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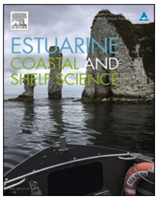

Decadal trajectories of phytoplankton communities in contrasted estuarine systems in an epicontinental sea

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ABSTRACT

In coastal areas, global changes are known to affect estuaries and their plume leading to water temperature increase and river discharge variations, which are two of the main drivers controlling phytoplankton dynamics. This paper aims at understanding the past 10 years' variations in term of communities' stability and trajectories along with their relationship with the environment. Considering the high environmental variability along coastal areas, we focused our study on six contrasted estuarine systems from the eastern English Channel. Using monthly monitoring from 2008 to 2019, the response of the micro-phytoplankton compartment was investigated through the abundances of a hundred taxa and several abiotic parameters' records. The results indicate an overall stability in community composition with an average of 30–40% similarity between pairs of samples over the study period. The phytoplankton assemblages also display greater spatial heterogeneity during summer in comparison with other seasons. The co-inertia analysis highlighted four separate systems linked to major drivers; a system under strong river and nutrient flows influence, a well-mixed and oxygenized estuary, a system challenged by offshore marine waters, and finally a system under shellfish farms pressure. This structuration is built from the dominance of a handful of species that differs from one place to another, which explains why phytoplankton is mostly site specific. Additionally, the low variations led a by few species' dominance also explains the inter-annual stability noticed during summer at each area, in spite of the high diversity observed.

1. Introduction

Phytoplankton, as primary producers, are at the base of the marine trophic network and heterotrophic biomass in coastal ecosystems. Understanding phytoplankton dynamics is crucial for explaining variations encountered at higher levels, and eventually leading to changes on an ecosystemic scale (Sumaila et al., 2011). However, there is a high diversity within the phytoplankton compartment, with thousands of species within the world's oceans (Dutkiewicz et al., 2020; Sournia et al., 1991; Tett and Barton, 1995). Physico-chemical environment and biotic pressures (grazers and parasites) are frequently highlighted as major drivers for these communities (Litchman et al., 2010). At the interface between the river's mouth and the sea, estuarine systems are particularly affected by parameters variability and seasonal patterns. River inputs as well as weather events (rainfall, upwelling, heatwaves and turbulences) trigger saline or thermal stratifications of the water column and affect the assemblage of the phytoplankton communities (Cloern and Jassby, 2008; Mallin et al., 1993). These factors vary through temporal and spatial scales, thus defining the seasonal patterns of phytoplankton structure from one ecosystem to another. Therefore, the primary producers' community assemblage, being dependant of long and short-term physical and chemical factors, is also the reflection of the ecosystem's dynamic.

Chlorophyll *a* (Chl-*a* - phytoplankton biomass indicator) in estuarine-coastal ecosystems are mainly due to micro-phytoplankton (cell size > 20 μm) (Carstensen et al., 2015; Wollschläger et al., 2015). Pattern variations within this compartment, such as the decrease of diatoms and the increase of dinoflagellates, have been recorded over

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the last 40 years with climate oscillations on a global scale (Xiao et al., 2018; Wasmund et al., 2011; Bode et al., 2009; Leterme et al., 2005). Moreover, changes in species seasonal assemblage with a higher homogeneity or even the increase of harmful algal blooms (HABs), have been documented for the past few decades in the North Sea (Nohe et al., 2020). The ongoing climate change is an environmental pressure playing a substantial role in the ecosystem's functioning and could lead to triggering changes within the primary producers. However, climate change can also induce mismatches between primary producers and consumers when differentially impacted (Hallegraeff, 2010). With eutrophication, primary producers may increase in numbers, the degradation that follows of such amounts of organic matter then causes low oxygen levels and water quality deterioration (Rabalais et al., 2014; Kimor, 1992). The combination of both global changes and eutrophication will likely intensify these symptoms (Rabalais et al., 2009). Indeed, with projections of rising temperatures, phytoplankton would be more efficient in nutrient use, causing mismatches with the upper trophic levels, which would alter the ecosystem's functioning (De Senerpont Domis et al., 2014).

Identifying temporal changes within the phytoplankton community's structure is made possible thanks to the study of time-series, which is also a mean to retrace and identify events like harmful algal blooms occurrences (Hernandez-Farinas et al., 2013; Wasmund et al., 2011). Long-term series at Helgoland Roads highlighted both a zooplankton species-specific response to an increasing temperature, as well as a close relation between these populations and phytoplankton cycling (Greve et al., 2004; Radach et al., 1990). This relation coupled with light penetration was seen as a major controlling factor of phytoplankton communities (Wiltshire et al., 2015). However, after a 30-year long time series study, Wiltshire et al. (2008) could not conclude any changes in spring bloom dynamics, or in their timing. This would indicate a persistent resiliency of the phytoplankton community over time. Amongst other analyses, namely on spring blooms and recurrent community structures, a 12-month periodicity was revealed through Chl-*a* monthly time series from temperate and sub-tropical zones, explaining most of the variance encountered between 1967 and 1979 (Winder and Cloern, 2010). However, more recent results within the English Channel, including satellite and in situ data, demonstrate a decline in Chl-*a* concentration over 1998 and 2017 (Gohin et al., 2019).

This study's objective is to target contrasted coastal ecosystems in order to cover a range of estuaries, within an epicontinental sea in a temperate area (Fig. 1). There are two separate areas along the French coast of the Channel. The western basin is mostly affected by oceanic and megatidal hydrologic features from the Atlantic Ocean (Dauvin, 2012; Gohin et al., 2019; Liénart et al., 2017). The eastern basin is mainly affected by the Seine Estuary with macrotidal environment and a coastal hydrodynamic system that drifts from the Seine estuary to the Northern parts of the Somme Estuary (Brunet et al., 1996; Brylinski et al., 1991). Such spatial diversity enquires about the relationship between an estuary and its local micro-phytoplankton community composition over time. Therefore, the aim of this study is to look at the decadal stability and reconstruct seasonal trajectories of phytoplankton communities in contrasted coastal areas. Moreover, it should highlights how the known different ecosystem's dynamics affect the community composition. Indeed, we could expect a binary differentiation between systems dominated by high fluvial influence and more marine systems with a tidal influence.

2. Material & methods

2.1. Study area

The study was conducted in the Eastern Channel, on France's coast, at the western Europe. Three coastal points located within the Bay of Seine (ANT – CAB – GEF), one point northward (ATSO), and two points in the Normanno-Breton Gulf (DONV – STCA) were selected (Fig. 1). The sites could be dissociated into two categories; ANT, CAB, GEF and ATSO that have high estuarine influence, mainly from the Seine river; whereas DONV and STCA are under marine influence. In addition, ANT is located southward of an artificial seawall, and within a restricted area where fuel cargo are unloaded. Finally, GEF is located in the small Bay of Veys, known for hosting several oyster farms.

2.2. Datasets compilations

Most of the data collected are from the French Research Institute for Marine Exploitation's (IFREMER) REPHY (Monitoring network for phytoplankton and phycotoxins), RHLN (Hydrologic Network for the Normandy Littoral) and SRN (Regional Nutrient Monitoring) programs. The flora dataset gathers information on phytoplankton abundance and diversity on the sub-surface level at a bi-monthly or monthly resolution for the time period of 2008–2019 (Neaud-Masson, 2016). The abiotic dataset either is from field sampling, or has been extracted from local weather networks (Météo France, Hydrological bank) on a daily

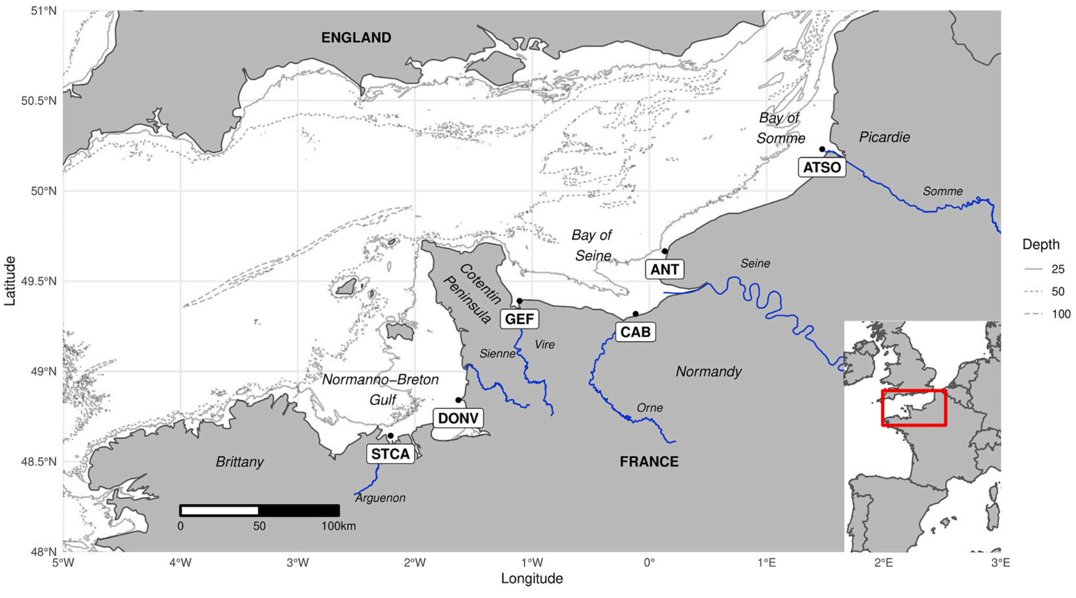

Fig. 1. Study area: The Eastern English Channel. (R package: rnaturalearthhires (South, 2020)).

resolution.

2.2.1. Phytoplankton datasets

The flora dataset was initially composed of 131 taxa (60% diatoms, 29% dinoflagellates) most of which were identified to the species or genus level or regrouped as sets of species or genus (85% of the taxa). In order to ensure robust analyses, taxa that represented more than 99% of the total abundance over the studied period and areas were selected. Moreover, only the abundances above 100 cells.L^{-1} were considered since this concentration is the detection limit with microscopy observations (Neaud-Masson, 2016). Special attention was put towards the naming convention so as to ensure temporal coherence. The final list for the 108 considered taxa is given in the supplementary data (Table S3).

2.2.2. Environmental variables

Abiotic parameters were obtained through the monitoring programs' quality protocols (Neaud-Masson, 2016). Hydroclimatic parameters were taken from the Météo France database from the closest meteorological station and the Hydrologic Bank (Table 1). Wind direction was transformed into a percentage of similarity from the local major wind (270°) (Table 1).

2.3. Numerical analyses

Data analyses were managed through R, version 3.5.1 (R Core Team, 2018), with the use of "ggplot2" package (Wickham, 2016) for the majority of the graphical outputs. Datasets and scripts are available on a GitHub repository (https://github.com/AngieLef/PhytoComm_Channel21). All phytoplankton cell counts were transformed to a logarithm base-10, with two decimals. Seasons are defined as three successive months with winter being the combination of the 12th month of year Y and the 1st and 2nd months of year Y+1.

2.3.1. Environmental exploration

For each station, parameter and year, every seasonal mean value was compared to the overall mean (μ_s) of the same season (s) over the 2008–2019 period, and the difference (μ_s - s) plotted. Due to important flow differences between rivers, the percentage to the mean of the difference ($\mu_s/s \times 100$) per station was plotted for this abiotic parameter only.

Table 1
Summary of the abiotic variables (with their unit) used for the numerical analyses and their measuring or calculation methods.

Parameter	Method		
Temperature (°C)	*In situ* temperature sensor		
Salinity (PSU)	*In situ* conductivity sensor		
Dissolved oxygen (mg.L^{-1})	*In situ* oxygen sensor		
Turbidity (NTU)	Optical turbidimeter		
N/P ratio	Spectrophotometry flows for the ammonium, nitrate, nitrite and phosphate nutrient (Aminot A. Kérouel R. 2007). $N/P = ([NH_4^+] + [NO_3^-] + [NO_2^-])/[H_3PO_4]$		
Rainfall (mm)	Amount of rainfall gathered between 06H00 UTC Day D and 06H00 UTC Day D+1 (1 mm = 1 L.m^{-2})		
Wind Speed (m.s^{-1})	Average of the maximum speeds recorded over 10 min		
Wind direction (% of a West wind)	Similarity of the wind direction (realWD) with a West wind (270°). NewWD = abs(100 – abs(realWD – 270)/180 *100)		
Daylight duration (min)	Duration of light (intensity over 120 W m^{-2}, enough to create distinct shades) over a period of 24h (from 00H00 UTC)		
Inflow ($m^3.s^{-1}$)	River	Average	Basin
	Seine (at Paris, Austerlitz)	315	78 650 km²
	Somme (at Bray sur Somme)	8.5	6 650 km²
	Vire (at Malloué)	7	1 969 km²
	Sienne (at St Cécile)	2	794 km²
	Arguenon (at Jugon Les Lacs)	0.8	534 km²

2.3.2. Phytoplankton stability approach

To investigate the stability over time of the communities found at each site, the Bray Curtis dissimilarity index (Bray and Curtis, 1957) was calculated for every pair of samples (not only consecutive) using the "vegan" package (Oksanen et al., 2018). The sampling protocol being bimonthly, all time intervals were rounded to be proportionate to 15 days, so as to allow the calculation of the average, Q1 and Q3 similarity between samples of same time intervals.

2.3.3. Seasonal temporal trajectories of phytoplankton

Trajectory analysis is an ordination that aims at comparing the behaviour of each community (trajectories) according to two main criteria; the resistance and resilience of communities, and the convergence or divergence for each year. For this, a recent Community Trajectory Analysis (CTA) was applied using the dissimilarity matrix described above (De Cáceres et al., 2019). It display, through annual arrows, the temporal evolution of the community assemblage over the study period. The function is part of the "vegclust" package (De Caceres et al., 2010) and the analysis was made independently for each season (ie: all years included).

2.3.4. Phytoplankton-environment relationship

Community and environment variables both varies in time and thus, there is a great interest to capture how their variations are related. COSTATIS (Co-inertia and organization of three way tables in statistics) is a method for the study of the relationship and structure of three way tables (referred as k-tables), that is to say the combination of community compositions, environment variations and time, altogether (Slimani et al., 2017; Thioulouse, 2011). Detailed in Thioulouse (2011), COSTATIS is the CO-Inertia Analysis (COIA) of 2 submatrices called 'compromises', obtained by 2 separates Partial Triadic Analysis (PTA) on each of the community and environment matrices. It was preferred to the similar STATICO analysis because of the relationship between environment and species that is strong and of main interest, and the chronological structure is not of primary importance in this case as it has been covered by the trajectory analysis described before (as advised in Thioulouse, 2011). Linking environmental and community datasets can draw out the structuration of each stations' community, depending on the main abiotic influences. For this analysis, both data tables needed to be scaled to the same temporal index, namely for the sites and years without any gaps. This is why only the seasonal scale was considered. However, STCA station was missing a value for the N/P variable during Winter of 2019; therefore, the mean value of all past winters' N/P ratio was used to complete the dataset.

3. Results

3.1. Environmental historical context

To better understand the temporal variations in phytoplankton community composition, it is important to know about past environmental events that occurred over the studied period (Fig. 2). Even when considering all sampled sites, two parameters indicated strong changes during the period of 2008–2019. The period from 2012 to mid 2013 displayed colder water temperatures, with successive negative anomalies values. The N/P ratio was at its highest in 2013, followed by lower values for the next two consecutive years, 2014 and 2015. Afterwards, a shift for both the water temperature and the N/P ratio occurred. Indeed, since 2014, the temperature variable indicated successive positives anomalies (except summers of 2015 and 2016). Also, the occurrences of positive anomalies concerning the N/P ratio are higher after 2013 compared to the 2008–2013 time period, due to lower phosphate

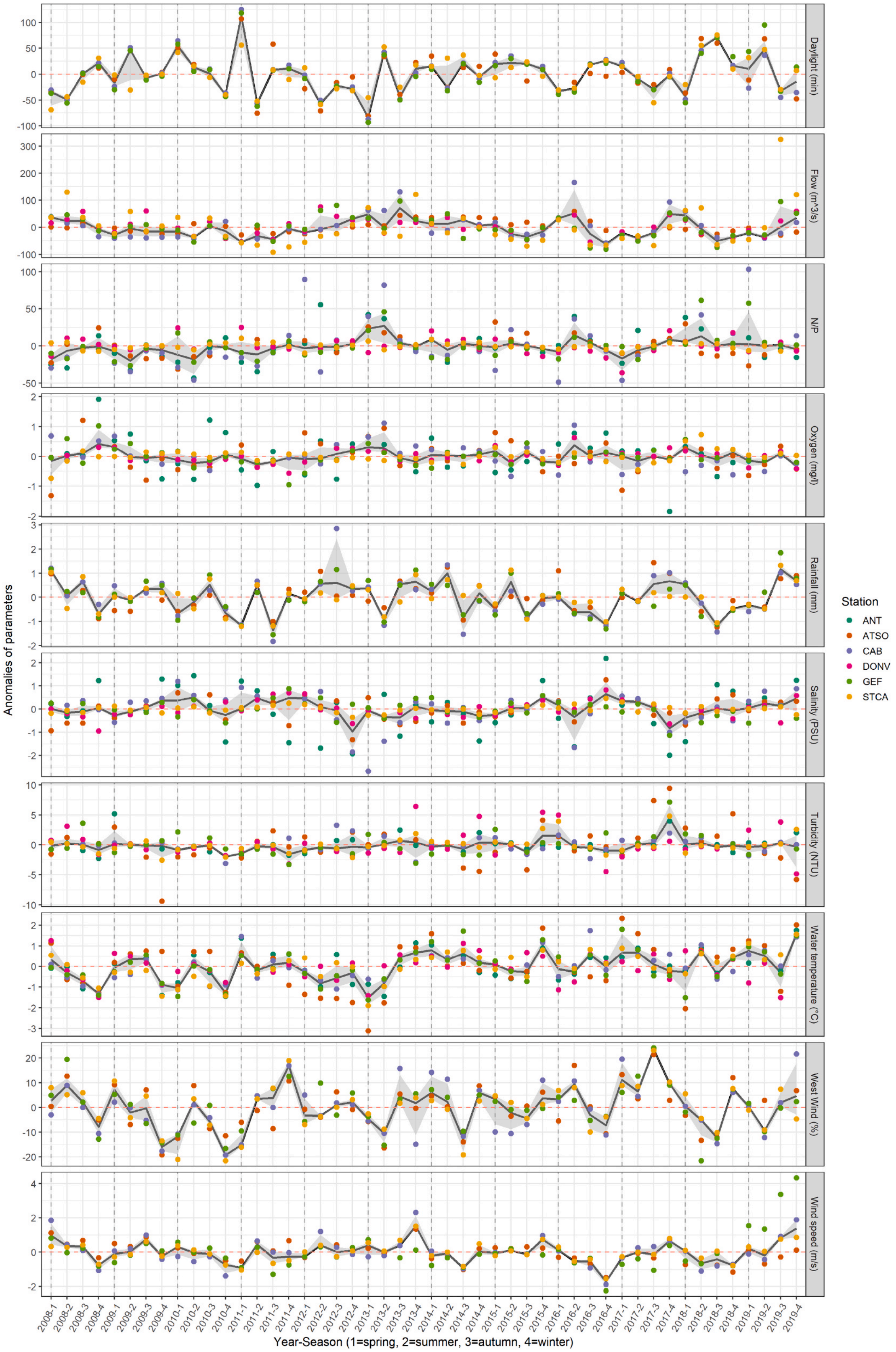

Fig. 2. Seasonal anomalies of environmental variables over the period of 2008–2019 (black line: median value between all stations; grey ribbon: Q1 and Q3 limits).

concentrations. This ratio is influenced by the ANT and CAB stations, and follows the flow input pulses from the Seine river. During 2018, and at the beginning of 2019, the conditions were exceptional with a longer light duration, low rainfall and less windy conditions. One can also notice that the GEF station was less affected by a wind speed changes and ATSO was the most affected by turbidity variations. The sampled sites' distributions allows different degrees of salinity influence, which is an important characteristic of each estuary's hydrodynamic situation.

3.2. *Community temporal stability along the French channel coastline*

The Bray Curtis index indicates a mean similarity of 0.35 for ANT, CAB, DONV and GEF, while the index is around 0.45 for ATSO and STCA (Fig. 3). This shows a stability between samples separated by nearly 11 years for most sites, and only ANT and GEF display a change of stability around the six years mark. Indeed, the mean similarity index decrease between samples separated by 15 days and those separated by 11 years is around 0.1 for ANT and GEF, and is below 0.05 for the other stations. The amplitude in similarity is stable and below 0.20 for STCA and CAB. Additionally, GEF displays the smallest amplitude.

One can notice that the oscillations present peaks of higher similarities for samples separated by a lapse period proportionate to 12 months. Whereas, the lowest similarities, indicated by a rounded end, occur between samples separated by a period proportionate to 6 months (but not to 12 months).

Kendall's index indicates a significant downward trend on the mean similarity for five over six stations (STCA is stable). Even though the trends of the mean level (μ) are not straight lines, the estimated slopes are very low for all sites, between -5e10^{-4} and 8e10^{-8} per two weeks.

3.3. *Community seasonal trajectories contrasts*

Community Trajectory Analysis (CTA) displays the annual variation undertaken by communities in term of species assemblage. Like in common ordination plots, the first two axes explain most of the variance; from 20% (spring and winter facets) to 27% (summer facet), which is correct considering it describes 12 years trajectories of 6 phytoplankton communities (Fig. 4). The seasonal display of the community trajectories undertaken by each site's community indicates that summer is

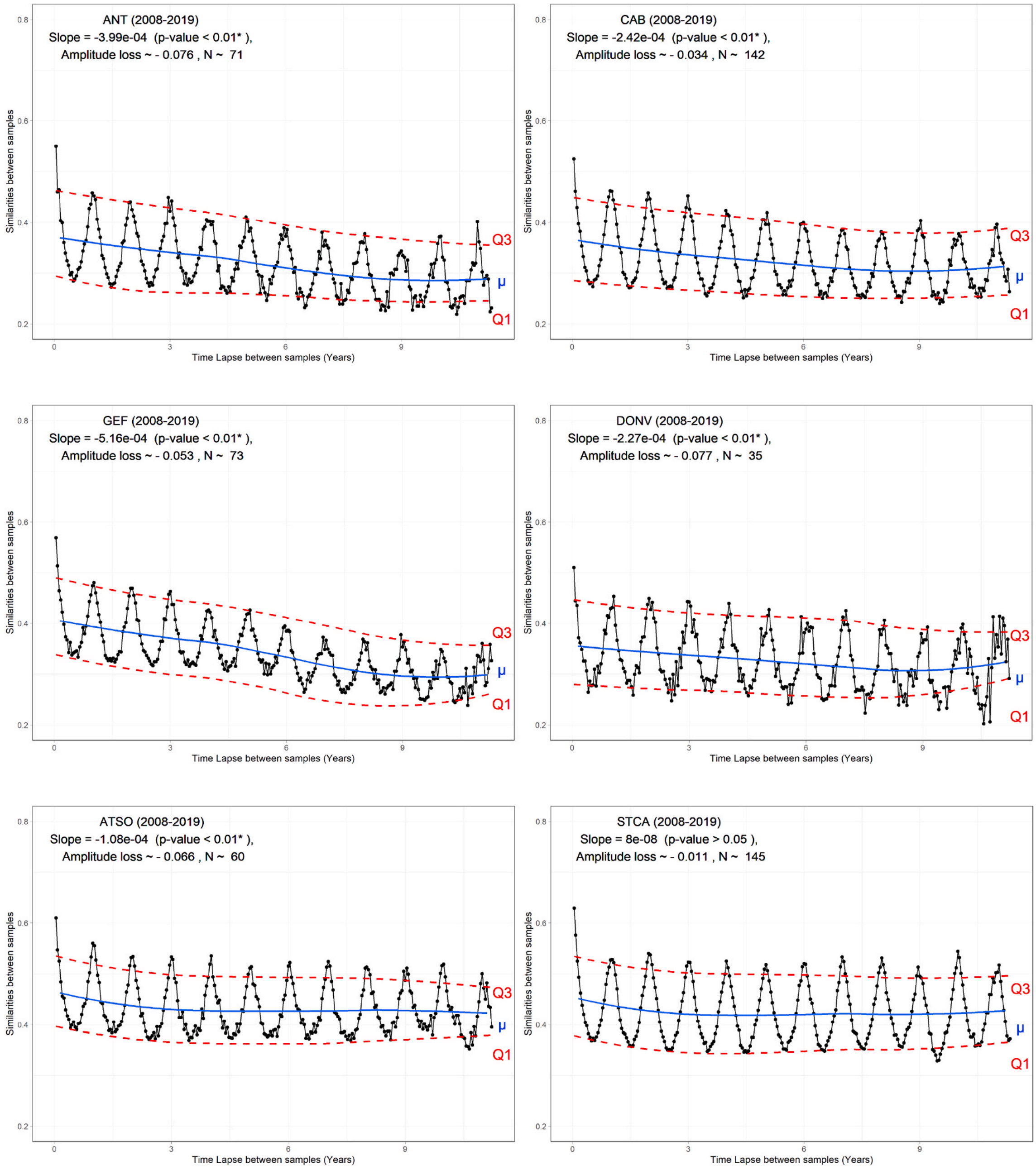

Fig. 3. Bray-Curtis similarity between samples sharing a same time lapse between sampling dates, per station. The slope is according to Sen's test and the associated p-value is part of Kendall's trend test (McLeod, 2011), (*) indicates significant downward trend of the blue line (mean similarity). The amplitude is estimated through the difference between Q3 and Q1 (third and first quantile). N is the average number of samples considered for the calculation of each similarity point (black dots).

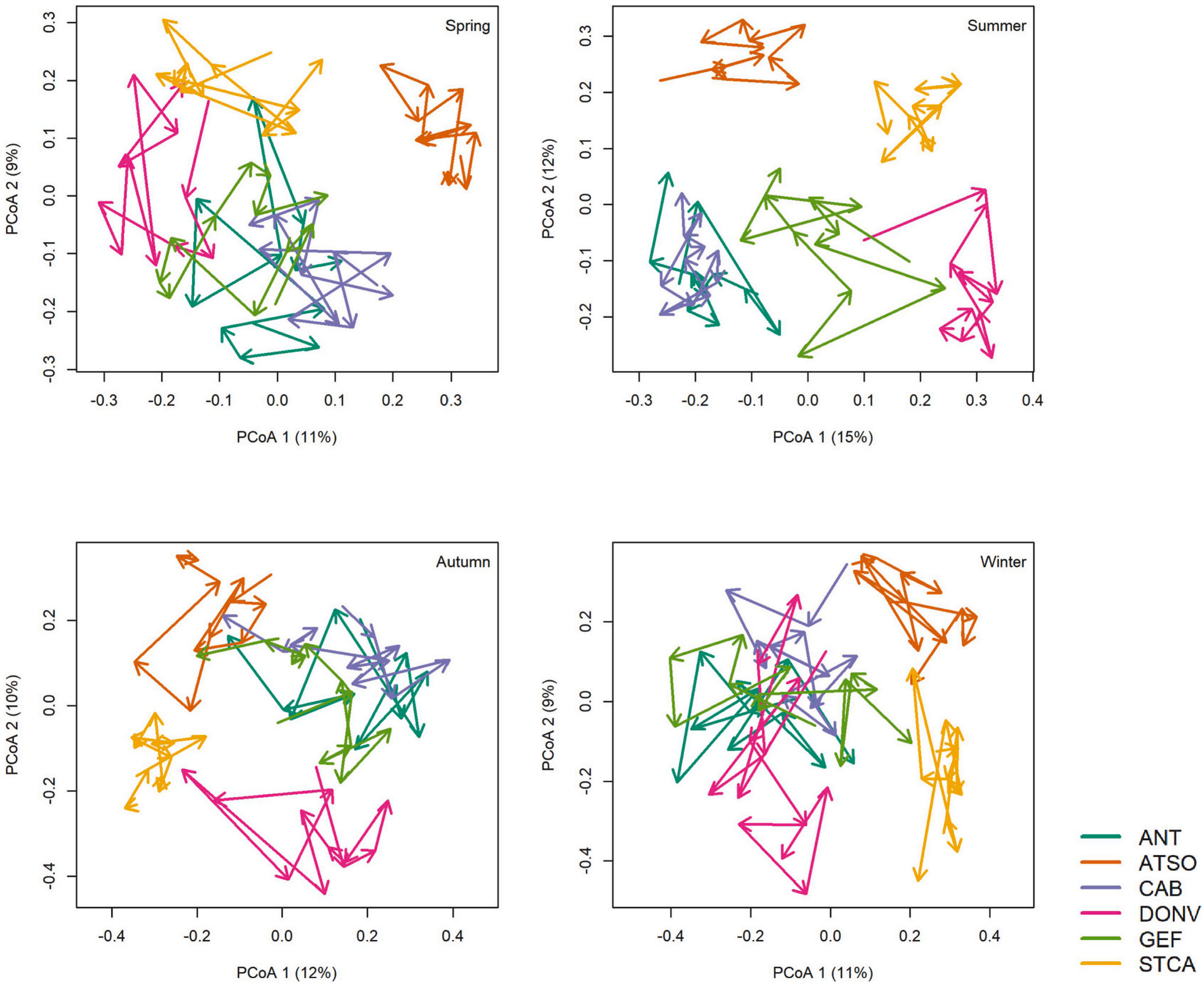

Fig. 4. Seasonal Community Trajectories Analysis (CTA) at 6 stations. The arrows drawing the trajectories represent the annual assemblage variations, from 2008 to 2019.

hosting the most site-specific communities. ANT and CAB, have overlapping trajectories due to their closeness with the Seine river's mouth. Summer is known as the season during which major blooms occur and when diversity is at its highest (Table S4). It is also the season during which the communities at each station show the least temporal variations but the most geographical distinctions.

Three types of patterns can be distinguished. (1) Bay of Seine sites follow similar global direction, taking similar paths and displaying the longest trajectories. (2) STCA displays a tight node of shorter trajectories every season as if all the years trigger very similar phytoplankton assemblages. (3) ATSO, always isolated from other trajectories, only differs in length from STCA during autumnal trajectory, which varies from one year to another (Table 2). DONV has a different temporal behaviour as it displays the longest trajectories like the Bay of Seine sites but also displays a path closer to STCA's communities' (Table 2, Table S5).

Table 2
Trajectories' length calculated from the CTA (Fig. 4) giving the community temporal evolution between 2008 and 2019, per season and station.

	Spring	Summer	Autumn	Winter	Total
DONV	1.728	1.180	2.303	3.283	**8.493**
ANT	1.830	1.169	2.262	2.690	**7.952**
GEF	1.165	1.790	1.475	2.282	**6.713**
CAB	1.659	0.870	1.592	1.985	**6.106**
ATSO	1.035	0.935	1.572	2.164	**5.706**
STCA	1.531	0.925	1.040	2.128	**5.625**

Two groups of sites can be identified. The first, composed of ANT and CAB, displays very close trajectories that sometimes overlap. The second group, with GEF, DONV and STCA show similar scores on axis 1 for spring and summer and axis 2 for autumn and winter (Table 2). Finally, on the axis scores, ATSO is closer to ANT and CAB sites compared to the three others.

Additionally, CTA scores indicate changes in trajectories' directions between 2013 and 2014 on the first axis (for winter and autumn) and second axis (for spring and summer but also autumn for GEF), mainly within the Bay of Seine (details in Table S5).

3.4. *Estuarine influence on phytoplankton community structure*

To better understand the community behaviour, we need to investigate the environment associated to each area, this is the purpose of the co-inertia analysis COSTATIS (Fig. 5). It gives two results; one displays the station's affinities to environmental parameters and the other indicates the most representative taxa found at the stations. The vectorial correlation coefficient (RV) between the environment and community k-tables is 0.809, which indicates a strong correlation displayed through this analysis.

On first hand, the axes display two major meanings; close to the x-

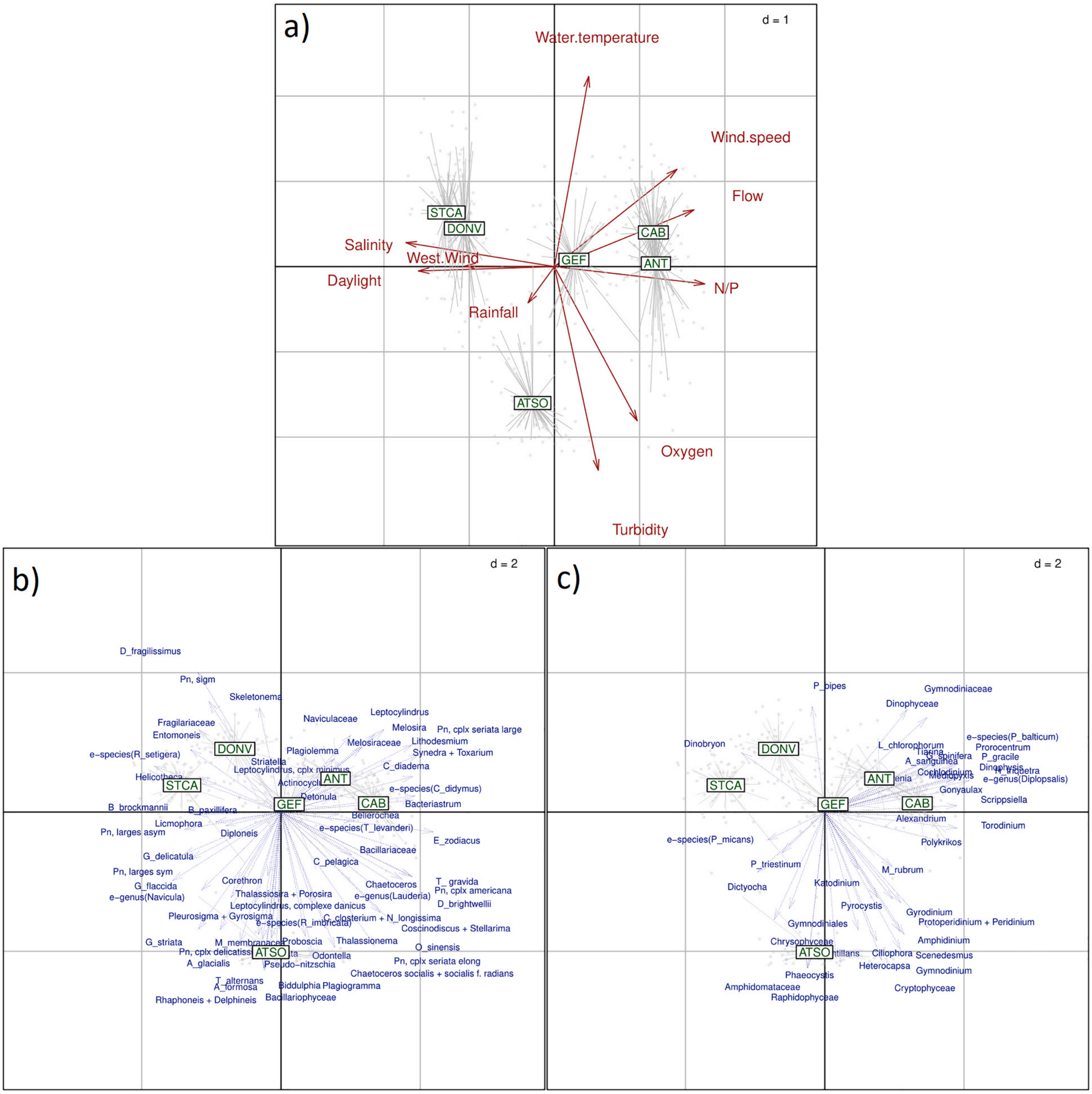

Fig. 5. 'Intrastructure' of the Costatis representing the community structure for each site superimposed with environment parameters (a) and phytoplankton taxa; diatoms (b) or other classes (c). Axis 1 and 2 represent respectively 63% and 29% of the variance, RV = 0.809 (correlation between the two k-tables). The grey points and lines represent the variability for each station, the 'd' mention at the upper right is the axes gradation. The detailed nomenclature for the taxa is in the supplementary data.

axis there is a marine-freshwater gradient running from flow to salinity arrows and close to the y-axis there is another gradient from oxygen and turbidity to water temperature arrows (Fig. 5a). There are four communities influenced by different parameters. (1) ANT and CAB, both affected by high value of N/P ratios, river flows and wind speed (with East-North-East wind direction). (2) ATSO that is greatly influenced by oxygen, low temperatures and turbidity. (3) DONV and STCA are mainly under the influence of oceanic waters and weather changes (daylight durations). (4) GEF is not driven by of any abiotic parameter more than another but displays a pattern closer to ANT and CAB.

On the other hand, looking at the species influences on the community structure, the four communities listed above are still distinct. At first look, the affinity of some species for certain area is noticeable. Thus, many diatoms are driven by ATSO's conditions, and most dinoflagellates by primarily ANT's and CAB's conditions and secondarily ATSO's.

Concerning the species distribution within these contrasted areas, there are a large diversity of taxa at the ANT and CAB stations, with *H. triquetra*, *O. sinensis*, *Prorocentrum* spp., *Lithodesmium* spp., *Leptocylindrus* spp. and some HABs forming species as *Pseudo-nitzschia* spp. complex seriata (large), *Dinophysis* spp., *L. chlorophorum*. ATSO present higher affinities with many diatoms and lesser other classes; *Rhaphoneis* spp., *Delphineis* spp., *T. alternans*, *Biddulphia* spp., *A. glacialis*, *Plagiogramma* spp., it is an area highly affected by *Phaeocystis* spp. blooms and some *Pseudo-nitzschia* spp. complex seriata (elongated). The taxa influencing communities at DONV and STCA are not numerous and nearly exclusively diatoms, *D. fragilissimus* and *R. setigera* are the main ones.

4. Discussion

The overall analysis indicates an overall stability of the communities for the time-period of 2008–2019. Nevertheless, historical analysis of environmental parameters highlight consequent variations between years for the temperature (increase) and nutrients (higher N/P ratio), with a notable shift in 2013. Local variations also occur at each station, due to the different environmental influences from their respective geographical areas. However, spatial clusters are noticeable within the selected contrasted estuarine systems depending on local drivers.

4.1. *Temporal variability over a decade of monitoring*

The question of phytoplankton community's stability over time in an unsteady environment is complicated due to seasonal patterns and cycling behaviour, especially in coastal environments being interfaces between tides and fresh water inputs. The similarity analysis applied to all samples, while taking into consideration their different sampling intervals, shows only a slight downward trend. Teubner and collaborators (2003) found comparable similarity values (average of 35%) between pair of months' samples in stable ecosystem such as alpine lakes, using species biovolumes. Moreover, a temporal study on a Hydroelectric Reservoir in Brazil has shown a decrease from 40% to 25% similarities between samples having 0 and 4 years apart, respectively (Schneck et al., 2011). Within the western Channel in the 70s, Maddock and collaborators (1981) could not find any trends in their 11 years-long study period, even though inter-annual fluctuations were noticeable. The present study shows Eastern-Channel coastal communities are displaying between 35% and 45% mean similarity from 2008 to 2019. Even with a year-by-year difference, the highest decrease in similarity goes from 40% to 30% between samples set 10 years apart. This suggests a decadal stability on the overall marine phytoplankton community over the studied period in the Eastern-Channel (Fig. 3). This also indicates limitations for community variations and highlights the fact that there are no substantial restructurings of the entire community over the studied period. Be that as it may, environmental variables along the western Channel have shown a sudden increase in water temperature and N/P ratio by the year 2013 (Fig. 2). Despite having a decade of stability, there is a clear sinusoidal pattern with a 20% amplitude between highest and lowest similarities (Fig. 3). This reflects a major 12 months similarity cycle that was also found by Winder and Cloern (2010) in 48% of 125 studied time series. However, only the communities within the Bay of Seine (namely ANT, CAB and GEF) show the most variations and decrease of similarities. The associated stations are under the influence of the main river that is the Seine. Moreover, even if GEF is further away and protected from the west winds in the Bay of Veys, models also indicate a westward water circulation from Seine water input that affects its water (Cugier and Le Hir, 2002).

Besides the overall stability over the decadal period, seasonal trajectories further highlight variabilities within phytoplankton assemblage's changes over time (Fig. 4). Autumn and winter seasons indicate, for all sites, a temporal shift in the trajectories around the years 2013–2014 (Table S5). The environment anomalies analysis indicates a corresponding change in abiotic parameters during autumn of 2013; sudden drops of N/P ratio and oxygen value that were higher than usual during spring and summer 2013, higher rainfalls from autumn 2013 to summer 2014, stronger flows and water temperature values and mainly; a strong west wind influence. These parameters changes are the consequence of positive North Atlantic Oscillation (NAO+) occurrences which also caused a very high mortality rate within Oyster farms in 2014 (Thomas et al., 2018). During spring and summer, another shift in the community composition is apparent around 2015 on the second axis of the CTA. No changes within the environmental parameters could be linked to this change. In their article covering 20 years of data for 12 sampling sites from the Bay of Somme, up to the border with Belgium, Hernández Fariñas and collaborators (2013) could define 2 distinct periods (1992–2001 and 2002–2007) with different community structures respectively separated by 9 and 5 years. Therefore, a community change around 2015 is not out of the ordinary but is discrete and mostly involves the blooming seasons (spring and summer) when species diversity is higher. Nonetheless, plankton shifts or changes in patterns should not be taken as a global change in forcing parameters; they could be due to a multitude of internal dynamics, like grazing and filtration by upper levels, as it was not taken into consideration during the analysis (Mazzocchi et al., 2012).

All sites' communities display a very strong seasonal pattern common to plankton communities (Fig. 4). Such stability and resilience among plankton communities was noticed in Italy through similar analysis applied to copepods assemblages over a two decades time period (Mazzocchi et al., 2012). In their study, the constant presence of abundant species and clear seasonal succession enabled this constancy. The zoo- and phytoplankton compartments are strongly linked to one another, which makes seasonal patterns very similar and successive (Greve et al., 2004; Wiltshire et al., 2015). The phytoplankton community structure observed is likewise marked by species encountered in high numbers on an annual scale, like *Chaetoceros* spp. and *Paralia sulcata*, and by the clear seasonal succession between species (Table S4). Amongst these species, *Skeletonema* spp., *Pseudo-nitzschia* spp., *Dactiliosolen fragilissimus, Leptocylindrus* spp., *Asterionellopsis glacialis, Phaeocytis* spp. and *Lepidodinium chlorophorum* present clear seasonal affinities, mainly for spring and summer. These blooming species were found to respond to temperature gradients in other studies (Carstensen et al., 2015). Summer is the most diverse season in terms of number of species observed per samples and bloom occurrences (Cloern and Jassby, 2008; Wiltshire et al., 2008). This season is however structured by the same specific blooming species that highly dominate successively the water composition. They show a fast response when seasonal changes occur in their local environment. This specific structuration, through the dominance of a handful of species, answers why phytoplankton is mostly site specific due to local bloom drivers and species. The low variations run over by few species' dominance also explains why the community's composition is stable from one year to another during this season specifically, in spite of the high species' diversity recorded.

4.2. *Phytoplankton community responses to different estuarine pressures*

Even though the micro-phytoplankton communities at the scale of this epicontinental sea are globally stable over time, they are affected by estuarine conditions, an effect from local environmental parameters on phytoplankton is expected. Beside the influence of the estuaries' size, this study pointed out four communities distinguished by their responses to the environment. The first is deeply impacted or dependant on river inputs and local winds (ANT & CAB). The second is challenged by water turbidity and high dissolved oxygen concentrations (ATSO). The third is mostly affected by oceanic and weather-like influences such as daily light duration and salinity (STCA and DONV). Finally, this study shows a fourth intermediate community structuration around a shellfish farming area (GEF).

The communities of the Seine estuary (ANT and CAB) display overlapping trajectories for each of the four seasons (Fig. 4) which can be explained by common environmental pressures due to the coastal drift of the Seine River (Brylinski et al., 1991). The ANT station most likely catches this Northward current of the Seine, while a wind change disturbance (East wind) seems to affect local phytoplankton communities' structure for both stations (Fig. 5). Besides their proximity, higher inter-annual variabilities within phytoplankton species assemblage were observed at the mouth of the Seine (ANT & CAB) compared to the northern station (ATSO).

For every season, at the Somme river mouth, ATSO clearly indicates a different phytoplankton community in both trajectory patterns and compositions (Fig. 4). This site is located 120 km North of ANT and is also partly affected by the Seine's coastal drift (Brylinski et al., 1996). Looking at the CTA scores, the phytoplankton's response tends to be closer to the ones of the Seine estuary (ANT and CAB) (Figs. 4 and 5). A first observation indicates that these communities are both under a largely estuarine influence (nutrient ratios, dissolved oxygen) and less under local weather dynamics (Morelle et al., 2018). However, ATSO is closer to the North Sea's influence. It is also known for having large and frequent *Phaeocystis* spp. blooms in spring and summer (Brunet et al., 1996; Dauvin et al., 2008; Lamy et al., 2006) (Table S4, this species is mainly recorded at this station). In that sense, beside the affinity to rivers-related parameters observed at the Seine and Somme stations (ANT, CAB and ATSO), the COSTATIS displays a different pattern between both estuarine systems (Fig. 5). The Seine basin and Somme basin are very different. The catchment basin is also ten times wider and the population density (200 inhab/km^2) is the double, mainly concentrated downstream, for the Seine basin compared to the Somme's (Thieu et al., 2009). In their complete comparison study, Thieu et al. (2009) highlight a higher N/P ratio due to lower phosphate in the Somme's estuary, along with higher dissolved oxygen and turbidity values, leading to low chl-*a* content. Moreover, the highly turbid water and high oxygenation of the Somme estuary suggest a well-mixed water column as well which is coherent with the species' life form observed at ATSO. Diatoms with benthic affinities such as the epipelic *Pleurosigma* spp., *Gyrosigma* spp., *Nitzschia longissima*, the set of genus around *Navicula* spp., and the tychoplanktonic *Rhaphoneis* spp., *Delphineis* spp., and *Cylindrotheca closterium* are observed on this site (Fig. 5) (Hernández Fariñas et al., 2017).

Considered as more marine influenced, the communities situated west of the Cotentin peninsula (DONV and STCA) are characterised by a lower diversity but a stable similarity over the studied period. The communities are grouped together in the co-inertia analysis, when taking into consideration their composition and affinities to environmental parameters (Fig. 5). They are dependant of local, short-termed variations (rainfalls, daily light availability). Studies indicate that short-term events can mainly affect phytoplankton's structure, as observed in the Bedford Basin in Nova Scotia with the passage of storms and during up-welling periods (Côté and Platt, 1983). Nevertheless, it is unlikely that these punctual events are responsible of significant long-term changes in community composition (Gohin et al., 2015; Henson et al., 2018), but it does explain the resiliency and why there is a decadal stability in this area (Fig. 3). The main difference between these two areas is the length of the seasonal trajectories, with the most notable difference for the autumnal and winter periods. This is due to the fact that one of the sites (STCA) is protected from the influence of the major west winds by its closeness to the western coast, unlike the other.

Lastly, the Bay of Veys is a very active shellfish farming area (GEF) (Costil et al., 2005; Timsit et al., 2004). It is a sheltered area from the winds, characterised by a high inter-annual variability and an unstable community composition compared to the stations mentioned above, and displays the smallest sinusoidal amplitude (Fig. 3). As previous studies have shown, filter feeders have a "top down" and "bottom-up" influence on primary producers (less Chl-*a*), through grazing and biodeposition (ammonium), they induce changes in turbidity and nutrient ratios and mitigate specific blooms (Gallardi, 2014; Grant and Pastres, 2019; Cugier et al., 2010). For the Bay of Veys, similar conclusions were drawn from models on bivalves and phytoplankton interactions (Grangeré et al., 2010). To conclude, being an intermediate point, the chosen abiotic variables are not the ones structuring the phytoplankton community in the Bay of Veys (Fig. 5). However, this study does not include indicators from the shellfish farms, their impact on the local community is thus only an hypothesis.

5. Conclusion

This study has highlighted an overall 12 years stability within the micro-phytoplankton communities thriving in epicontinental Sea (Bay of Seine, Bay of Somme and Northern Brittany). In accordance with Cloern and Jassby, 2010 hypothesis, with the slight environmental and community changes in 2013 and with a higher inter-annual variability for a shellfish farming area, our results show that seasonal patterns of community changes were linked to environmental cycling and year-to-year variability was a slow process to be correlated with anthropic or climate shift. Moreover, being in a macro and mega tidal environment, seasonal patterns within each sites are both strong and regular.

As shown through this study, no long-term changes were evident despite environmental variations. Taking a closer look at the functional groups within the phytoplankton could highlight some community variation, as suggested by Zingone and collaborators (2010). Moreover, a comparative analysis with English estuarine systems along the Channel could give a more detailed and complete mapping of the English Channel's influence on phytoplankton communities (Iriarte and Purdie, 2004; Pirani et al., 2016).

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Data access

The datasets supporting this article have been downloaded from the Quadrige^2 platform (http://quadrige.eaufrance.fr), acquired on demand from the Méteo-France network (https://donneespubliques.meteofrance.fr) and extracted from the hydrological data bank (http://www.driee.ile-de-france.developpement-durable.gouv.fr). All the sets and script as used for the production of graphical outputs are available on the GitHub repository: https://github.com/AngieLef/PhytoComm_Channel21.

CRediT authorship contribution statement

Angéline Lefran: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Tania Hernández-Fariñas:** Investigation, Writing – review & editing, Supervision, Project administration. **Francis Gohin:** Investigation, Writing – review & editing, Supervision. **Pascal Claquin:** Investigation, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107409.

References

Bode, A., Alvarez-Ossorio, M.T., Cabanas, J.M., Miranda, A., Varela, M., 2009. Recent trends in plankton and upwelling intensity off Galicia (NW Spain). Prog. Oceanogr., Eastern Boundary Upwelling Ecosystems: Integrative and Comparative Approaches 83, 342–350. https://doi.org/10.1016/j.pocean.2009.07.025.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.

Brunet, C., Brylinski, J.M., Bodineau, L., Thoumelin, G., Bentley, D., Hilde, D., 1996. Phytoplankton dynamics during the spring bloom in the south-eastern English Channel. Estuar. Coast Shelf Sci. 43, 469–483.

Brylinski, J.M., Brunet, C., Bentley, D., Thoumelin, G., Hilde, D., 1996. Hydrography and phytoplankton biomass in the eastern English Channel in spring 1992. Estuar. Coast Shelf Sci. 43, 507–519.

Brylinski, J.M., Lagadeuc, Y., Gentilhomme, V., Dupont, J.P., Lafite, R., Dupeuble, P.A., Huault, M.F., Auger, Y., 1991. Le fleuve côtier: un phénomène hydrologique important en Manche Orientale. Exemple du Pas-de-Calais. Oceanol. Acta Spec. Issue.

Carstensen, J., Klais, R., Cloern, J.E., 2015. Phytoplankton blooms in estuarine and coastal waters: seasonal patterns and key species. Estuar. Coast Shelf Sci. 162, 98–109.

Cloern, J.E., Jassby, A.D., 2010. Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. Estuar. Coast 33, 230–241. https://doi.org/10.1007/s12237-009-9195-3.

Cloern, J.E., Jassby, A.D., 2008. Complex seasonal patterns of primary producers at the land–sea interface. Ecol. Lett. 11, 1294–1303.

Costil, K., Royer, J., Ropert, M., Soletchnik, P., Mathieu, M., 2005. Spatio-temporal variations in biological performances and summer mortality of the Pacific oyster Crassostrea gigas in Normandy (France). Helgol. Mar. Res. 59, 286–300.

Côté, B., Platt, T., 1983. Day-to-day variations in the spring-summer photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. 28, 320–344.

Cugier, P., Le Hir, P., 2002. Development of a 3D hydrodynamic model for coastal ecosystem modelling. Application to the plume of the Seine river (France). Estuar. Coast Shelf Sci. 55, 673–695. https://doi.org/10.1006/ecss.2001.0875.

Cugier, P., Struski, C., Blanchard, M., Mazurié, J., Pouvreau, S., Olivier, F., Trigui, J.R., Thiébaut, E., 2010. Assessing the role of benthic filter feeders on phytoplankton production in a shellfish farming site: mont Saint Michel Bay, France. J. Mar. Syst. 82, 21–34. https://doi.org/10.1016/j.jmarsys.2010.02.013.

Dauvin, J.-C., 2012. Are the eastern and western basins of the English Channel two separate ecosystems? Mar. Pollut. Bull. 64, 463–471. https://doi.org/10.1016/j.marpolbul.2011.12.010.

Dauvin, J.-C., Desroy, N., Denis, L., Ruellet, T., 2008. Does the Phaeocystis bloom affect the diel migration of the suprabenthos community? Mar. Pollut. Bull. 56, 77–87.

De Cáceres, M., Coll, L., Legendre, P., Allen, R.B., Wiser, S.K., Fortin, M.-J., Condit, R., Hubbell, S., 2019. Trajectory analysis in community ecology. Ecol. Monogr. 89.

De Caceres, M., Font, X., Olivia, F., 2010. The management of vegetation classifications with fuzzy clustering. J. Veg. Sci.

De Senerpont Domis, L.N., Van de Waal, D.B., Helmsing, N.R., Van Donk, E., Mooij, WolfM., 2014. Community stoichiometry in a changing world: combined effects of warming and eutrophication on phytoplankton dynamics. Ecology 95, 1485–1495. https://doi.org/10.1890/13-1251.1.

Dutkiewicz, S., Cermeno, P., Jahn, O., Follows, M.J., Hickman, A.E., Taniguchi, D.A.A., Ward, B.A., 2020. Dimensions of marine phytoplankton diversity. Biogeosciences 17, 609–634. https://doi.org/10.5194/bg-17-609-2020.

Gallardi, D., 2014. Effects of bivalve aquaculture on the environment and their possible mitigation: a review. Fish. Aquacult. J. 5 https://doi.org/10.4172/2150-3508.1000105.

Gohin, F., Bryère, P., Griffiths, J.W., 2015. The exceptional surface turbidity of the North-West European shelf seas during the stormy 2013–2014 winter: consequences for the initiation of the phytoplankton blooms? J. Mar. Syst. 148, 70–85. https://doi.org/10.1016/j.jmarsys.2015.02.001.

Gohin, F., Van der Zande, D., Tilstone, G., Eleveld, M.A., Lefebvre, A., Andrieux-Loyer, F., Blauw, A.N., Bryère, P., Devreker, D., Garnesson, P., Hernández Fariñas, T., Lamaury, Y., Lampert, L., Lavigne, H., Menet-Nedelec, F., Pardo, S., Saulquin, B., 2019. Twenty years of satellite and in situ observations of surface chlorophyll-a from the northern Bay of Biscay to the eastern English Channel. Is the water quality improving? Remote Sens. Environ. 233, 111343. https://doi.org/10.1016/j.rse.2019.111343.

Grangeré, K., Lefebvre, S., Bacher, C., Cugier, P., Ménesguen, A., 2010. Modelling the spatial heterogeneity of ecological processes in an intertidal estuarine bay: dynamic interactions between bivalves and phytoplankton. Mar. Ecol. Prog. Ser. 415, 141–158. https://doi.org/10.3354/meps08659.

Grant, J., Pastres, R., 2019. Ecosystem models of bivalve aquaculture: implications for supporting goods and services. In: Smaal, A.C., Ferreira, J.G., Grant, J., Petersen, J.K., Strand, Ø. (Eds.), Goods and Services of Marine Bivalves. Springer International Publishing, Cham, pp. 507–525. https://doi.org/10.1007/978-3-319-96776-9_25.

Greve, W., Reiners, F., Nast, J., Hoffmann, S., 2004. Helgoland Roads meso-and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgol. Mar. Res. 58, 274–288.

Hallegraeff, G.M., 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge1. J. Phycol. 46, 220–235.

Henson, S.A., Cole, H.S., Hopkins, J., Martin, A.P., Yool, A., 2018. Detection of climate change-driven trends in phytoplankton phenology. Global Change Biol. 24, e101–e111. https://doi.org/10.1111/gcb.13886.

Hernández Fariñas, T., Ribeiro, L., Soudant, D., Belin, C., Bacher, C., Lampert, L., Barillé, L., 2017. Contribution of benthic microalgae to the temporal variation in phytoplankton assemblages in a macrotidal system. J. Phycol. - Wiley Online Libr. 53, 1020–1034.

Hernandez-Farinas, T., Soudant, D., Barillé, L., Belin, C., Lefebvre, A., Bacher, C., 2013. Temporal changes in the phytoplankton community along the French coast of the eastern English Channel and the southern Bight of the North Sea. ICES J. Mar. Sci. 71, 821–833.

Iriarte, A., Purdie, D.A., 2004. Factors controlling the timing of major spring bloom events in an UK south coast estuary. Estuar. Coast Shelf Sci. 61, 679–690. https://doi.org/10.1016/j.ecss.2004.08.002.

Kimor, B., 1992. The impact of eutrophication on phytoplankton composition in coastal marine ecosystems. Mar. Coast. Eutrophication 871–878. https://doi.org/10.1016/B978-0-444-89990-3.50075-4.

Lamy, D., Artigas, L.F., Jauzein, C., Lizon, F., Cornille, V., 2006. Coastal bacterial viability and production in the eastern English Channel: a case study during a Phaeocystis globosa bloom. J. Sea Res. 56, 227–238.

Leterme, S.C., Edwards, M., Seuront, L., Attrill, M.J., Reid, P.C., John, A.W.G., 2005. Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic. Limnol. Oceanogr. 50, 1244–1253. https://doi.org/10.4319/lo.2005.50.4.1244.

Liénart, C., Savoye, N., Bozec, Y., Breton, E., Conan, P., David, V., Feunteun, E., Grangeré, K., Kerhervé, P., Lebreton, B., Lefebvre, S., L'Helguen, S., Mousseau, L., Raimbault, P., Richard, P., Riera, P., Sauriau, P.-G., Schaal, G., Aubert, F., Aubin, S., Bichon, S., Boinet, C., Bourasseau, L., Bréret, M., Caparros, J., Cariou, T., Charlier, K., Claquin, P., Cornille, V., Corre, A.-M., Costes, L., Crispi, O., Crouvoisier, M., Czamanski, M., Del Amo, Y., Derriennic, H., Dindinaud, F., Durozier, M., Hanquiez, V., Nowaczyk, A., Devesa, J., Ferreira, S., Fornier, M., Garcia, F., Garcia, N., Geslin, S., Grossteffan, E., Gueux, A., Guillaudeau, J., Guillou, G., Joly, O., Lachaussée, N., Lafont, M., Lamoureux, J., Lecuyer, E., Lehodey, J.-P., Lemeille, D., Leroux, C., Macé, E., Maria, E., Pineau, P., Petit, F., Pujo-Pay, M., Rimelin-Maury, P., Sultan, E., 2017. Dynamics of particulate organic matter composition in coastal systems: a spatio-temporal study at multi-systems scale. Prog. Oceanogr. 156, 221–239. https://doi.org/10.1016/j.pocean.2017.03.001.

Litchman, E., de Tezanos Pinto, P., Klausmeier, C.A., Thomas, M.K., Yoshiyama, K., 2010. Linking traits to species diversity and community structure in phytoplankton. In: Naselli-Flores, L., Rossetti, G. (Eds.), Fifty Years after the “‘Homage to Santa Rosalia”’: Old and New Paradigms on Biodiversity in Aquatic Ecosystems, Developments in Hydrobiology 213. Springer Netherlands, Dordrecht, pp. 15–28. https://doi.org/10.1007/978-90-481-9908-2_3.

Maddock, L., Boalch, G.T., Harbour, D.S., 1981. Populations of phytoplankton in the western English Channel between 1964 and 1974. J. Mar. Biol. Assoc. U. K. 61, 565–583. https://doi.org/10.1017/S0025315400048050.

Mallin, M.A., Paerl, H.W., Rudek, J., Bates, P.W., 1993. Regulation of estuarine primary production by watershed rainfall and river flow. Mar. Ecol. Prog. Ser. 93, 199.

Mazzocchi, M.G., Dubroca, L., García-Comas, C., Di Capua, I., d'Alcalà, M.R., 2012. Stability and resilience in coastal copepod assemblages: the case of the Mediterranean long-term ecological research at Station MC (LTER-MC). Prog. Oceanogr. 97, 135–151.

McLeod, A.I., 2011. Kendall Rank Correlation and Mann-Kendall Trend Test. R Package, version 2.2.

Morelle, J., Schapira, M., Orvain, F., Riou, P., Lopez, P.J., Pierre-Duplessix, O., Rabiller, E., Maheux, F., Simon, B., Claquin, P., 2018. Annual phytoplankton primary production estimation in a temperate estuary by coupling PAM and carbon incorporation methods. Estuar. Coast 41, 1337–1355. https://doi.org/10.1007/s12237-018-0369-8.

Neaud-Masson, N., 2016. Observation et dénombrement du phytoplancton marin par microscopie optique photonique-Spécifications techniques et méthodologiques appliquées au REPHY. Doc. Méthode.

Nohe, A., Goffin, A., Tyberghein, L., Lagring, R., De Cauwer, K., Vyverman, W., Sabbe, K., 2020. Marked changes in diatom and dinoflagellate biomass, composition and seasonality in the Belgian Part of the North Sea between the 1970s and 2000s. Sci. Total Environ. 716, 136316. https://doi.org/10.1016/j.scitotenv.2019.136316.

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. Vegan: Community Ecology Package. R Package Version 2.

Pirani, M., Panton, A., Purdie, D.A., Sahu, S.K., 2016. Modelling macronutrient dynamics in the Hampshire Avon river: a Bayesian approach to estimate seasonal variability and total flux. Sci. Total Environ. 572, 1449–1460. https://doi.org/10.1016/j.scitotenv.2016.04.129.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rabalais, N.N., Cai, W.-J., Cartensen, J., Conley, D.J., Fry, B., Hu, X., Quiñones-Rivera, Z., Rosenberg, R., Slomp, C.P., Turner, R.E., Voss, M., Wissel, B., Zhang, J., 2014. Eutrophication-driven deoxygenation in the coastal ocean. Oceanography 27, 172–183.

Rabalais, N.N., Turner, R.E., Díaz, R.J., Justić, D., 2009. Global change and eutrophication of coastal waters. ICES J. Mar. Sci. 66, 1528–1537. https://doi.org/10.1093/icesjms/fsp047.

Radach, G., Berg, J., Hagmeier, E., 1990. Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at Helgoland and at LV ELBE 1 in the German Bight. Continent. Shelf Res. 10, 305–328. https://doi.org/10.1016/0278-4343(90)90054-.

Schneck, F., Schwarzbold, A., Rodrigues, S.C., Melo, A.S., 2011. Environmental variability drives phytoplankton assemblage persistence in a subtropical reservoir. Austral Ecol. 36, 839–848. https://doi.org/10.1111/j.1442-9993.2010.02224.x.

Slimani, N., Guilbert, E., El Ayni, F., Jrad, A., Boumaiza, M., Thioulouse, J., 2017. The use of STATICO and COSTATIS, two exploratory three-ways analysis methods: an application to the ecology of aquatic heteroptera in the Medjerda watershed (Tunisia). Environ. Ecol. Stat. 24, 269–295.

Sournia, A., Chrdtiennot-Dinet, M.-J., Ricard, M., 1991. Marine phytoplankton: how many species in the world ocean? J. Plankton Res. 13, 1093–1099. https://doi.org/10.1093/plankt/13.5.1093.

South, A., 2020. Rnaturalearthhires: High Resolution World Vector Map Data from Natural Earth Used in Rnaturalearth.

Sumaila, U.R., Cheung, W.W.L., Lam, V.W.Y., Pauly, D., Herrick, S., 2011. Climate change impacts on the biophysics and economics of world fisheries. Nat. Clim. Change 1, 449–456. https://doi.org/10.1038/nclimate1301.

Tett, P., Barton, E.D., 1995. Why are there about 5000 species of phytoplankton in the sea? J. Plankton Res. 17, 1693–1704. https://doi.org/10.1093/plankt/17.8.1693.

Teubner, K., Tolotti, M., Greisberger, S., Morscheid, Heike, Dokulil, M.T., Morscheid, Harald, 2003. Steady state phytoplankton in a deep pre-alpine lake: species and pigments of epilimnetic versus metalimnetic assemblages. In: Naselli-Flores, L., Padisák, J., Dokulil, M.T. (Eds.), Phytoplankton and Equilibrium Concept: the Ecology of Steady-State Assemblages, Developments in Hydrobiology. Springer Netherlands, Dordrecht, pp. 49–64. https://doi.org/10.1007/978-94-017-2666-5_5.

Thieu, V., Billen, G., Garnier, J., 2009. Nutrient transfer in three contrasting NW European watersheds: the Seine, Somme, and Scheldt Rivers. A comparative application of the Seneque/Riverstrahler model. Water Res. 43, 1740–1754.

Thioulouse, J., 2011. Simultaneous analysis of a sequence of paired ecological tables: a comparison of several methods. Ann. Appl. Stat. 5, 2300–2325.

Thomas, Y., Cassou, C., Gernez, P., Pouvreau, S., 2018. Oysters as sentinels of climate variability and climate change in coastal ecosystems. Environ. Res. Lett. 13, 104009.

Timsit, O., Sylvand, B., Lefeuvre, J.-C., 2004. Évolution du macrozoobenthos intertidal de la baie des Veys de 1985 à 2000. C. R. Biol. 327, 51–64. https://doi.org/10.1016/j.crvi.2003.11.002.

Wasmund, N., Tuimala, J., Suikkanen, S., Vandepitte, L., Kraberg, A., 2011. Long-term trends in phytoplankton composition in the western and central Baltic Sea. J. Mar. Syst. 87, 145–159. https://doi.org/10.1016/j.jmarsys.2011.03.010.

Wickham, H., 2016. H. Wickham. Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, 2016.

Wiltshire, K.H., Boersma, M., Carstens, K., Kraberg, A.C., Peters, S., Scharfe, M., 2015. Control of phytoplankton in a shelf sea: determination of the main drivers based on the Helgoland Roads Time Series. J. Sea Res. 105, 42–52. https://doi.org/10.1016/j.seares.2015.06.022.

Wiltshire, K.H., Malzahn, A.M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B.F.J., Boersma, M., 2008. Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. Limnol. Oceanogr. 53, 1294–1302. https://doi.org/10.4319/lo.2008.53.4.1294.

Winder, M., Cloern, J.E., 2010. The annual cycles of phytoplankton biomass. Philos. Trans. R. Soc. B Biol. Sci. 365, 3215–3226.

Wollschläger, J., Wiltshire, K.H., Petersen, W., Metfies, K., 2015. Analysis of phytoplankton distribution and community structure in the German Bight with respect to the different size classes. J. Sea Res. 99, 83–96.

Xiao, W., Liu, X., Irwin, A.J., Laws, E.A., Wang, L., Chen, B., Zeng, Y., Huang, B., 2018. Warming and eutrophication combine to restructure diatoms and dinoflagellates. Water Res. 128, 206–216. https://doi.org/10.1016/j.watres.2017.10.051.

Zingone, A., Phlips, E.J., Harrison, P.J., 2010. Multiscale variability of twenty-two coastal phytoplankton time series: a global scale comparison. Estuar. Coast 33, 224–229. https://doi.org/10.1007/s12237-009-9261-x.