdal” (Bivand and al., 2021), “scatterpie” (Yu, 2021) and “wesanderson” (Ram and Wickham, 2018) were performed using the R software (R Development Core Team, 2021). The map (Figure 1) was created with QGIS (QGIS Development Team, 2021).

3. Results

3.1. Overall characteristics of the ecosystems based on nutrient concentrations and ratios

3.1.1. Mean levels and temporal trends

NO_x concentrations ranged between nearly 0 and 385 µM (Figure 3). The highest and lowest annual average concentrations were recorded in the Gironde Estuary at station 18 (127 µM) and in the Bay of Marseille at station 27 (0.834 µM), respectively. NH₄⁺ concentrations ranged between nearly 0 and 14.0 µM. The highest and lowest annual mean concentrations were recorded in the Arcachon Bay at station 21 (4.38 µM) and in the Bay of Banyuls at station 28 (0.187 µM), respectively. PO₄³⁻ concentrations ranged between nearly 0 and 7.76 µM. The highest and lowest annual average concentrations were recorded in the Gironde Estuary at station 19 (2.18 µM) and in the Bay of Banyuls at station 28 (0.0320 µM), respectively. Si(OH)₄ concentrations ranged between nearly 0 and 264 µM. The highest and lowest annual mean concentrations were recorded in the Gironde Estuary at station 18 (120 µM) and in the Bay of Banyuls at station 28 (1.49 µM), respectively. N/P ratio highest and lowest average were recorded in the Arcachon Bay (194) and in the EEC (15) respectively. Si/N ratio highest and lowest mean were recorded in the Arcachon Bay (27) and in the WEC (0.75) respectively. Si/P ratio highest and lowest mean were recorded in the Arcachon Bay (302) and in the North Sea (10) respectively. All nutrients related models can be found in Supplementary material B.

Although the four nutrients concentrations tended to show either no or decreasing trends at most of the stations within the studied period, their changes as well as changes in ratios,

316 differed both between and within ecosystems. Most of the time (except for NO_x), when no
317 significant changes were detected over the bi-decadal period, a trend inversion was
318 highlighted (Figure 4), meaning that some changes occurred during the study period.

319 Overall, NO_x significantly increased only in the Gironde Estuary (station 18) and in the
320 Arcachon Bay (stations 21, 22, 23, 26) and NH_4^+ increased only in the Western English
321 Channel (station 14). PO_4^{3-} significantly increased at a few scattered stations, one station
322 out of four in the Bay of Somme (station 12), the two stations of the Western English
323 Channel (stations 13 and 14), the Bay of Brest station (station 15), one out of three
324 stations sampled in the Gironde Estuary (station 20) and the one station recorded in the
325 Bay of Banyuls (station 28). Si(OH)_4 significantly increased in the inner Bay of Somme
326 (station 9), in the Bay of Quiberon (station 16), in the Bay of Vilaine (station 17), in the
327 Gironde Estuary (stations 18 to 20) and in the Arcachon Bay (stations 21, 22, 23 and 26).

328 The inner Arcachon Bay (stations 21 to 26) was one of the scarce ecosystems where NO_x
329 and Si(OH)_4 significantly increased at most stations: NO_x concentrations tripled at some
330 stations and Si(OH)_4 was multiplied by 1.5 on average. However, NH_4^+ showed no
331 significant monotonic trend and PO_4^{3-} decreased by almost two folds at all the stations of
332 this ecosystem.

333 Following these nutrients concentrations changes, ratios significantly increased or
334 showed no significant monotonic trends at most stations. In the Eastern English Channel,
335 N/P decreased at two (stations 7 and 8) out of five stations (stations 4 to 8) and was
336 associated with significant decreasing NO_x and NH_4^+ concentrations and stable PO_4^{3-}
337 concentrations with no inversion. The same patterns were spotted for the Si/P and Si/N
338 as the Si(OH)_4 concentrations significantly decreased. In the Western English Channel and
339 the Bay of Brest (stations 13, 14 and 15), N/P and Si/P decreased following the PO_4^{3-}

concentrations increase and Si/N decreased at the one station where NH_4^+ concentrations increased. In the Arcachon Bay (stations 21 to 27), Si/N significantly decreased because the NO_x concentrations increase was higher than for $\text{Si}(\text{OH})_4$. N/P also decreased in the Bay of Banyuls (stations 28) due to the decreasing NO_x and NH_4^+ and increasing PO_4^{3-} .

3.1.2. Spatial discrimination and drivers

Because it was complicated to synthesise the observed diversity in terms of nutrients concentrations and their bi-decadal variability, ordination techniques such as the BGCOIA enabled to discriminate the coastal ecosystems to have an overall image.

The BGCOIA discriminates the stations along a 'nutrients ratio axis' (first axis on Figure 5a) from the English Channel (lower Si/P ratio) to the Arcachon Bay (higher Si/P ratio) and along a 'concentration axis' (second axis on Figure 5a) from the Gironde estuary (higher concentrations) to the Mediterranean Sea (lower concentrations) (Figure 5a and b). Also, the BGCOIA discriminates the stations along a 'temperature axis' (first axis on Figure 5c) from the northern (lower temperature) to the southern (higher temperature) stations and along a 'salinity axis' (second axis on Figure 5c) from the Gironde estuary (lower salinity) to the Mediterranean Sea (higher salinity) (Figure 5c and d).

Two ecological gradients were highlighted by both the nutrients and drivers. First, a latitudinal-like gradient expressed through temperatures, nutrient ratios, and wind directions that opposed the warm southernmost stations located in the Gironde Estuary, the Arcachon Bay and the Mediterranean Sea, which exhibited a high Si/P ratio, to the cold northernmost stations located in the North Sea, the English Channel and the northern Bay of Biscay, which exhibited a low Si/P ratio. Secondly, a 'trophic status' gradient expressed through continental inputs (river flow, nutrient concentration) and chlorophyll *a*

concentrations opposed the eutrophic Gironde Estuary to the oligotrophic Mediterranean ecosystems. High nutrient concentrations were thus associated with low salinity and high precipitations, river flow and chlorophyll *a* concentrations. Apart from wind intensity, only local drivers showed up in the expression of these gradients and therefore discriminated the stations and ecosystems from one another.

3.2. Ecosystem trajectories and typologies

3.2.1. Nutrient trajectories

Four groups of stations were identified based on the observed temporal variability. Nutrients concentrations and ratios changes were expressed as trajectories and mean trajectories for each of the four identified groups. These trajectories were projected onto the correlation circle. They indicate the changes in nutrients concentrations and ratios. When a trajectory is directed towards a parameter, it means that this parameter increased. Inversely, when a trajectory is directed away from a parameter, it means that this parameter decreased.

NO_x, NH₄⁺ and Si(OH)₄ were opposed to the Si/N ratio on the first axis and PO₄³⁻ was opposed to both the N/P and Si/P ratios on the second axis. N and Si both being opposed to Si/N indicated that N-changes range were relatively wider than Si changes. P being opposed to both N/P and Si/P indicated that P-changes range were relatively wider than for N and Si.

The Arcachon Bay group

Group A (Figure 6b top left, purple in Figure 6c) encompassed all the stations of the Arcachon Bay (stations 21 to 27). Thus, group A was defined as “The Arcachon Bay group”. This group was characterised by increasing NO_x and Si(OH)_4 , rather stable NH_4^+ and decreasing PO_4^{3-} concentrations (Figure 4) and by increasing N/P and Si/P ratio as well as decreasing Si/N (Figure 4). The trajectories of the six inner stations were very close one from another and were directed from the top right corner to the bottom left, meaning that the stations were mostly characterised by increasing NO_x , Si(OH)_4 and N/P as well as decreasing Si/N (Figure 6a and b).

The group of strong continental influence

Group B (Figure 6b top left, blue in Figure 6c) encompassed the two inner-most stations of the Bay of Somme (stations 9 and 10), Ouest Loscolo (station 17) in the Bay of Vilaine, the Gironde Estuary (stations 18, 19 and 20) and Frioul (station 29) in the Bay of Marseille. This group was characterised by rather stable NO_x and PO_4^{3-} , rather decreasing NH_4^+ and rather increasing Si(OH)_4 (Figure 4). Regarding nutrients ratios, this group was characterized by stable N/P and increasing Si/N and Si/P. Including the estuarine stations and the closest stations to the river mouths, apart from Frioul, it was defined as “The group of strong continental influence”. Frioul apart (mean salinity index: 0.991), the mean salinity index of each station ranges between 0.080 and 0.922. The trajectories of the stations within this group were all directed along the horizontal axis, from left to right, with variations on the vertical axis. The stations within this group were mostly characterised by decreasing ammonium, by increasing Si/N for the first half of the period and increasing Si/P for the second half (Figure 6a and b).

409 *The group of moderate continental influence*

410 Group C (Figure 6b bottom left, red in Figure 6c) encompassed six out of eight stations of
411 the North Sea (stations 1, 2 and 3) and the Eastern English Channel (stations 4, 5 and 6),
412 the two outermost stations of the Bay of Somme (stations 11 and 12) and station Men er
413 Roue (station 16) in the Bay of Quiberon. This group was characterised by decreasing NO_x ,
414 NH_4^+ and Si(OH)_4 and rather stable PO_4^{3-} concentrations (Figure 4). Regarding the
415 nutrients ratios, this group was characterized by increasing Si/P and Si/N as well as rather
416 stable N/P (Figure 4) so that it was defined as “The group of moderate continental
417 influence”. The mean salinity index of each station ranges between 0.937 and 0.973. The
418 trajectories of all the stations were close from one another and were positioned along the
419 horizontal axis, from left to right with very little variations along the vertical axis. The
420 stations within this group were mostly characterised by decreasing NO_x and NH_4^+ as well
421 as increasing Si/N and Si/P (Figure 6).

422

423 *The group of poor continental influence*

424 Group D (Figure 6b bottom right, green in Figure 6c) encompassed the remaining two
425 stations of the Eastern English Channel (stations 7 and 8), the two stations of the Western
426 English Channel (13 and 14), Portzic (station 15) in the Bay of Brest and Sola (station 28)
427 in the Bay of Banyuls. This group was characterised by decreasing NO_x , NH_4^+ and Si(OH)_4 ,
428 and increasing PO_4^{3-} concentrations. Regarding the nutrients ratios, this group was
429 characterized by rather stable or decreasing Si/P and Si/N as well as decreasing N/P. It
430 was thus defined as “The group of poor continental influence”. Except for Point C (station
431 7; mean salinity index: 0.963) the mean salinity index of each station ranges between
432 0.980 and 0.994. The trajectories of the stations were not very close from one another, but

the mean trajectory was directed from the bottom left to the top right corner. All the stations were mostly characterised by decreasing NO_x , Si(OH)_4 and N/P.

3.2.2. Drivers changes

Similarly to nutrients, it was possible to project the drivers changes once the spatial effect was removed (Figure 7a) and to group the stations by common trajectories (Figure 7b).

Two groups with different drivers changes were detected (Figure 7c). Unlike for nutrients, these drivers segregated the stations along a north-south gradient. Group A gathered the northern stations from the North Sea to the Bay of Vilaine (stations 1 to 17) apart from the Bay of Quiberon (station 16), whereas group B gathered the southern stations from the Gironde Estuary to the Mediterranean Sea (stations 18 to 29) in addition to the Bay of Quiberon (station 16). The northern stations exhibited a V-shaped trajectory and the southern stations a more linear trajectory. Despite the differences in trajectories, precipitations, wind-speed and direction, as well as pressure were the most involved drivers. Temperature also accounted through the NHT but to a lesser extent. It should be noticed that local drivers, apart from local wind intensity (I_{wind}), are poorly represented on the correlation circle of the WGCIOA (Figure 7a) in contrast to the correlation circle of the BGCIOA (Figure 5c and section 3.1.2.).

4. Discussion

4.1. Differences between ecosystems

Although the studied ecosystems are not very distant from one another, various studies pointed out their contrasted characteristics. Using a panel of particulate, dissolved and hydro-physical parameters, it was showed that the French coastal ecosystems experienced both similar (salinity) or opposed (dissolved and particulate organic matter) changes during the last two decades (Goberville et al. 2010, Lheureux et al. 2021). At an annual timescale, the contribution of organic matter sources to coastal particulate organic matter along the French coast (including common stations with the present study) followed a continent-ocean gradient (Liénart et al. 2017, 2018). In other French coastal ecosystems where phytoplankton biomass was used as a proxy of ecosystems trophic status, their eutrophication trajectories were different (Derolez et al. 2020, Le Fur et al. 2019; Ratmaya et al. 2019). The bay of Vilaine showed trajectories towards eutrophication despite decreasing continental discharges (Ratmaya et al. 2019), whereas the French Mediterranean lagoons showed trajectories towards oligotrophication. The latter were mainly influenced by air temperature, winds and rainfall (Derolez et al. 2020). At a higher trophic level and at a wider spatial scale, different trophic pathways structures and fish assemblages were identified between the three French ecoregions: the English Channel Bay, the Bay of Biscay and the Gulf of Lions (Cresson et al. 2020). These differences were mainly driven by primary production and environmental drivers, highlighting the contrast between the French ecosystems.

The *in-situ* parameters used in the present study highlighted the patent contrasts between the studied ecosystems in terms of temperature or continental discharges, in addition with their differences in geomorphology, tidal regime and trophic status (Table 1).

First, the studied stations and ecosystems were segregated along a temperature gradient (Figure 5). Indeed, there is a patent contrast between the French local climatic characteristics (Joly et al. 2010): the Mediterranean climate experiences higher temperatures (e.g., yearly average temperature of 16°C in the Bay of Marseille) than the oceanic climate of northern France (e.g. yearly average temperature of 11°C in the North Sea). Differences in wind conditions were also pointed out (Figure 5b). The latter two ecoregions (Mediterranean Sea and North Sea) were two extremes between which the other ecosystems, all under oceanic climate (Joly et al. 2010) were gradually characterised by higher temperatures and lower precipitations (from the Eastern English Channel in the North to the Bays of Marseille and Banyuls in the South). The gradient in nutrients ratios was in the same direction: higher ratios values were recorded in the Mediterranean ecosystems than in the northern ecosystems.

Secondly, the stations and ecosystems were segregated along a continental influence and trophic status gradient (i.e., the eutrophic Gironde Estuary was opposed to the oligotrophic Mediterranean bays). Both river flows and salinity were proxies of continental discharges. These two parameters were related to the differences in trophic status as illustrated by the nutrients and chlorophyll *a* concentrations. Analysis 1 (Figure 5) also highlighted the fact that nutrients were mainly brought by rivers in the French temperate coastal ecosystems. The other studied ecosystems were gradually distributed between the Gironde Estuary and the Mediterranean bays. Such a gradient in trophic

status of ecosystems has also been previously pointed out as a driver of the composition of the particulate organic matter for similar ecosystems (Liénart et al. 2017, 2018).

The fact that the studied ecosystems are subjected to different drivers and / or to their different magnitudes implies local consequences, either directly or indirectly due to the drivers. For example, the western Mediterranean Sea is subjected to direct atmospheric deposition with a higher N/P ratio than the seawater (Durrieu de Madron et al. 2011). Differences in wind and precipitation regimes could therefore modify the atmospheric deposition, which could have major consequences on the functioning of Mediterranean ecosystems due to their oligotrophic conditions (Durrieu de Madron et al. 2011). In meso- or eutrophic ecosystems, such differences might not have similar consequences on nutrients concentrations and ratios. The influence of precipitations on nutrients concentrations and ratios does not only stand at local scale but also at the scale of the watershed through a combination of processes. Precipitation leads to nutrient leaching from the soils toward the rivers and contributes to river flow (Blöschl et al. 2007). Differences in precipitations then resulted in differences in continental discharges, and consequently in nutrients concentrations and ratios due to the strong connection between rivers and coastal ecosystems (Seitzinger et al. 2002). The consequences of such differences depend on the continental influence in each ecosystem but also on the land use and the associated run-off waters in the watersheds. The consequences were thus expected to be very different between the agricultural lands of French Brittany including the Western English Channel (stations 13 and 14) and Bay of Brest (station 15), both under lower continental influence, and the urban and yet subjected to low continental discharges Bay of Marseille (station 29). At last, differences in water temperature may

induce differences in nutrients concentrations and ratios because higher water temperatures induce stronger stratification that can disrupt vertical nutrient inputs and remineralisation processes (Doney, 2006).

4.2. Temporal changes of ecosystems

Despite the importance of local drivers to characterise the French coastal ecosystems, it appeared that regional and large-scale drivers were involved in the temporal changes. Ecosystem responses to large-scale climate and anthropogenic drivers are complex to assess because of their non-linearity. This non-linearity can be attributed to the involved processes (Cloern et al. 2010) and to the rather indirect influence of the drivers. For example, precipitation rates and rivers discharge as well as the Eastern Atlantic Pattern (EAP) influenced winter nutrients concentrations in the Bay of Brest (Tréguer et al. 2014). Yet, river discharge is locally influenced by local precipitations (Blöschl et al. 2007), themselves under the spectrum of large-scale precipitations and wind circulation and thus under the prism of the teleconnection indices that summarize climate at a large scale (Kingston et al. 2006, Steirou et al. 2017).

In addition, ecosystems answers can follow different pathways: ecosystems can come back to a previous state or switch to another equilibrium (Scheffer & Carpenter 2003, Scheffer et al. 2009). Many studies detected abrupt changes during the late 1990s and early 2000s in the western Europe and French coastal ecosystems either using biogeochemical parameters (Goberville et al. 2010, Lheureux et al. 2021), phytoplankton communities (David et al. 2012; Hernández-Fariñas et al 2014), zooplankton communities (Richirt et al. 2019), fish assemblages (Chaalali et al. 2013) or birds (Luczak

et al. 2011). Although the processes that triggered these changes had not been explicitly described as a whole, it appeared that it was due to a combination of both climatic and direct anthropogenic pressures that were hard to disentangle. The obvious assessment was that the French coastal ecosystems were struggling with obvious changes during the past decades.

4.2.1. Overall changes in nutrients and drivers

Along the 20-year studied period the overall nutrients concentrations in the French coastal ecosystems tended to decrease. The main exception was the Arcachon Bay where inorganic dissolved nitrogen and silicic acid concentrations increased due to internal ecosystem functioning (Lheureux et al. 2022).

The overall decrease in nutrients concentrations could be attributed to both changes in climatic and continental drivers as well as to management policies. Local and regional precipitations appeared to be decreasing and changes in regional winds were also spotted (Supplementary material C and D). Rainfall decline (except in south-western France) and changes in winds affected continental discharges (Blöschl et al. 2007) at local (i.e., local run-off) and larger (i.e. watershed) scale and might be responsible for continental discharges overall stability or decrease (Supplementary material E; Friedland et al. 2021), which might have induced the overall decrease in nutrients concentrations in the coastal ecosystems (Seitzinger et al. 2002). In addition, continental nutrients concentrations also decreased (Supplementary material E) probably due to such decreases of precipitations and continental discharges, as reported in the North Sea (Radach & Pätsch 2007) and of management policies.

Indeed, France had reduced the use of phosphate in domestic detergent from the middle of year 2007 (Decree n°2007-491, March 29, 2007). During the studied period, PO_4^{3-} concentrations dropped in many of the studied ecosystems. This could be a consequence of this decree although such decreasing trends were observed from the 1990 in numerous south-western Europe rivers, including the biggest French rivers (Romero et al. 2013). This highlights the importance and the need of appropriate management policies and mitigation to fight against eutrophication (Friedland et al. 2021) as PO_4^{3-} was often the limiting nutrient in the French coastal ecosystems at the beginning of the productive period considering the Redfield ratio as the reference value (Glé et al. 2008, Souchu et al. 2010) as PO_4^{3-} limitation could arise during the spring period during dry years. However, it was hard to disentangle the real impact of this measure from the change in precipitation and associated river discharge that occurred at the same period.

Changes in regional climate and atmospheric circulation had already been raised and suspected to have caused an abrupt change *ca* 2005 in the French coastal ecosystems (Goberville et al. 2010; Lheureux et al, 2021). Our study was framed by the above mentioned early 2000s abrupt changes as it was noticeable in the nutrients and drivers groups mean trajectories between 2005 and 2010. It was also probable that the Atlantic Meridional Overturning Circulation (AMOC) played a role in the regional climate changes. The AMOC was reported to be decreasing with a starting point between 2005 (Chen & Tung 2018) and 2009/2010 (Roberts et al. 2013). A decreasing AMOC leads to a decrease of precipitations and changes in the atmosphere circulation patterns over Europe (Jackson et al. 2015), as seen above. A decreasing AMOC would also alter the heat transfer from the tropical regions to Europe and would result in decreasing temperature as seen from 2000 to *ca* 2010. The increase in temperature from 2010 onwards should also

participate in strengthening water stratification and thus might have reduced the vertical advection of nutrients from deeper waters.

However, quantifying the importance of the AMOC was not the goal of this study but not mentioning a potential role of the AMOC would have been a shortage as it is known that the hydrosphere and the atmosphere are connected.

In theory, following these climatic and anthropogenic changes, nutrients concentrations decrease (or trend inversions) as well as changes in their ratios should arise. This happened in most but not all the studied ecosystems. Such discrepancies highlight the need to focus on the local scale with local climatic variations, land use in the watersheds and ecosystems functioning in multi-ecosystemic studies.

4.2.2. Typology of ecosystem trajectories based on changes in nutrients concentrations and ratios

Ecological trajectories are useful tools to analyse and compare changes between ecosystems (Lamothe et al. 2019). They do not only provide synthetic information regarding changes, e.g., in nutrients concentrations and ratios, but also enables to characterize ecosystem status and to identify its potential changes. Ecosystem state changes could either be inexistent, linear, abrupt and sustained or abrupt and temporary (Ratajczak et al. 2018). Identifying state changes could greatly help to understand the temporal variability and its implications for ecosystems.

614 The Arcachon Bay Group

615 The Arcachon Bay was the only ecosystem where both N- and Si-nutrients concentrations
616 increased during the studied period. The processes involved in these changes are only
617 summarized here as they are deeply described and discussed in Lheureux et al. (2022).
618 The main hypothesis behind the increase in N- and Si-nutrients concentrations is linked
619 to the decrease in the biomass and sediment surface coverage of the seagrass (*Zostera*
620 *noltii*) meadow (Plus et al. 2010). This decrease led to a lowered nutrients consumption
621 by the seagrass as well as, on the other hand, to wobblier sediments, the latter causing an
622 increase in benthic nutrient advection and particulate resuspension. Both processes
623 explained the increase in N- and Si-nutrients concentrations, which led to an increase in
624 phytoplankton biomass (Lheureux et al. 2022). Because of both the difference in nutrients
625 needs between *Zostera* and phytoplankton and the higher need in P relatively to N and Si
626 for the phytoplankton than for *Zostera*, the increase in N- and Si-nutrients concentrations
627 and in phytoplankton biomass induced a decrease in PO_4^{3-} concentrations in this
628 ecosystem where the phytoplankton production is mainly P-limited (Glé et al. 2008).
629 Consequently, the N/P and Si/P ratios increased.

630 Following the classification of Ratajczak et al. (2018), the mean trajectory of the Arcachon
631 Bay group can be considered as a potential sustained change of state: the ecosystem
632 shifted between 2002 and 2013 before stabilising in a rotating movement indicating a
633 relative stability during the last years of the studied period. The *Zostera* meadow decrease
634 is likely responsible for the nutrients changes (Lheureux et al. 2022). Studying the
635 Arcachon Bay using this statistical approach enabled to detect a potential beginning of the
636 abrupt change in 2002. It might have been triggered by the extremely low river discharges
637 in 2002 that could then have induced a disequilibrium in the bay.

638

639 *The group of strong continental influence*

640 All stations of this group, except Frioul (station 29) in the Bay of Marseille, were either in
641 an estuary or close to an estuary within a bay. It is important to note that station Frioul is
642 the station with the lowest affiliation to this group compared to the six others.

643 Frioul is geographically close to the Rhône river (40 km eastward the delta) but is in fact
644 slightly under its influence: 1) the Coriolis acceleration flushes the Rhône plume
645 westward, 2) the intrusion of Rhône water in the Bay of Marseille is scarce (up to 8 times
646 a year and for less than three days each time) and mainly limited to the northern part of
647 the bay while Frioul is located in its southern part and is protected on its west-side by the
648 Frioul island (Frayse et al. 2014). It is more likely that the proximity of the city of
649 Marseille is a factor explaining the presence of station Frioul into this group. The
650 Huveaune river (Marseille's river) is a small stream with low continental inputs but with
651 the greatest urban lands share among the studied watersheds. In addition, some of the
652 Huveaune river waters are derived to an outlet in the south of the city (5km eastward the
653 bay of Marseille) and mixed with effluents from waste-water treatment plants (WWTPs).
654 Although the outlet flow is composed by equal proportions of WWTPs and Huveaune
655 waters, more than 80% of the NH_4^+ , NO_2^- and PO_4^{3-} concentrations come from the urban
656 effluents (Oursel et al. 2013). It was therefore possible that the "estuarine-like"
657 characteristics of the trajectory of station Frioul were due to this outlet influence.

658 The stations of the group of the strong continental influence were the only stations (with
659 the Arcachon Bay stations) where Si(OH)_4 concentrations increased. Si(OH)_4 main origin
660 in the coastal ecosystems is continental, mainly due to rock weathering. Thus Si(OH)_4
661 concentrations should have decreased following the decrease of both global precipitation

and river discharge. The increase in Si(OH)_4 concentrations might have been due to the recovery from eutrophication processes in the rivers, which can induce the release of the retained Si(OH)_4 and consequently can result in the increase in Si(OH)_4 export to the coastal ecosystems (Prins et al. 2012). Similar hypotheses have been pointed out for the Bay of Vilaine (station 17), and for the Bay of Somme (station 9 and 10). Regarding the Bay of Vilaine, PO_4^{3-} and chlorophyll-*a* concentrations decreased in the Loire and Vilaine rivers as well as in the bay, whereas Si(OH)_4 concentrations increased in the bay, in line with internal benthic regeneration (Ratmaya et al. 2019). The eutrophication processes also decreased upstream the Bay of Somme with an increase in Si(OH)_4 concentrations in the inner bay (Lefebvre et al. unpublished). We assume that similar hypotheses also stand for the Gironde estuary.

The mean trajectory of this group enabled to detect a potential abrupt and temporary change of state in 2005. The mean trajectory indicated a shift from the direction towards lower NO_x concentrations and higher Si/P ratio to the direction towards lower PO_4^{3-} concentration and higher Si/P ratio, with an overall net trajectory toward lower ammonium concentrations. The shift is coherent with both the start of the AMOC decrease (see section 4.2.1) and the removal of PO_4^{3-} from public detergents. However, this abrupt change was not obvious in the trajectories of all the stations of this group, probably because of the high diversity of local drivers encountered in the concerned ecosystems.

The group of medium continental influence

All stations of this group belong to four ecosystems located in the northern half of the study area. The nutrient concentrations changes of this group were the closest to the expected changes following the decrease of precipitations, continental discharges and the

implementation of management policies on land. The mean trajectory is linear and seemed to indicate relatively slow changes at the beginning of the study period (small gaps between points). It exhibited an overall change towards a decrease of the N- and Si-nutrients, indicating changes towards mesotrophy, and an increase of Si/N and Si/P ratios. The fact that eight (over nine) stations of the group of medium continental influence belong to drivers group “1” indicates that changes in nutrients concentrations and ratios are clearly in relation to the decrease in precipitations and to changes in wind intensity and directions. The year of inflexion corresponds to the period of change of the AMOC (see section 4.2.1).

Since the trajectory of this group exhibited a “smooth” shape, it could be interesting to have a look at the speed of the changes in order to check if the ecosystems of this group are potentially rather moving away or drawing near a state of “stability”. Stability has lots of different definitions due to its different aspects and thus different index to define it (e.g. resistance, resilience, robustness; Saint-Béat et al. 2015). One way to check this is to study the distance between each observation. If the distance is decreasing, it indicated that the ecosystems might draw near a state of ‘stability’ (Lamothe et al. 2019). The distance between each observation were greater at the beginning of the study and kept decreasing between 2016 and 2019. Although declaring that these ecosystems are approaching a period of higher stability was not possible by lack of time span, it would be interesting to test the hypothesis in the upcoming years.

The group of poor continental influence

The stations of this group belong to four ecosystems distributed along the French coasts. Despite Point C in the Eastern English Channel (station 7; discussed below), the stations

710 of this group are under poor continental influence. Estacade and Astan in the Western
711 English Channel (stations 13 and 14) are subjected to very poor continental influence
712 from the Penzé river, a small stream which nutrients concentrations and discharge data
713 were not available for the studied period. Portzic in the inlet of the Bay of Brest (Station
714 15) is located in a semi-enclosed ecosystem receiving freshwater from the Aulne River
715 and the Elorn River. However, its location in the inlet of a macrotidal bay combined with
716 the fact that the samplings have been performed at high tide, implies that the sampling
717 water mass is mainly influenced by oceanic waters (Le Pape & Menesguen, 1997). This is
718 well illustrated by the averaged salinity index of 0.981, indicating that on average over the
719 study period, the sampled water is composed at 98% of marine water. Sola in the Bay of
720 Banyuls (station 28) is under a very low influence of some Southern France rivers (mean
721 salinity index of 0.98) since it is southward because of the overall water circulation in the
722 continental shelf of the Gulf of Lion. Point C and L, found in the Eastern English Channel
723 (stations 7 and 8), such as stations 4, 5 and 6 but these five stations were segregated into
724 two groups: the groups of poor and medium continental influence, respectively. In
725 contrast to station 8, which showed a mean salinity index of 0.980 characteristic of this
726 group of 'poor continental influence', station 7 in the English Channel exhibited an
727 averaged salinity index of 0.963, which is rather characteristic of the group of 'moderate
728 continental influence'. In fact, this station is located within the 'coastal flow' — a water
729 mass composed by the diluted river plumes of the Seine River, the Somme River and other
730 minor rivers — that is directed eastward along the French coast because of the overall
731 water circulation (Brylinski et al. 1991). Station 7 shared the same characteristics than
732 the other stations of this group (stations 8, 14, 15 and 28), i.e., the only group where the
733 N/P ratio decreased over the study period. Surprisingly, stations 4; 5 and 6 do not belong
734 to the same group as stations 7 and 8. This is probably because the former stations are

under the influence of the Liane River, a small stream (38 km) pouring in the city of Boulogne-Sur-Mer.

The group of poor continental influence was the only group encompassing stations at which the N/P ratio decreased during the study period. This decrease was due to the increase in PO_4^{3-} concentration and/or the decrease in DIN concentration. Interestingly, these stations exhibited, among all other stations, the lowest mean PO_4^{3-} concentrations over the study period (except Frioul). The concerned ecosystems were characterised by low human population density and watershed made of slow-weathering and nutrient-poor bedrock from which low P pattern should result (Farmer et al. 2018).

The mean trajectory of this group displayed overall changes towards decreasing NO_x , NH_4^+ and $\text{Si}(\text{OH})_4$ concentrations and N/P ratio as well as increasing PO_4^{3-} concentrations. The hypotheses explaining these changes in nutrient concentrations and ratios are not straightforward yet. Since these stations are of poor continental influence, possible explanation had to be found among internal processes of the water masses. However, from our data sets, there is no straightforward evidence of specific higher or lower remineralization processes and because changes may be due to other reasons, e.g., changes in phytoplankton community that may have different needs in N/P/Si ratios nowadays compared to the beginning of the study period.

4.3. Conclusion

The nutrients concentrations and their ratios in the studied French coastal ecosystems were influenced both by local and large-scale drivers, as well as by climatic and anthropogenic drivers (e.g., AMOC decrease and its implications on temperature and

atmospheric circulation, as well as the PO_4^{3-} regulation policies). Although it was hard to truly ascertain the role of one specific driver at one given scale because they are all interconnected, it was possible to point out significant cascade effects. Such effects resulted from the non-linear and dynamic characteristics of the drivers (Cloern et al. 2010) and were previously reported in some of our studied ecosystems (i.e., Chaalali et al. 2013). In addition, studying a longer time period (at least 30 years) might have enabled to have better large-scale climate signals and thus to point out better connections between the different spheres. Unfortunately, such long time periods data sets are not yet available for these ecosystems. Interestingly, the data sets showed that the spatial variability of nutrients concentrations and ratios mainly depended on local drivers (local climate and river flow) while their overall bi-decadal variability depends on large-scale drivers (mainly regional climate). Nevertheless, a form of geographical typology of the bi-decadal variability appeared and was linked to local drivers: e.g., the seagrass meadow for the Arcachon Lagoon and the freshwater influence for the other groups of stations. In different words, while large-scale drivers were tangled with local drivers in the definition of the overall nutrients concentrations and ratios changes, it seemed that even under different local characteristics and influences the ecosystems responded in a similar way in function of their continental influence.

The need for multi-scaled data in environmental studies to identify as many patterns as possible is therefore highlighted. However, studying one ecosystem at a time (e.g., Lheureux et al. 2022) remained important as it allowed going deeper into the local processes that were of importance to understand ecosystems functioning.

Nutrients concentrations and ratios are essential drivers of phytoplankton production (and primary production as a whole). Their (pluri-)decadal change should undoubtedly

affect phytoplankton production and probably phytoplankton diversity, and subsequent trophic levels, which have been reported to change at this time scale (David et al. 2012; Hernández-Farinas et al. 2014). Coupling studies of (pluri-)decadal changes of nutrients concentrations and ratios with phytoplankton diversity would allow to have a broader view and understanding of the ecosystem functioning and its changes in the era of global change.

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