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Temporal changes in the phytoplankton community along the French coast of the eastern English Channel and the southern Bight of the North Sea

Hernandez- Farinas Tania [1,] *, Soudant Dominique [1], Barille Laurent [2], Belin Catherine [1], Lefebvre Alain [3], Bacher Cedric [4]

[1] IFREMER, Dyneco VIGIES, F-44311 Nantes 03, France.
[2] Univ Nantes, Fac Sci & Tech, F-44322 Nantes 3, France.
[3] IFREMER, LER, F-62321 Boulogne Sur Mer, France.
[4] IFREMER, Dyneco BENTHOS, F-29280 Plouzane, France.

* Corresponding author : Tania Hernandez-Farinas, email address : tania.hernandez.farinas@ifremer.fr

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Abstract :

Long-term trends in the phytoplankton community along the French coast of the English Channel and southern Bight of the North Sea were studied and related to physico-chemical factors and large-climatic indices. Phytoplankton and hydrological data were acquired through three transects. Sampling took place between 1992 and 2011 as part of the French Phytoplankton Monitoring Network (REPHY) and the Regional Nutrients Monitoring Network (SRN). Trends in time-series were identified with dynamic linear models tailored to environmental monitoring data characteristics (e.g. irregular sampling frequency, missing data). Temporal and spatial patterns in the phytoplankton community were explained with a partial triadic analysis. Relationships between the phytoplankton community composition, environmental factors, and climatic indices were assessed using a redundancy analysis (RDA). The analyses revealed long-term changes in the community composition, characterized by a temporal structure that remained common to all transects. The abundance of some groups of taxa such as the one composed by Gymnodinium and Gyrodinium, as well as the group of Pseudo-nitzschia increased during the study period, whereas the abundance of other taxa as for example Guinardia and the group of Coscinodiscus and Stellarima globally decreased. More generally, the proportion of dinoflagellates relative to diatoms increased. Trends in environmental variables were also observed in most sites and related to decreases in nutrient concentrations and an increasing trend in salinity. The RDA indicated that the Atlantic Multidecadal Oscillation index and salinity were the main factors defining the temporal structure of the phytoplankton community. This suggests that variations observed in the phytoplankton community are linked to hydro-climatic changes in the coastal environment.

Keywords : climatic indicators, dynamic linear model, environmental drivers, multivariate analysis, phytoplankton

1. Introduction

In a context of climate change and concerns about anthropogenic pressures over coastal ecosystems, understanding the response of biological communities has become a necessity. In marine ecosystems, the phytoplankton is at the base of marine foodwebs, and its specific composition determines the pathways and efficiencies of the energy transfer through the upper trophic levels (Cloern and Dufford, 2005; Dickman *et al.*, 2008). The relative species abundance and the community composition contribute to the characterization of phytoplankton assemblage structure. This structure is governed by various environmental factors, allelopathic interactions and grazing, affecting cellular processes, and determining the population growth, community composition, and algal succession (e.g. Tilman *et al.*, 1982; Marshall *et al.*, 2006). These factors lead to recurrent patterns of phytoplankton composition observed at different temporal scales. However, these community properties may vary significantly with climate change and water-quality trends in coastal areas.

Long-term variations in phytoplankton communities have been recently observed and related to hydro-climatic changes, affecting biomass, community composition, and phenology (Edwards and Richardson, 2004; Suikkanen *et al.*, 2007). These modifications in phytoplankton communities are often studied at different taxonomic scales. Thereby, recent works show a modification of the relative proportion between diatoms and dinoflagellates (Klais *et al.*, 2011; Zhai *et al.*, 2013) and significant variations in the biomass of some taxonomic groups such as chrysophytes and chlorophytes (Suikkanen *et* *al*., 2007). Functional approaches have also been used to assess temporal changes in phytoplankton communities related to physical factors and climate (David *et al*., 2012). On the French coast of the eastern English Channel and the southern Bight of the North Sea, some studies highlighted the link between large-scale climatic features, local meteorological and hydrographical conditions, modulating phytoplankton dynamics (Breton *et al*., 2006, Goberville *et al*., 2010). These studies have proved the importance of monitoring networks to assess long temporal changes in phytoplankton communities.

The Phytoplankton Monitoring Network (REPHY) is implemented and managed by the French Research Institute for the Exploitation of the Sea (IFREMER). This program aims to describe spatial and temporal dynamics of phytoplankton populations and to detect and monitor phycotoxin-producing species involved in toxic shellfish outbreaks and affecting human health (Amzil *et al*., 2001; David *et al*., 2012; Gailhard *et al*., 2002). Previous works with these data have greatly improved our knowledge on spatial patterns of microphytoplankton and highlighted the influence of hydrodynamic features in the geographical structure of microalgal populations (David *et al*., 2012, Gailhard *et al*., 2002). Seasonal variability and temporal succession patterns have also been characterized through the analyses of phytoplankton events, defined by the phases of sudden growth, reached maxima and decline of abundance (Beliaeff *et al*., 2001). In addition, Guarini *et al*. (2004) showed the importance of the interaction between benthic and planktonic communities through assessing the contribution of the microphytobenthos to the total phytoplankton abundance. Regarding the eastern English Channel, Lefebvre *et al*. (2011) analyzed the long-term variability of the major phytoplankton groups and gave a first insight of establishing a link between environmental conditions and phytoplankton. However, even though several studies have been conducted on the REPHY data sets, temporal tendencies have been only partially addressed, either for the major phytoplankton components or the specific community composition. At present, data on phytoplankton have been collected over 20 years, and completed by a regional network which targets relations between phytoplankton and nutrients.

Besides these ecological results, it should be noted that the analyses of these time series requires methods able to identify structures in space and time with data that exhibit a very large variability. Several methods have been used with data coming from monitoring programs, specially multivariate and time-series analyses techniques (*e.g.* David *et al*., 2012, Goberville *et al*., 2010, Wasmund *et al*., 2011).

The main objective of this paper is to characterize and quantify long temporal changes in the phytoplankton community structure at three sites in the French coast of the eastern English Channel and the southern Bight of the North Sea, and to explain these changes in relation to physico-chemical factors and large-scale climatic indices. We examine if variations of the phytoplankton community can be observed at different scales, from specific community composition, to groups such as diatoms and dinoflagellates. A statistical framework is developed to deal with common issues in the analysis of long-term monitoring time series and depict the spatial structure of temporal patterns.

Material and Methods

Study area

The study of the phytoplankton community was conducted in three coast-to-offshore transects, along the French coast: Bay of Somme (SOM), Boulogne (BL), and Dunkerque (DK) (Figure 1). Each transect consists of three to four sampling stations. Boulogne and the Bay of Somme are located in the eastern English Channel, and are characterized by a coastal flow system often separated from the open sea by a frontal area (Brylinski *et al*., 1996). The sampling area of Dunkerque, located in the southern Bight of the North Sea, is characterized by shallow and well-mixed waters (Lefebvre *et al.*, 2011). In addition, the sampling zone is influenced by a macrotidal regime and by freshwater inputs coming from the Seine, Somme and other tributaries (such as Canche, Authie and Liane rivers).

Data sets

Data was collected as part of the REPHY and the Regional Nutrients Monitoring Network (SRN). Water samples were acquired from fortnightly to a monthly frequency from 1992 to 2011 between 0 and 1 meter, along with physical measurements and completed with chemical analyses. Finally, the environmental variables included in this study were water temperature (°C), salinity (psu), dissolved inorganic nitrogen ($DIN = NH_4^+ + NO_3^- + NO_2^-$, $\mu mol\ l^{-1}$), silicate ($\mu mol\ l^{-1}$) and phosphates ($\mu mol\ l^{-1}$). For quantitative phytoplankton analyses, samples were fixed with Lugol's solution and counted according to the Utermöhl method (Utermöhl, 1958). Organisms were identified to the lowest possible taxonomic level. Taxa that are difficult to discriminate with optical microscopy were grouped. This was the case of various groups representing a set of multiple species or even genus (*e.g.* *Pseudo-nitzschia* "*seriata* complex", *Gymnodinium-Gyrodinium*). These groups correspond to the taxonomic units extracted from the database. In addition, within sample observation conditions, phytoplankton experts identified and counted organisms whose size is greater than 20 µm but also species whose size is smaller but have a chain structure or form a colony. Smaller species were also counted if they are potentially toxic/noxious (*e.g.* *Chrysochromulina*, *Phaeocystis*). Further details about sampling and processing of phytoplankton and physico-chemical parameters are available in the literature (Aminot and Kérouel, 2004, 2007; Belin and Neaud-Masson, 2012; Grossel, 2006; Lefebvre *et al.*, 2011).

Two large-scale climatic indices were used: the winter North Atlantic Oscillation index (NAO_w, Hurrell, 1995) and the Atlantic Multidecadal Oscillation (AMO, Kerr, 2000). The NAO index can be defined as the difference in atmospheric pressure at sea level between the high pressure centre near the Azores and the low pressure centre near Iceland (Rodwell *et al.*, 1999). This oscillation has been related with factors such as temperature, precipitation, wind, storms and mixed-layer depth (Hurrell and Deser, 2009; Trigo *et al.*, 2002). The winter NAO index (December-March) was used for its more pronounced correlation with temperature, wind and precipitation, and because its influence persists in subsequent months (Ogi *et al.*, 2003; Stenseth *et al.*, 2003). This index was obtained from the website http://climatedataguide.ucar.edu/. The AMO is a pronounced signal of climate variability in the North Atlantic sea surface temperature (Dijkstra *et al.*, 2006). The AMO index was downloaded from http://www.esrl.noaa.gov/psd/data/timeseries/AMO/.

Preliminary processing of phytoplankton data

Despite the use of taxonomic units as described previously, some confusions due to changes in phytoplankton taxonomists or any other expertise variation during the period may arise. These changes may lead to heterogeneous data regarding taxonomic classification and hence to a misinterpretation of phytoplankton time series. To homogenize the data, taxonomic units were grouped into the lowest common taxonomic level. For example, *Coscinodiscus*, *Coscinodiscus radiatus- marginatus*, *Coscinodiscus-Stellarima* are three different labels available in the database and were finally replaced by *Coscinodiscus-Stellarima*. In total, 91 of such taxonomic units were identified over the selected period. Furthermore, discussions with observers and phytoplankton experts were undertaken to ensure the reliability of the analysis performed.

To normalize data and reduce the effect of dominant taxa, abundances were $\log_{10}(x + 1)$-transformed. In addition, a simple phytoplankton community index was defined as the proportion of dinoflagellates relative to diatoms. This proportion was calculated as the abundance of total dinoflagellates divided by the sum of total abundance of diatoms and dinoflagellates.

Data analyses

Univariate and mutlivariate analyses were performed to assess changes in phytoplankton community, taking into account different scales of variability either taxonomic, temporal or spatial. The Figure 2 shows the pathways of statistical analyses applied in this study. All analyses and graphical representations were performed with the R software (R Core Team, 2012).

Univariate analyses of phytoplankton and environmental data

In order to characterize seasonal patterns of the main taxonomic groups, monthly median abundances, less sensitive to extreme values, were calculated over 1992–2011. Bacillariophyceae, Dinoflagellata, and Prymnesiophyceae were previously identified as the most common classes in this zone (Lefebvre *et al.*, 2011).

Dynamic Linear Models (DLM, West and Harrison, 1997) were used to study long-term trends in phytoplankton and environmental variables (Figure 2). DLM were previously used in other studies for analysing phytoplankton time series (Cottingham and Carpenter, 1998; Soudant *et al.*, 1997). They are indeed time series models, *i.e.* they take into account the temporal structure. Moreover, the parameters of the model can evolve with time, hence the "dynamic" designation. This class of models was chosen because they are well tailored to environmental monitoring data characteristics (*e.g.* irregular sampling frequency, missing data, outliers). Furthermore, as for all time series models, exogenous information can be taken into account using an "intervention", that is, modifying some model parameters. This was particularly useful for incorporating information such as changes in measurement methods applied to physico-chemical variables. All these changes in measurement methods were analysed. For example, from 1992 to 2011, two main methods have been used for the measurement of salinity: Knudsen titration and conductivity sensors. In such cases, using the intervention allows to correct the time series and thus, ensures comparability and continuity of measurements through the time series.

To extract trends in time series, a common model structure was used for all variables. The first component is a second order polynomial trend: it remains simple and allows to capture complex evolutions. The second component is a 12-month seasonal factor. This was chosen since sampling frequency was mainly monthly. Furthermore, this temporal unit is fine enough to capture different annual periodic patterns. Finally, when more than one observation was available within the month, the median was used to aggregate the data. Outliers were detected by examination of standardized residuals. Under the assumption of a normal distribution of standardized residuals, it is expected that about 95% of them are within the ± 1.96 interval. Values standing outside this interval were considered as outliers. They were not removed but treated using interventions. Model checking was assessed by residual diagnosis. Serial autocorrelation and normality were tested by plotting the autocorrelation function of the standardized residuals as well as their normal QQ-plot. Deviations from normality were rare. In the case where serial autocorrelation was present, an AR(1) term was added to the model. The results showed that adding this term does not affect trends. Thus, models have been kept in the original structure as described above.

DLM were first used to study long-term trends in diatoms and dinoflagellates functional groups, as well as trends of some taxonomic units, selected through multivariate techniques (explained below). Physico-chemical trends were identified with DLM, and the annual mean trend was used for multivariate analyses. Time series analyses with DLM were conducted with the *dlm* package for R (Petris, 2010).

Multivariate analyses of phytoplankton community composition

For multivariate analyses, the genus was used as the smallest taxonomic level. Aggregating the data at this level allows to capture most of the information considering that little information is lost using the genus level rather than the species one (Cottingham and Carpenter, 1998). In order to focus on the main changes in phytoplankton community, rare taxa were excluded from the analyses, based on the occurrence frequency over 1992–2011. A taxa was discarded when its occurrence frequency was less or equal to three years in all sites. This resulted in a loss of less than one percent of the total abundance for each site, which represents 29 discarded taxonomic units. Sixty-two taxonomic units remained for mutivariate analyses.

Spatial and temporal characteristics of the phytoplankton data led to obtain a three-dimensional table (taxonomic units; sites; years). Partial Triadic Analysis (PTA), used with such multi-table data, was computed to elucidate temporal patterns of the phytoplankton community composition (Figure 2, package *ade4* for R, Dray *et al.*, 2007). This method allows simultaneous principal component analyses of a set of tables by searching for an average temporal structure called compromise, and studying the spatial stability of this structure (Blanc and Beaudou, 1998). In addition to the analysis performed at genus level, the PTA was also carried out at upper levels (*e.g.* family, order, class).

Relationships between phytoplankton, environmental factors and climatic indices

A Redundancy Analysis (RDA) was conducted with data from all sampling stations in order to study the relationships between patterns in the phytoplankton community composition, environmental variables and climatic indices (Figure 2, package *vegan* for R, Oksanen *et al*., 2012). The significance of the analysis and all variables was assessed using permutation tests (499 permutations).

Results

From 1992 to 2011, Bacillariophyceae, Dinoflagellata, and Prymnesiophyceae were the most abundant groups, averaging 81% of the total abundance. Among these groups, diatoms and dinoflagellates represented over 84% of the total diversity. Principal diatom taxa in terms of abundance were the genus *Guinardia*, *Chaetoceros*, *Rhizosolenia*, *Pseudo-nitzschia*, *Paralia*, *Skeletonema* and *Leptocylindrus*. The group *Gymnodinium-Gyrodinium* was the major dinoflagellate present over the period. *Phaeocystis* (Prymnesiophyceae) was a major contributor to the phytoplankton total abundance between March and May. When present, *Phaeocystis* median contribution varies from 74% to 90%, with the highest concentrations generally observed in stations near the coast. The complete list of taxa identified is given in the Supplementary Material (Table S1) with information on the taxonomic groups they belong to, and highlighting those mainly discussed in this study.

Seasonal patterns in phytoplankton and environmental data

Although all sites within a same transect generally present the same patterns, three sampling sites, each one belonging to a different transect were chosen as their results present the most pronounced variations. Consequently, these sampling sites will be used for graphical representations. Among the major phytoplankton groups, *Phaeocystis* (Prymnesiophyceae) showed a clear seasonal pattern, with peaks that appear generally in April (Figure 3). Diatoms were present throughout all the year with highest abundance usually observed between June and July in Boulogne and the Bay of Somme (Figure 3). In contrast, in Dunkerque, diatoms showed high abundances early in the year (March). Seasonal patterns of diatoms, dinoflagellates and Prymnesiophyceae are showed for each sampling station in Figure S1 in the Supplementary Material (SM).

Spring-summer diatoms generally included the genus *Guinardia*, *Chaetoceros*, *Pseudo-nitzschia* and *Rhizosolenia* while *Leptocylindrus* was characteristic in summer. The autumn-winter period was characterized by the presence of the diatom *Skeletonema*, the groups *Thalassionema-Thalassiothrix-Lioloma*, *Thalassiosira-Porosira*, *Coscinodiscus-Stellarima* and the genus *Ditylum*. Others groups present at this period of the year included the small single-cell flagellate *Dictyocha*. Dinoflagellate abundances increased from the beginning of the year peaking between July and September, then decreasing at the end of the year (Figure 3). The dinoflagellates *Gymnodinium-Gyrodinium*, *Protoperidinium-Peridinium*, and *Prorocentrum* are common genera during this period.

Seasonal patterns of environmental variables are illustrated for each sampling station in Figure S2 (SM). Nutrients data reflected typical temperate seasonal patterns, remaining almost similar between sites. DIN, phosphate and silicates reached maxima during the winter and decreased over the spring and early summer to levels close to the detection limits (Figure 4). A further increase in nutrients was observed in the late summer-autumn period. During winter, the Bay of Somme showed the highest concentration of DIN and silicates, with average values between 22.7 μmol l^{-1} and 44.3 μmol l^{-1} for DIN and between 9.1 μmol l^{-1} and 20.7 μmol l^{-1} for silicates. Lower concentrations of DIN and silicates were found at Boulogne with ranges of 11–23.8 μmol l^{-}

^{1} and 5.1–8.7 µmol l^{-1}, respectively. At Dunkerque the concentration of these nutrients varied from 14.5 to 31.5 µmol l^{-1} for DIN and from 7.7 to 12.9 µmol l^{-1} for silicates.

The phosphates concentration varied from 0.73 to 1.1 µmol l^{-1} at Boulogne and reached comparable values at Dunkerque and the Bay of Somme (0.83–1.27 µmol l^{-1} and 0.82–1.76 µmol l^{-1} respectively). Furthermore, a spatial heterogeneity of the nutrient concentrations was observed in "coast-to-offshore" transects, with higher concentrations near the coast. The temperature varied from an average minimum of 5.9°C between January and February to a maximum of 18.9°C between July and August. The salinity varied between 31.6 and 34.4 psu. In addition, the sampling station of Bif was characterized by a lower salinity (minima 9.1 psu), related to a major influence of freshwater inputs from the Somme river.

Long-term trend in diatoms and dinoflagellates groups and environmental data based on univariate analysis

The long-term trends in the diatoms and dinoflagellates abundance are showed in Figure 5. Minor changes in the abundance of diatoms are observed at Dunkerque and in the Bay of Somme while a decrease in the abundance is observed in Boulogne between 1992 and 1997, followed by an increase between 1998 and 2005. The abundance of dinoflagellates between 1992 and 2011 showed more pronounced variations. From 2000 to 2007, the mean level of the dinoflagellates logarithmic abundance increased by 60% (from 2.5 to 4 $\log_{10}$ cells l^{-1}). Spatial differences in the trend of dinoflagellates are observed among transects between 1992 and 2000, but abundance patterns showed minor variations within sampling stations of the same transect. The abundance of dinoflagellates decreased at Dunkerque and Boulogne between 1992 and 2000, while minor changes were observed at the Bay of Somme. The phytoplankton community showed an increasing trend in the proportion of dinoflagellates relative to diatoms, with values generally below 0.1 between 1992 and 2001 and frequently above this value after 2002 (Figure 5). In addition, increases in dinoflagellates abundance were observed throughout all the seasonal cycle after 2001.

Regarding physico-chemical variables, dissolved inorganic nitrogen decreased in Dunkerque from the beginning of the period (Figure 6 a) and after 2000 at Boulogne. The phosphate concentration decreased at Dunkerque and the Bay of Somme at the start of period with a minor increase after 2000s (Figure 6 b). A decrease was observed at Boulogne over the period. No trend was observed for silicates at Dunkerque while it seems to slightly increase at Boulogne after 2000s (Figure 6 c). At the Bay of Somme, DIN and silicates seem to vary cyclically, with periods of higher concentrations (1994–1995, 2000–2001) followed by years with lower concentrations (1996–1998, after 2002). Time series of salinity at Boulogne and the Bay of Somme showed large increases during the period (Figure 6 d).

Long-term changes in the phytoplankton community based on multivariate analysis

As suggested by the PTA results, the community structure changed between 1992 and 2011 (Figure 7). The first two axes account for 58.7% of the total variability. PTA objects, corresponding to (site;year) pairs, were projected on the first and second axis of the compromise (Figure 7 a). Each dotted line represents a given sampling station. The first axis globally distinguishes two periods: 1992−2001 and 2002−2011. In the latter period, the second axis splits the period into two groups: 2002−2007 and 2008−2011. This temporal trajectory was generally seen at all the sampling stations. Such result highlights a temporal structure of the phytoplankton community composition and a trend in taxa abundances that change largely during the sampling period while remaining almost constant in space. Among diatoms, *Melosira*, and *Stephanopyxis* were usually common in early years but rarely observed after 2002. Other taxa such as the dinoflagellates *Amphidinium*, *Alexandrium*, and *Polykrikos* were characteristic after 2002 (Figure 7 b). Finally, *Heterocapsa* (dinoflagellate), *Torodinium* (dinoflagellate), and *Eutreptiella* (euglenid) were mostly common over the third period.

Changes in the abundance of some taxonomic units were observed over the period (Figure 8 and Figure S3 in SM). The diatom *Guinardia* generally decreased at the Bay of Somme and Dunkerque while no pronounced variation was detected at Boulogne. Other taxa, mainly diatoms, showed a decline in their abundances (*e.g. Coscinodiscus-Stellarima*, *Eucampia-Climacodium*, *Ceratulina*) while the abundance of *Pseudo-nitzschia* increased during the period of study. Among dinoflagellates, the group of *Gymnodinium-Gyrodinium* showed a strong increase in abundance, which has more than doubled (in logarithmic scale) between 2002 and 2007. *Phaeocystis* showed no trend in the Bay of Somme, while a minor increase was observed at Dunkerque and Boulogne.

The analyses of taxonomic groups from family to class indicate a similar temporal structure. Nevertheless, with the increase in the level of aggregation, presence/absence patterns of specific taxonomic units are more difficult to detect while changes in abundances tend to become more apparent.

Relationships between phytoplankton community, environmental factors and climatic indices

The redundancy analysis accounted for 21.8% of the total variance of the data (all canonical axes). Of this, 68.8% was explained by the first two axes. These canonical axes and the seven variables were significant ($p < 0.01$). On the first axis, the AMO index, salinity, NAO_w index, and temperature were the main explanatory variables (Figure 9 a). The first axis describes a temporal structure, with two different periods, before and after

2001 (Figure 9 a, c). The second axis is mainly defined by silicates, dissolved inorganic nitrogen, but also salinity (Figure 9 a). It shows a spatial pattern between transects. Sampling stations in the Bay of Somme are characterized by high concentrations of silicates and dissolved inorganic nitrogen, and a low salinity (Figure 9 a). Temporal patterns were observed in transects of Dunkerque and Boulogne in relation to a decreasing trend in nutrients concentrations (mainly dissolved inorganic nitrogen) over 1992–2011 (Axis 2–RDA, Figure 9 a).

The distribution of phytoplankton taxonomic units along the first gradient was positively related to the salinity, AMO index and temperature, and negatively to the NAO_w index and phosphates concentration. The AMO index, salinity and temperature vectors pointed to the second period (after 2001) when dinoflagellates increased (Figure 9 a, b). Diatoms were mostly grouped in the lower-left quadrant and thus positively linked to silicates, DIN and NAO_w index. However, some diatoms such as *Pseudo-nitzschia* showed their highest abundance during the second period (positive score on the first axis), suggesting that these diatoms were favoured under an increased salinity and positively associated with the AMO index and temperature. Other genera show low scores in both axes, thus suggest its presence along all transects and over mostly the whole period of study (*e.g. Rhizosolenia*, *Skeletonema*).

Discussion

Patterns of phytoplankton community changes

During the past 20 years, the structure of the phytoplankton community of the eastern English Channel and the southern Bight of the North Sea was subject to changes. We observed an increasing trend of dinoflagellates during the last decade while minor changes were observed for diatoms between 1992 and 2011. The PTA allowed us to understand these changes at a finer taxonomic scale. Some diatoms taxa globally showed a declining trend in their abundances (*e.g. Guinardia*, *Coscinodiscus-Stellarima*). In contrast, the abundance of *Pseudo-nitzschia* appears to increase over the 20 years of study. Diatoms like *Melosira* and *Stephanopyxis* were mainly found before 2001. Some dinoflagellates such as *Gymnodinium-Gyrodinium* showed a strong increasing trend in their abundances after 2001. Other genera such as *Alexandrium*, *Amphidinium* and *Polykrikos* were mostly found in the last decade (2002–2011).

In our study, the PTA enabled to describe temporal patterns and also facilitated comparisons between multiple sampling stations, determining if the long-term trend is spatially constant. This analysis was previously used to study the temporal and spatial structures of phytoplankton communities (David *et al.*, 2012). Globally, three periods were identified (1992–2001, 2002–2007 and 2008–2011), and such temporal pattern is globally exhibited by all transects. In combination with RDA to further assess relationships between phytoplankton communities, physical-chemical variables and climatic indices, we found a clear separation between the periods before and after 2001, and some of the observed trends in the phytoplankton community could be related with physico-chemical variations and climatic indices. The time at which the changes in the phytoplankton community structure occurred is consistent with a shift observed in the French coastal system after 2001, manifested through an increasing salinity and decreasing nutrients, impacting chlorophyll *a* concentrations (Goberville *et al.*, 2010). Similar temporal patterns were observed in the functional and specific diversity along the French Atlantic coast, although spatial patterns were most apparent, mainly related to a latitudinal gradient and hydrodynamic characteristics (David *et al.*, 2012). Moreover, during the last decades, major modifications in the phytoplankton composition, leading to an increasing importance of some groups such as dinoflagellates, have been documented in the central North Atlantic Ocean, North Sea and Baltic Sea (Klais *et al.*, 2011; Leterme *et al*., 2005; Zhai *et al.*, 2013). The rather low percentage of the variance explained by the RDA in this study has also been observed in previous analyses of phytoplankton data (Suikkanen *et al.*, 2007, Wasmund *et al*., 2011). This has been related to environmental factors usually not considered in the analyses, but having influence in phytoplankton populations, such as allelopathic interactions, interspecific competition and grazing.

It should be noted, however, that changes in staff involved in the identification of microalgal species, or any other expertise variation, may lead to a misinterpretation of phytoplankton time series. These issues have been already questioned, especially with long term phytoplankton data sets (Wasmund and Uhlig, 2003; Wiltshire and Dürselen, 2004). Obviously, with more than 20 years of REPHY monitoring network along the French coast, such changes did occur. To deal with these biases, other studies have suggested a regrouping of taxonomic units (Gailhard *et al.*, 2002, Guarini *et al*., 2004). In our study, clustering taxonomic units has been carried out with morphologically close taxa. Furthermore, discussions with observers directly involved in the identification and counting, as well as phytoplankton experts, suggest that our trends are reliable. In addition, the results of PTA performed with different taxonomic grouping, from family to class, show a similar temporal structure, which supports our interpretation.

Previous studies have highlighted temporal changes in the phytoplankton community structure at different scales. In the English Channel, Widdicombe *et al.* (2010) identified major changes in the community such as the decrease of the average abundance of diatoms and the increase of some dinoflagellates abundance. For the study area, changes have also been observed in chlorophyll *a* concentrations, used as an indicator of phytoplankton biomass trends (Goberville *et al.*, 2010; Lefebvre *et al.*, 2011). Other approaches can also be suitable with available species data sets. Modifications in the ecological niche of species have been detected using long-term species data (Gebühr *et al.*, 2009; Grüner *et al.*, 2011). Moreover, a functional approach can be particularly relevant to understand prey-predator processes and assess factors driving the structure of phytoplankton communities (David *et al.*, 2012).

Links between phytoplankton changes and environmental variables

Several dinoflagellates genera have shown an increasing trend over the period and such trend seems to be linked to AMO index, salinity and water temperature. In our study, the AMO index was one of the principal factors defining the temporal structure observed in the phytoplankton community, suggesting a possible link between large-scale climate variability and phytoplankton. Similar temporal patterns were globally observed in all transects, suggesting that the climate forcing may be stronger than local prevailing conditions. The link between phytoplankton community structure and climate forcing has been previously discussed in literature (Breton *et al.*, 2006; Irigoien *et al.*, 2000; Leterme *et al.*, 2005). The AMO index reflects changes in the sea surface temperature, a main factor governing the changes in the coastal environment (Beaugrand, 2009) and may favour dinoflagellates growth. Although the AMO seems to be more related with the phytoplankton community structure, the NAO index was also positively associated with some diatoms and negatively related to dinoflagellates, a relation previously observed in the North Atlantic Ocean and the English Channel (*e.g.* Irigoien *et al.*, 2000; Zhai *et al.*, 2013).

Regional climate conditions modify coastal environment, influencing physico-chemical parameters (Goberville *et al.*, 2010). Along the French coast of the English Channel, observed changes in environmental conditions, such as salinity increases and decreasing nutrient concentrations were related with the sea surface temperature increase, reduced rainfall and intensity of zonal winds (Goberville *et al.*, 2010). Oceanic-atmospheric drivers such as AMO and NAO are likely to impact precipitation patterns and may affect the river run-off as well as inputs on terrestrial-derived nutrients, salinity and turbidity (*e.g.* Enfield *et al.*, 2001; Harley *et al.*, 2006, Trigo *et al.*, 2004). In a study of the three main Iberian river basins, Trigo *et al.*, (2004) have shown an influence of the NAO on precipitation patterns and river flow, but also highlighted the irregularity and the high inter-decadal variability of this impact. The river flow patterns may also reflect human impacts such as damming and channels. Concerning the Somme river, we found a weak correlation between the NAO and the river flow (Pearson correlation coefficient r = 0.15, $p < 0.02$) although some influence can be observed. These results may suggest more local influencing conditions over the river flow. When analysing the influence of the Somme river flow on the nutrient concentrations and salinity trends in the Bay of Somme, we generally observed a significant ($p < 0.05$) and a high correlation coefficient (highest values $r_{DIN} = 0.89$, $r_{SIOH} = 0.77$, $r_{SALI} = -0.52$, r_{PO4} not significant). Both, NAO and river flow seem to modulate separately the Bay of Somme hydrologic conditions. In addition, the frequency of important flow events in the Somme river seems to decrease after 2004. In 2001, the maxima river flow was about 96 $m^3 s^{-1}$, while from 2004 to 2011, the maxima river flows ranges between 30 and 49 $m^3 s^{-1}$ (Data: Artois–Picardie Water Agency).

Generally, our results suggest an increasing trend in salinity and a decreasing trend in dissolved inorganic nitrogen and phosphates, while a certain variability in trends between sampling sites has to be noted. At Dunkerque, DIN concentrations decreased throughout the study period and during the 2000's in Boulogne. In the Bay of Somme, a period of low concentrations was observed from 2002. Our analysis suggests a decreasing trend in phosphates in Boulogne over the whole period while at Dunkerque and the Bay of

Somme it decreases at the start of 1990's with minor increases in 2000's. The decreasing trend in phosphates has been already highlighted in SRN data series and attributed to a result of phosphates-reduction practice since 1970s (Lefebvre *et al.*, 2011). Similar results were observed by Romero *et al.* (2013) while assessing nutrients export for a large number of rivers in south-western Europe (including France). The authors highlighted a general decrease in phosphorus, a general decrease in phytoplankton biomass during summer, as well as an increase in the summer abundance of dinoflagellates over the past 20 years. It is well-known that the nutrient availability is a major factor for algal growth (Tilman *et al.*, 1982). In general, diatoms dominate under high-nutrient and turbulent conditions whereas dinoflagellates prevail under periods of stratified conditions and low nutrient concentrations (Margalef, 1978). Under low-nutrient conditions, the use of mixotrophy in algal flagellates may represent an advantage, making the growth not strictly dependent on the inorganic nutrients supply (Cloern and Dufford, 2005; Smayda, 2002). Considering the heterogeneity of phytoplankton taxonomic classification levels in the REPHY database, we were not able to associate species, mainly dinoflagellates, to mixotrophic and heterotrophic functional groups. However, potential groups where mixotrophic species are present, like *Gymnodinium-Gyrodinium*, showed an increasing trend in abundance.

Phytoplankton changes are usually not disconnected from other ecosystem changes and interactions between ecosystem components may amplify or attenuate changes at the ecosystem level. Multiple studies have recently highlighted the response of marine ecosystems to climate change (*e.g.* Beaugrand, 2009; Harley *et al*., 2006; Hays *et al*., 2005). These changes can be observed at several levels of the ecosystem such as primary producers, zooplankton and fish communities (Beaugrand, 2004; Beaugrand, 2009; Hawkins *et al*., 2003). Thus, they may alter community properties like diversity, dominance, community composition and lead to modifications in the marine ecosystems functioning (Beaugrand, 2004; Wernberg *et al*., 2011). However, the lack of long-term data on other biological components makes difficult to separate ecosystem responses to changes. There is a growing interest in analysing phytoplankton data sets in coastal areas, establishing trends for phytoplankton as well as for associated variables such as inorganic nutrients. These constitute the activities being addressed by the ICES Working Group on Phytoplankton and Microbial Ecology (WGPME, Li *et al*., 2011).

Conclusion and future works

The analysis of the phytoplankton time series allowed the identification of important temporal changes in the phytoplankton community structure between 1992 and 2011 along the French coast of the eastern English Channel and the southern Bight of the North Sea. We found some evidence of changes in the community composition as well as significant long-term trends in the abundance of some taxonomic units that seem to reflect climate-driven changes in the coastal environment. Since phytoplankton plays a key role in the pathways and efficiency of energy transfer through the upper trophic levels and participates in the nutrients cycles, the observed long-term changes in the phytoplankton community structure may have important ecological consequences (*e.g.* Edwards and Richardson, 2004; Hays *et al*., 2005). However, further studies are necessary to assess the modifications of the phytoplankton community and the factors forcing these changes. In particular, the causal relationships between climate and environmental drivers on one hand, and phytoplankton communities and species phenology on the other hand, need to be described to assess whether changes correspond to a major shift in the ecosystem structure and functioning. Future works will therefore follow two lines of research: 1) apply the same statistical framework to other REPHY monitoring sites, test for similar occurrences of changes and relate changes to environmental drivers, 2) determine the ecological niche of the most significant species and assess whether and how the phytoplankton phenology responds to environmental changes.

Supplementary material

The following supplementary material is available at ICESJMS online version of the manuscript:

Table S1 A list with assigned codes and taxonomic groups of phytoplankton taxa identified.

Figure S1 Seasonal patterns of the three main phytoplankton groups at ten stations along the French Coast of the English Channel and the southern Bight of the North Sea between 1992 and 2011.

Figure S2 Seasonal patterns of environmental variables at ten stations along the French Coast of the English Channel and the southern Bight of the North Sea between 1992 and 2011.

Figure S3 Long-term trends in the abundance of six taxonomic units over the sampling period at Dunkerque, Boulogne and the Bay of Somme.

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Figures

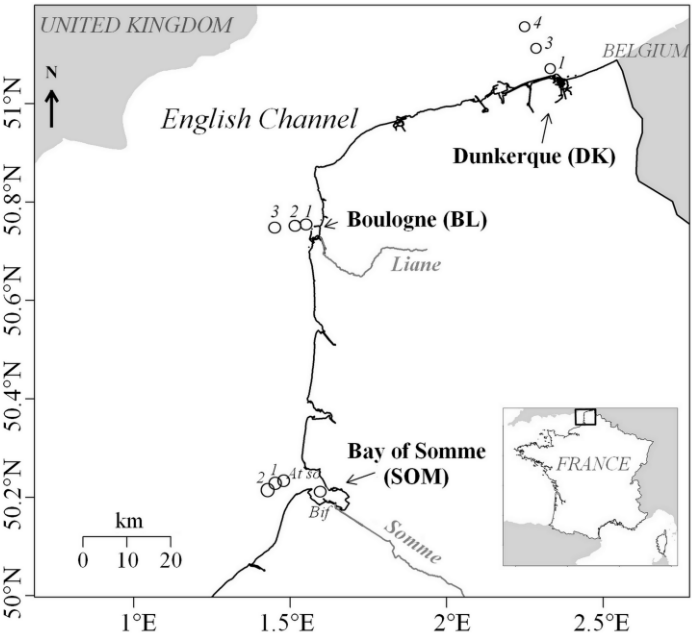

Figure 1. Location of the phytoplankton sampling stations in the Bay of Somme and Boulogne transects (English Channel) and Dunkerque transect (southern Bight of the North Sea).

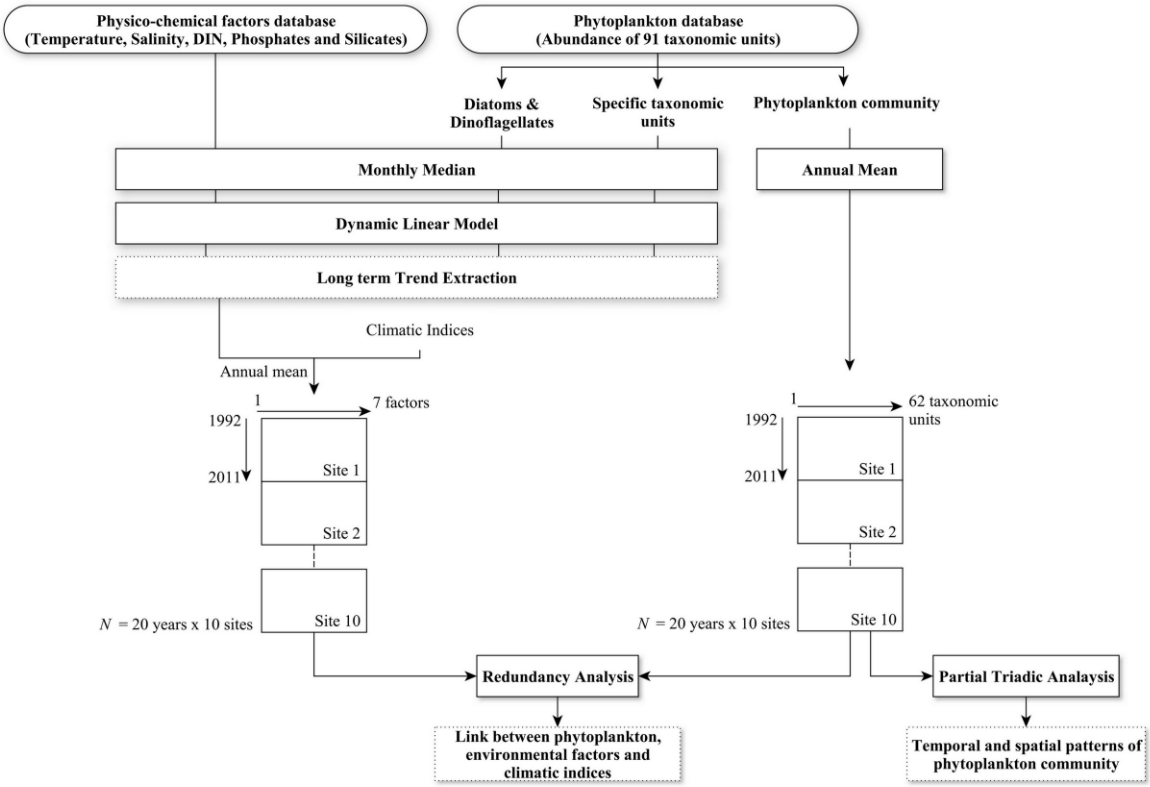

Figure 2. Pathways of statistical analyses followed in this study.

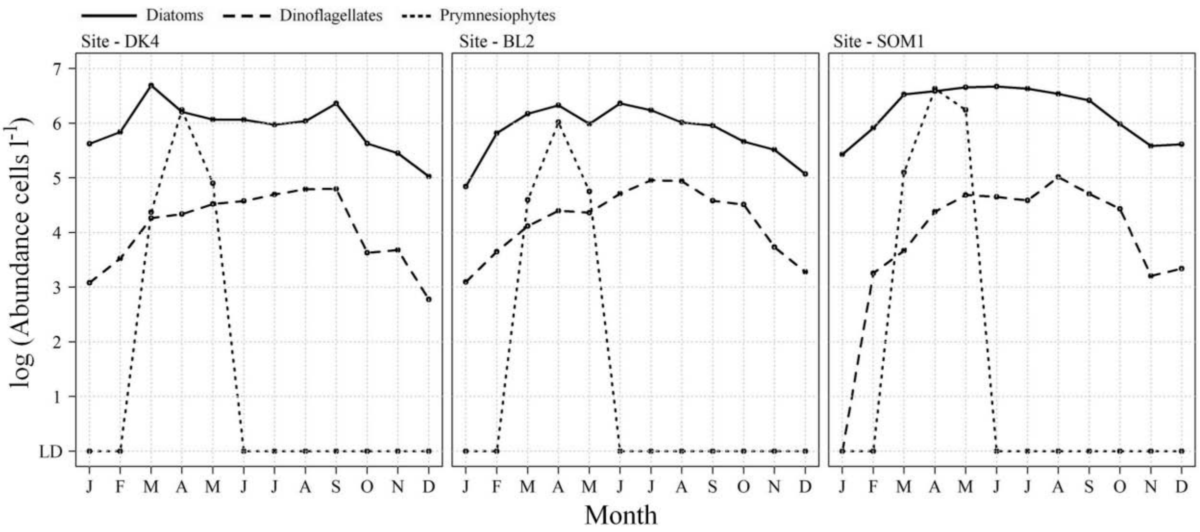

Figure 3. Median monthly abundance of the main phytoplankton taxonomic groups in the three transects between 1992 and 2011. *LD (detection limit).*

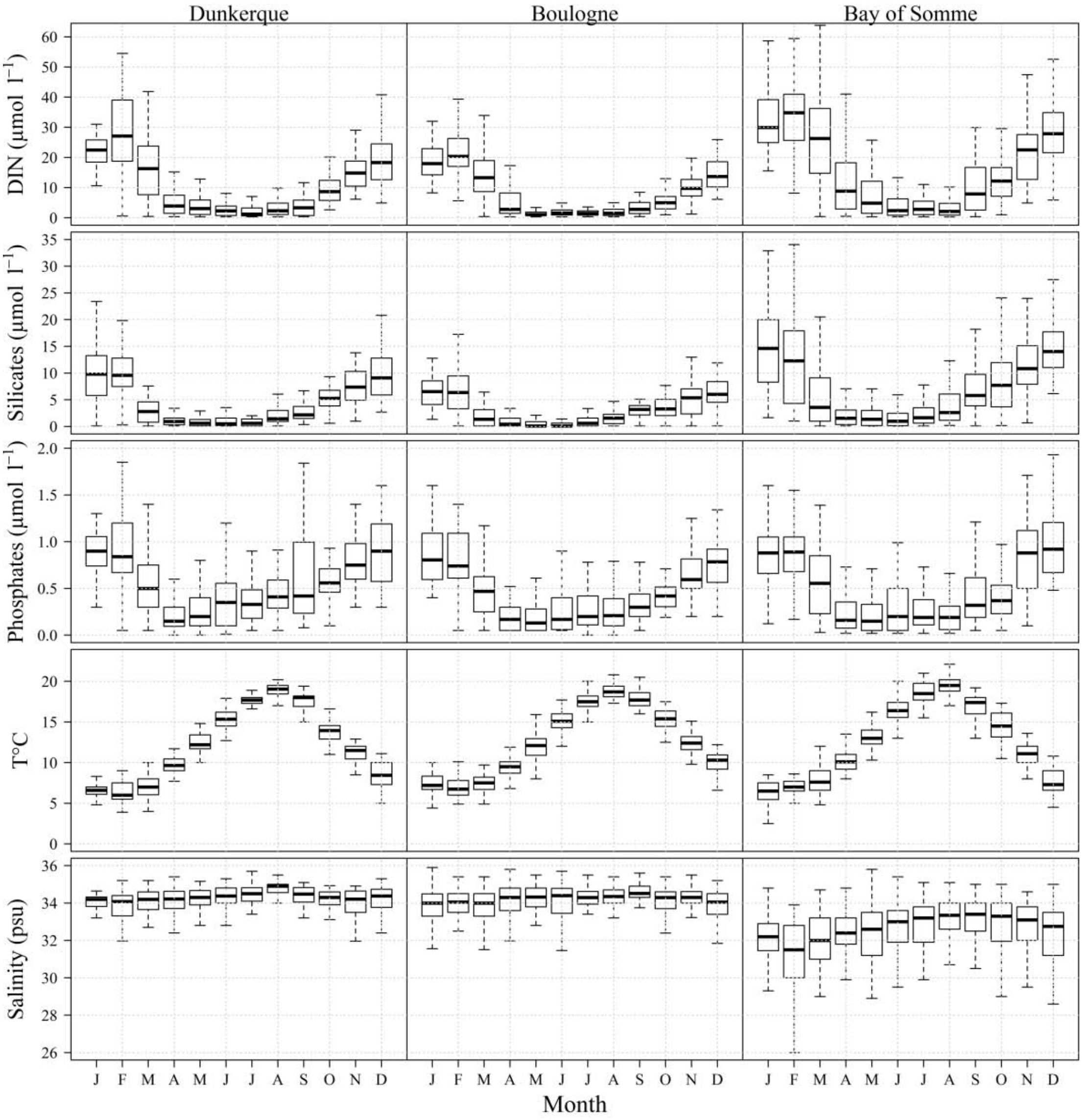

Figure 4. Box-and-whisker plot of the annual variation of physico-chemical measurements between 1992 and 2011 at Dunkerque, Boulogne and the Bay of Somme. Horizontal line denotes the median value for each month, box represents first and third quartiles and whisker represents last value within 1.5 times the interquartile distance.

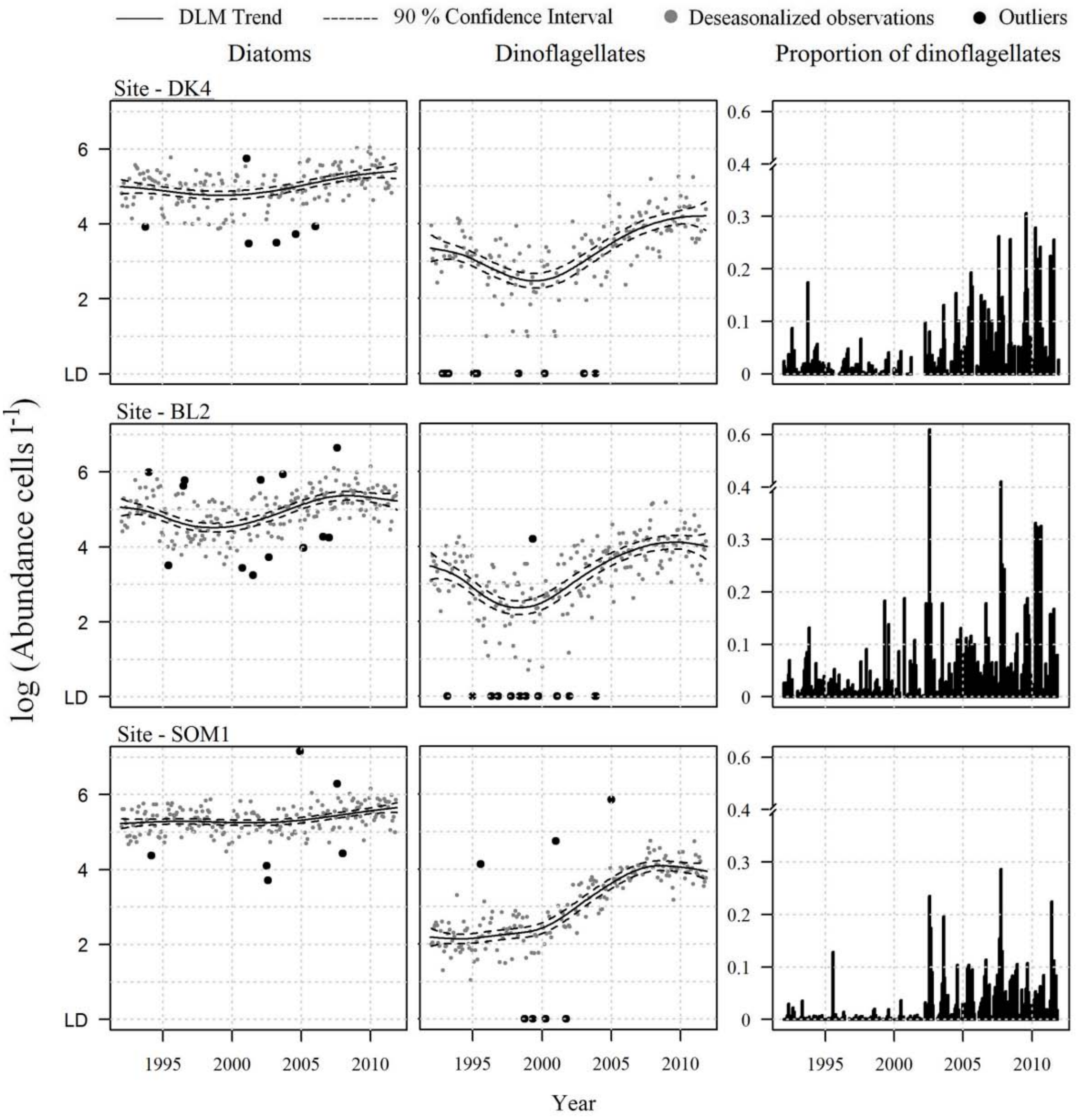

Figure 5. Long-term trends of diatoms (first column) and dinoflagellates (second column) abundances, and proportion of dinoflagellates relative to diatoms (third column) between 1992 and 2011 in three sampling sites. Solid black lines and dotted lines represent trends and 90% confidence interval respectively, as predicted by the Dynamic Linear Model. Gray and dark dots correspond to deseasonalized observations and outliers respectively. *LD (detection limit).*

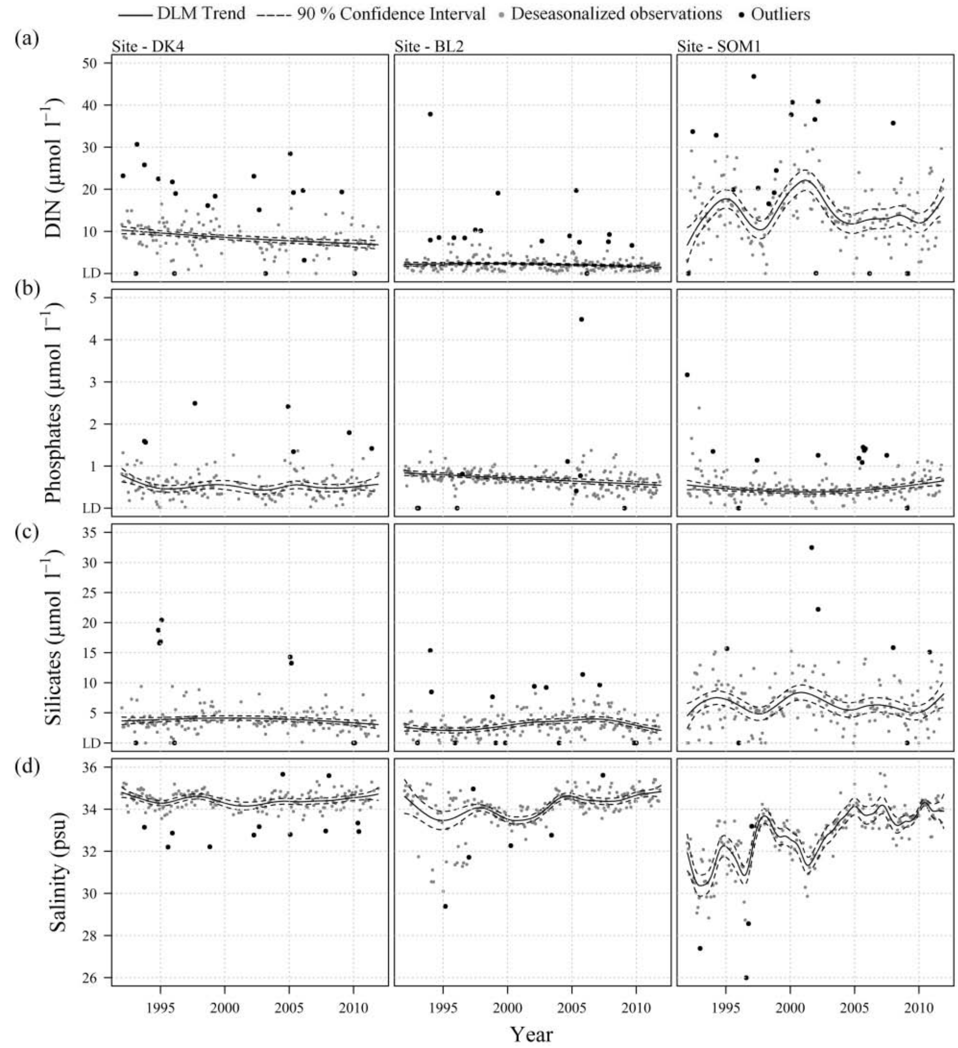

Figure 6. Long-term trends of (a) DIN, (b) phosphates, (c) silicates concentration and (d) salinity between 1992 and 2011 at Dunkerque (Site DK4), Boulogne (Site BL2) and Bay of Somme (SOM1). Solid black lines and dotted lines represent trends and 90% confidence interval respectively, as predicted by the Dynamic Linear Model. Gray and dark dots correspond to deseasonalized observations and outliers respectively**.** *LD (detection limit).*

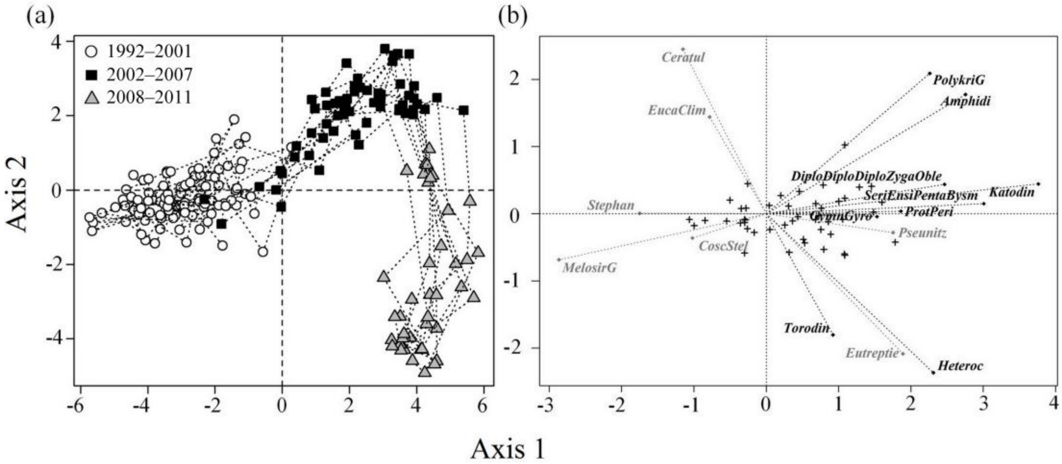

Figure 7. Partial triadic analysis results conducted on the phytoplankton community data from ten sampling stations with the periods 1992–2001, 2002–2007 and 2008–2011. (a) First and second axis for (site; year) objects. Each dotted line represents a given sampling station. (b) First and second axis for taxonomic units. For readability, only taxonomic units with large coordinates in the first and second axis were represented, the other taxa were represented with black crosses. The plot displays 43.3% and 15.4% of the variance in the first and second axis respectively. For details in codes and taxonomic groups of phytoplankton units, see Table S1 in SM.

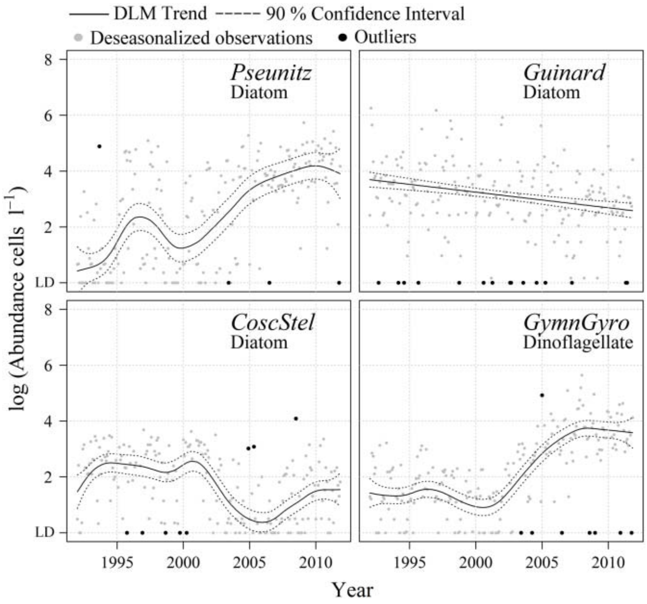

Figure 8. Long term trend in the abundance of four selected taxonomic units over the sampling period at the Bay of Somme, the transect showing the most pronounced variations. Solid black lines and dotted lines represent trends and 90% confidence interval respectively, as predicted by the Dynamic Linear Model. Gray and dark dots correspond to deseasonalized observations and outliers respectively. *LD (detection limit). CoscStel Coscinodiscus-Stellarima, Guinard Guinardia, GymnGyro Gymnodinium-Gyrodinium, Pseunitz Pseudo-nitzschia.*

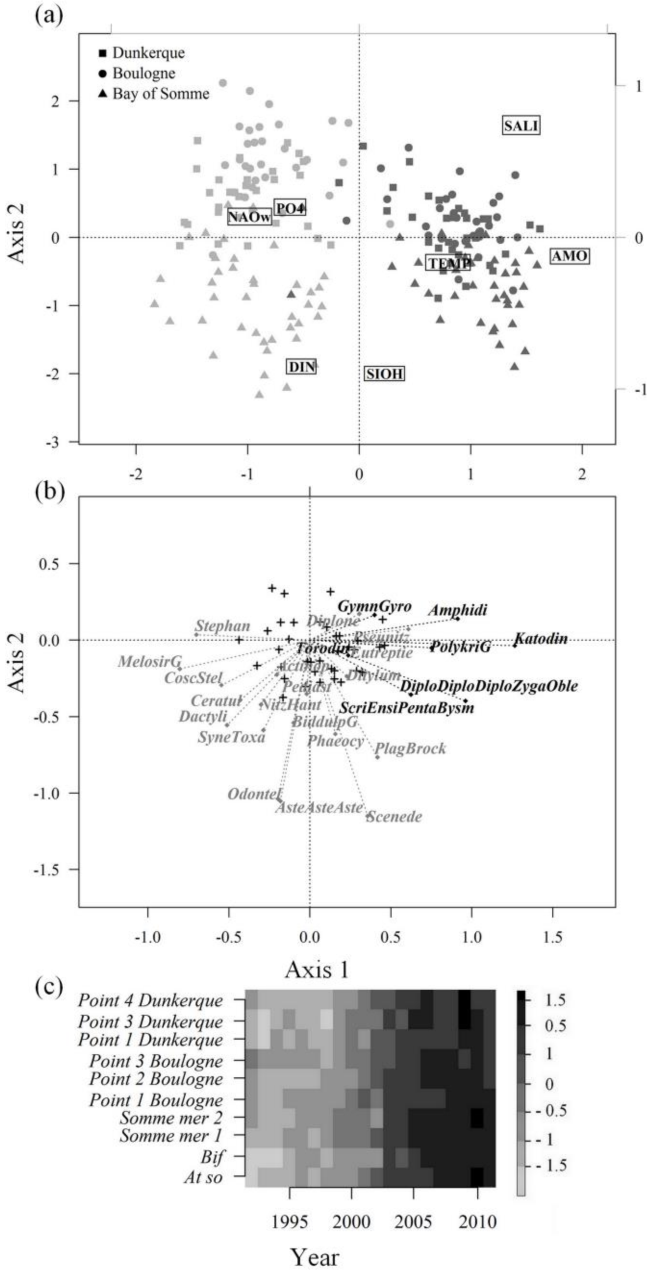

Figure 9. Redundancy analysis of phytoplankton units between 1992 and 2011. (a) RDA biplot (site; year) score (filled symbols), and environmental variables (box). The bottom-left scale corresponds to site-year objects and top-right scales to environmental variables, respectively. Colours on filled symbols represent periods (light gray symbols for years before 2001, dark gray symbols after 2001. (b) Details for phytoplankton genera (black labels for dinoflagellates, gray labels for other taxa), genera which percentage of variance explained in RDA is lower than 20% are indicated by black crosses. (c) Sites-temporal trajectories represented for the first axis. Abbreviations of environmental variables: DIN

(dissolved inorganic nitrogen), SIOH (silicate), PO4 (phosphates), TEMP (temperature), SALI (salinity), NAO_w (winter North Atlantic Oscillation index), AMO (Atlantic Multidecadal Oscillation index). For details in codes and taxonomic groups of phytoplankton units, see Table S1 in SM.