

Phytoplankton community structure responses to episodic summer storms in a temperate coastal ecosystem

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Abstract. Extreme events potentially modify the physical and biogeochemical environment resulting in dramatic changes of phytoplankton community structure. In this study the impact of ~~ten~~ well-identified storms on phytoplankton communities was explored in a productive ~~temperate~~ coastal ~~temperate~~ ecosystem, the eastern English Channel (EEC). ~~Our study targeted the summer season, which is typically characterised by low nutrient availability, yet transient phytoplankton blooms often occur~~We focussed in summer because it is a low-nutrient season where phytoplankton major shifts and blooms are not expected. ~~From 2012–2022, low-frequency (weekly to fortnightly) flow cytometry measurements of phytoplankton abundance were combined with high-frequency meteorological data (precipitation and wind) and river flow rates as a proxy for riverine influence~~Low-frequency (weekly to fortnightly) flow cytometry measurements of phytoplankton abundance were combined with high-frequency meteorological data (precipitation and wind) and hydrological records from 2012 to 2022. Storm impacts occurred in three distinct forms: high river inflow events, high wind stress–low inflow events, and low wind stress–low inflow events. ~~Regardless of wind conditions, high inflow storms favoured diatoms, as nutrient-rich river plumes supported their growth. In contrast, low inflow events paired with strong winds enhanced vertical mixing and nutrient availability, favouring nanophytoplankton. Finally, weak winds and relatively low-nutrient conditions favoured picophytoplankton~~ High inflow storms, whether accompanied by weak or strong winds, promote coastal advection of riverine plumes enriched in nutrients, sustaining diatom dominance and, under high wind stress, favouring nano-sized phytoplankton (nanophytoplankton and cryptophytes). ~~In contrast, low inflow conditions limit riverine nutrient supply, shifting reliance to regenerated nutrients from vertical mixing. When combined with strong winds, these conditions support nanophytoplankton growth, while short, low-wind storms favour pico-sized phytoplankton (*Synechococcus* spp. and picoeukaryotes). Across years, storms repeatedly reset seasonal succession and maintained environmental heterogeneity, leading to transient monospecific peaks of phytoplankton. These findings highlight storms as recurrent structuring forces in the EEC, mediating nutrient availability and driving shifts in phytoplankton composition; as such, storm-driven dynamics might be an important input to prediction models for phytoplankton across the summer months.~~

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1 Introduction

Coastal marine ecosystems are vulnerable to changes in weather patterns, particularly extreme events such as storms and heatwaves. ~~The coastal marine ecosystems are vulnerable to changes in weather patterns and various extreme events, such as storms and heatwaves.~~ The impact of extreme events can lead to deoxygenation, eutrophication, or the formation of harmful algal blooms in aquatic systems (Bianucci et al., 2018; Carpenter et al., 2022; Stockwell et al., 2020). ~~Existing studies~~ Studies in lakes and oligotrophic seas in tropical and subtropical

regions showed an increase in the ~~chlorophyll-a Chl-a (Chl-a chlorophyll-a)~~ with cooling of the sea surface temperature (Babin et al., 2004; Jena et al., 2012) usually lasting for 1–3 weeks following storm passage and inducing changes in phytoplankton composition by altering seasonal succession (Thyssen et al., 2014). ~~At higher~~
40 ~~latitudes, While studies in polar environments have observed appreciable Chl-a increases in oligotrophic Arctic waters (Pozdnyakov et al., 2014) and elevated primary production in the Barents and southern Chukchi Seas following cyclones (Crawford et al., 2020), the influence of such storms in coastal temperate waters remains poorly documented (Pozdnyakov et al., 2014) (Crawford et al., 2020) storm forcing has been associated with enhanced primary productivity; for example, Pozdnyakov et al., (2014) observed appreciable Chl-a increase in oligotrophic~~
45 ~~Arctic waters within days of a cyclone, while Crawford et al., (2020) reported elevated net primary production in inflow regions such as the Barents and southern Chukchi Seas. Despite these insights, the responses of rapidly changing temperate and high-latitude coastal seas to extreme events remain poorly resolved, particularly in terms of their influence on phytoplankton community structure.~~ Most existing studies rely on Chl-a and derived productivity estimates from satellite data (Crawford et al., 2020; Pozdnyakov et al., 2014; Zhao et al., 2009), yet
50 the ecological consequences of storms are reflected not only on biomass but also on shifts in community composition and seasonal succession (Robache et al., 2025; Thyssen et al., 2014).

~~In this context, we focus on the eastern English Channel (EEC), a temperate coastal sea characterized by strong atmospheric frontal activity and regularly influenced by frequent extratropical storms. Originating in the North Atlantic, these storms track towards north-western Europe, where they exert substantial physical forcing on the~~
55 ~~region's coastal waters. The English Channel is a temperate coastal sea generally characterized by strong atmospheric frontal activity and frequent extratropical storms, occasionally accompanied by thunderstorms. These systems typically originate in the North Atlantic and track towards north-western Europe, bringing prevailing south-westerly winds and enhanced precipitation (Kaspi and Schneider, 2013; Priestley et al., 2020; Priestley and Catto, 2022).~~ With rising global temperatures, weakening of the polar midlatitude temperature gradient is reducing
60 jet stream stability, leading to more persistent weather patterns and a higher frequency of extreme precipitation events in temperate regions (Crawford et al., 2023; Dietze et al., 2022; Francis et al., 2020; Pfleiderer et al., 2019). Within the English Channel, the ~~eastern English Channel (EEC)~~ is characterized by a nutrient-rich regime (Dulière et al., 2019; Lefebvre et al., 2011), particularly with an excess of nitrogen originating mainly from local rivers
65 ~~(e.g., the Somme; Loquet et al., 2000 (Loquet et al., 2000)).~~ The EEC coastline hosts numerous estuaries, including the Seine, the Somme, and several smaller systems such as the Authie, Canche, Liane, Wimereux, and Slack, which collectively contribute substantial nutrient inputs to coastal waters (Dulière et al., 2019). As a result, nutrient concentrations typically peak during the end of the winter leading to massive *Phaeocystis globosa* blooms in April–
70 ~~May each year (e.g., Breton et al., 2021; Lefebvre et al., 2011; Skouroliahou et al., 2022).~~ By contrast, the end of spring is characterized by nutrient depletion, yet episodic summer blooms of diatoms as well as ~~pico-~~
~~nanophytoplankton~~ and ~~nano-sized-pico~~phytoplankton have been observed (e.g., Houliez et al., 2023; Skouroliahou et al., 2022). Over recent decades, ~~the~~ summer season in the EEC has been increasingly dominated by ~~pico-sized~~ phytoplankton (Hubert et al., 2025a), accompanied by a decreasing trend in Chl-a concentrations (Hubert et al., 2025a; Huguet et al., 2024). Nevertheless, the causes of interannual variability in summer Chl-a concentrations and seasonal succession patterns remain poorly understood, reflecting the complex interplay among
75 hydrodynamic processes, nutrient dynamics, and meteorological forcing. In a recent study (Skouroliahou et al., 2022), the summer phytoplankton succession in the EEC has been characterized as largely stochastic, with drift

mechanisms accounting for more than 69% of community turnover. However, these authors did not identify *any* specific environmental drivers underlying these stochastic processes. In the present work, we extend phytoplankton observations over a ~~10-ten~~-year period and explore summer storm events as drivers of changes in phytoplankton composition.

The main objective of the present study was to better understand the occurrence of the summer phytoplankton blooms and *in particular* to investigate the possible effect of summer storm events on the magnitude of the blooms and *also* the phytoplankton community. ~~We were particularly interested to examine how varying intensities of river inflow and wind affect phytoplankton community structure.~~ We hypothesized that varying intensities of river inflow and wind *stress* drive distinct changes in abundance and community composition ~~during otherwise more stable summer conditions.~~ *Transient phytoplankton blooms during the nutrient-limited summer months in the eastern English Channel are a key feature of interest. A 10-year dataset (2012–2022) was used to evaluate biological responses alongside local meteorological forcing and riverine inputs.* The phytoplankton community was characterized using ~~size-based~~-functional groups derived from flow cytometry along a coastal–offshore gradient in the Strait of Dover, known as the DYPHYRAD (Dynamics of PHYtoplankton on RADiale) transect (Hubert et al., 2026) ~~(Hubert et al., 2025b) by the Strait of Dover. The dataset comprises 1835 samples collected on 268 dates during a ten-year survey (2012–2022). Storm characterization was based on Météo France meteorological data (wind and precipitation) from the Boulogne-Sur-Mer station (<https://meteo.data.gouv.fr/>) and river discharge records from Eaufrance (<https://www.eaufrance.fr/>) near the DYPHYRAD transect. In this study,~~ we examine phytoplankton community composition before and after storm events, assess the various impacts of storms on the marine environment and phytoplankton structure, and conclude with a synthesis of our findings.

2 Materials and ~~m~~Methods Section

2.1 Sampling strategy

The ~~The eastern English Channel~~ (EEC) is a shallow coastal sea where depths rarely exceed 50 m, with an average depth of 45 m between Calais and Dover (Fig. 1). The region is subject to macro- and mega-tidal regimes, with tidal amplitudes often surpassing 8 m, and it receives substantial nutrient inputs from multiple estuaries along the Picardy and Opale coasts, most notably the Seine, *and* Somme (Huguet et al., 2024), ~~Authie, Canche, Liane, Wimereux, and Slack rivers (Fig. 1).~~

*Phytoplankton data were collected between 2012 and 2022 as part of the DYPHYRAD transect (Dynamics of PHYtoplankton on RADiale; Hubert et al., 2025b). The transect spans approximately 9.7 km from coast to offshore and consists of nine stations ranging from R0 (50.8° N, 1.59° E) to R4 (50.8° N, 1.45° E) (Fig. 1). Sampling was performed aboard the research vessel *Sepia II* (CNRS INSU-FOF, Centre National de la Recherche Scientifique Institut National des Sciences de l'Univers – Flotte Océanographique Française). The “coastal–offshore” distinction was defined within the frontal area to ensure each category consistently represented coastal and offshore waters, regardless of tidal state. Because frontal waters are strongly mixed, they span both categories, and tides mainly influence only the direction of flow (northwards or southwards; Brylinski et al., 1991). To account for tidal influences on phytoplankton communities, the sampling strategy used a high-resolution (~1 km) coast–offshore transect comprising 9 stations (Fig. 1; Table 1). The transect spans approximately 9.7 km from coast to offshore, from* ~~The transect spans approximately 9.7 km from coast to offshore and consists of nine stations ranging from~~

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115 R0 (50.8° N, 1.59° E) to R4 (50.8° N, 1.45° E) (Fig. 1). To facilitate analysis of spatial patterns, stations were categorized into two zones based on their proximity to shore: coastal (R0–R2) and offshore (R2'–R4). Sampling was conducted approximately weekly from February 2012 to December 2022, providing a long-term dataset suitable for both temporal and spatial analysis. Sampling was conducted approximately weekly from February 2012 to December 2022, providing a long-term dataset suitable for both temporal and spatial analyses. The

120 DYPHYRAD network includes nine sampling stations, with tThe highest sampling frequency was recorded at station R1 he highest sampling frequency at station R1 (227 samples, Table 1). Additional details regarding data acquisition and validation are provided in Hubert et al. (2025b2026).

In addition to DYPHYRAD, we incorporated datasets from two French National Observation Systems (Systèmes Nationaux d'Observation, SNO): SNO-SOMLIT and SNO-PhytobsPHYTOBS. SNO-SOMLIT contributed data

125 from two stations (SOMLIT C and SOMLIT L) sampled 2–4 times per month (Table 1). SOMLIT (Savoye et al., 2024) contributed data from two stations (SOMLIT C and SOMLIT L), sampled two to four times per month (Table 1). SNO-PhytobsPHYTOBS contributed data from Boulogne and from station C, which is co-located with SOMLIT C. Data from SOMLIT C and PHYTOBS C were classified as coastal, while SOMLIT L represented offshore conditions. (Lemoine et al., 2024) provided data from two additional stations Wimereux (SOMLIT C) and Boulogne–I also sampled two to four times per month. Data from the SOMLIT C and Phytobs stations were classified as coastal, whereas data from SOMLIT L were considered offshore. Phytobs station Wimereux and SNO SOMLIT C share the same location.

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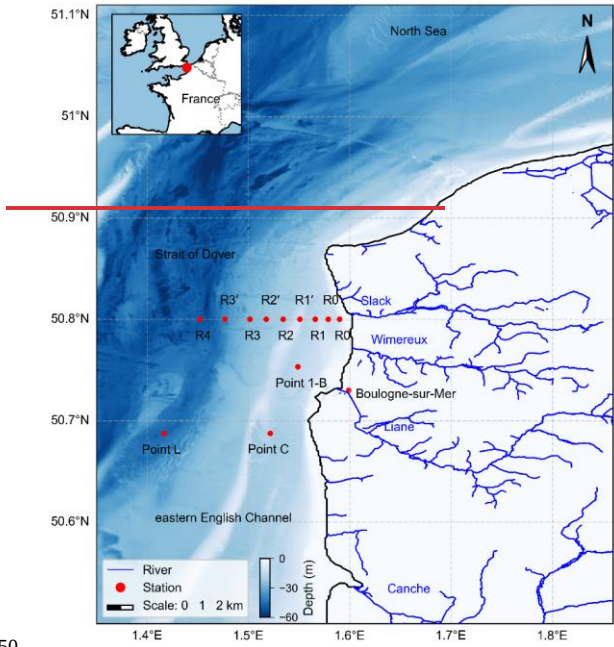
2.2 Environmental and biological parametersNutrients and Chlorophyll-a

At each station (R0–R4), sea surface temperature (T, °C) and salinity (S, PSU) were measured using a

135 conductivity-temperature-depth profiler (CTD Seabird SBE 25). Subsurface water samples (1–2 m depth) were collected along the DYPHYRAD transect to measure Chl-a, nutrients and phytoplankton abundance. Dissolved inorganic nutrients i.e., nitrite (NO_2^-), nitrate (NO_3^-), orthophosphate (PO_4^{3-}) and orthosilicic acid ($\text{Si}(\text{OH})_4$)Subsurface water samples were collected for dissolved inorganic nutrients (NO_2^- , NO_3^- , PO_4^{3-} and $\text{Si}(\text{OH})_4$. Nutrient concentrations were quantified using an autoanalyzer (AutoAnalyzer ALLIANCE SpA, Italy until 2016; then AA3 HR AutoAnalyzer, SEAL Analytical GmbH, Germany) following a protocol based on Aminot and Kérouel, (2004). Dissolved nutrients are referred to hereafter as DIN ($\text{NO}_2^- + \text{NO}_3^-$), DIP (PO_4^{3-}) and DiSi ($\text{Si}(\text{OH})_4$). Chl-a concentrations were measured using a Turner Designs 10-AU field fluorometer (Turner Designs Ltd, USA), as described in the equations developed by (Lorenzen, 1966).

140 SOMLIT SNO measurements used in this study include temperature, salinity, nutrients (nitrate, nitrite, phosphate, and silicate), all collected according to the standardized SOMLIT protocol. In addition to the DYPHYRAD transect, chlorophyll-a concentrations from the Phytobs stations (Wimereux SOMLIT C and Boulogne-I) were included in the analysis to provide a broader overview of the EEC. Further details on environmental data acquisition and sample processing are available on the SOMLIT observation network website (<https://www.somlit.fr/en/>).

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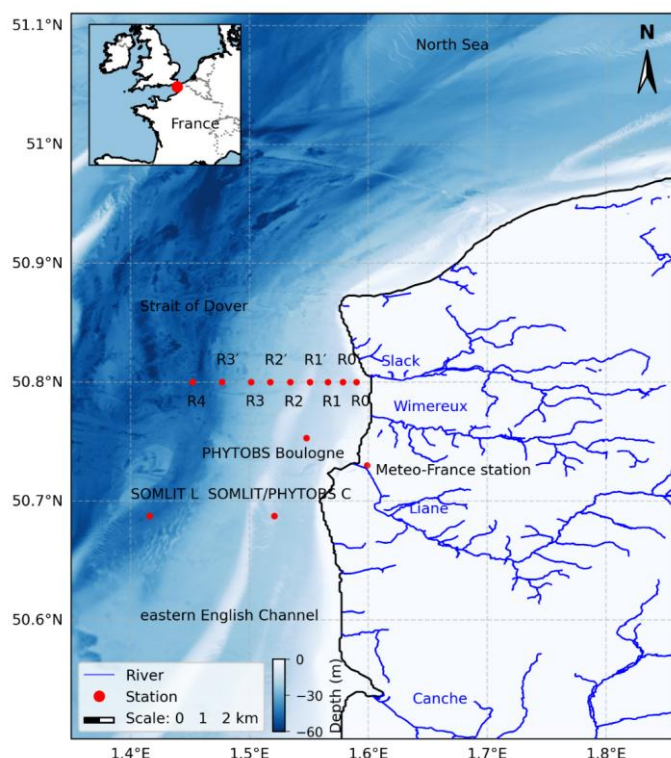


Figure 1. Map of the study area showing the locations of the DYPHYRAD stations (R0–R4), the co-located SOMLIT/PHYTOBS C, SOMLIT L, and PHYTOBS Boulogne station in the EEC near the Strait of Dover. The Météo-France station at Boulogne-sur-Mer is situated on the adjacent coastline of the EEC. Map of the study area showing the locations of DYPHYRAD stations (R0–R4), SOMLIT stations (Point L and Point C), the Phytobs station Point 1 Boulogne (Point 1-B), and the Météo-France station Boulogne-Sur-Mer in the eastern English Channel near the Strait of Dover.

2.3 Phytoplankton abundance

The DYPHYRAD dataset comprises 1835 samples collected over 268 dates during a 10-ten-year survey (2012–2022, Table 1). Single-cell optical analyses were conducted using pulse-shape recording flow cytometers (CytoSense and CytoSub, manufactured by CytoBuoy b.v., Woerden, the Netherlands), which are designed for high-resolution in vivo characterization of phytoplankton based on their optical properties. Four cytometers were used over the 11-year time series. These instruments count particles ranging from 0.1 to 800 μm in width, covering practically the entire phytoplankton size range. Technical specifications for each flow cytometer are detailed in previous studies—(Hubert et al., 2026)(Bonato et al., 2015, 2016; Hubert et al., 2025a; Louchart et al., 2020). Briefly, two protocols were employed: the "Pico" protocol used low detection thresholds (10 mV red fluorescence), low pump speed ($5 \mu\text{L s}^{-1}$), and short sampling time (5 min) to target 0.1–3 μm cells with low fluorescence and high abundance. The second protocol targeted nanophytoplankton- and microphytoplankton using higher detection thresholds (25 mV red fluorescence), high pump speed ($1013 \mu\text{L s}^{-1}$), and longer sampling time (8–10 min). The flow cytometers are equipped with a blue laser (488 nm, 50 mW) to allow discrimination between phototrophic and non-phototrophic particles. Cytoqram analysis (biplots combining scatter and fluorescence data, Hubert et al.,

2025a) was performed using CytoClus 4 software (CytoBuoy b.v., the Netherlands). Five P-phytoplankton functional groups (PFGs) were manually discriminated and characterized based on their size distribution, structural complexity, and fluorescence signals, following the interoperable vocabulary of (Thyssen et al., 2022). Five major phytoplankton groups were distinguished: picoeukaryotes (RedPico), nanophytoplankton (RedNano), microphytoplankton (mainly diatoms; RedMicro), *Synechococcus* spp. (OraPicoProk), and cryptophytes (OraNano) (Hubert et al., 2025a; Thyssen et al., 2022; Table 2).

Phytobs stations located south of the DYPHYRAD transect (50.8° N, Fig. 1) provide taxonomic information on diatoms, while SOMLIT stations supply additional pico- and nano-phytoplankton data. Bi-weekly microscopic counts from PHYTOBS PHYTOBS-Boulogne (Point 1-Boulogne) and Wimereux (SOMLIT-C) were used to identify dominant phytoplankton species in the study area. Additional datasets from SOMLIT stations C and L were used to compare pico- and nano-phytoplankton abundances with DYPHYRAD observations. microscopy data (<https://www.phytobs.fr/en>) were used only to check for the species related to the observed phytoplankton blooms, while SOMLIT data (<https://www.somlit.fr/>) provided complementary measures of temperature, salinity, nutrients (DIN, DIP and DiSi), Chl-a and flow cytometry counts of nanophytoplankton and picophytoplankton for comparison with the DYPHYRAD transect (see Fig.1 for the locations). All samples from both networks were collected at the subsurface (1–2 m) at a bimonthly frequency. SOMLIT datasets were used solely to construct the climatologies of nutrients, salinity, temperature, and Chl-a for the study area. Chl-a was the only variable for which SOMLIT and DYPHYRAD datasets also contributed to the statistical analyses. These complementary observations were not included in the statistical analysis.

Table 1. Sampling station characteristics. DYPHYRAD samples provided chlorophyll a, nutrients, and flow cytometry counts of micro-, nano-, and pico-phytoplankton. SOMLIT data (C and L) provided additional chlorophyll a and flow cytometry counts of nano- and pico-phytoplankton. PHYTOBS data provided microscopy-based counts of microphytoplankton to identify dominant taxa.

Station	Longitude (° E)	Latitude (° N)	Distance from the coast (km)	Sampling frequency	Number of samples
R0	1.59	50.8	0.95	once/twice a week	192
R0'	1.57	50.8	1.7		189
R1	1.56	50.8	2.6		227
R1'	1.55	50.8	3.7		164
R2	1.53	50.8	4.3		166
R2'	1.51	50.8	6.1		147
R3	1.50	50.8	7.3		150
R3'	1.47	50.8	9		137
R4	1.45	50.8	10.9		150
SOMLIT-PHYTOBS-C	1.52	50.68	2	fortnightly	168
SOMLIT-L	1.41	50.68	9.8		125
PHYTOBS-Boulogne	1.55	50.75	3.2		197

2.3 Storm event identification and characterization

Storm events in this study were identified as periods when wind speeds exceeded the 90th percentile (Fig. A1) (11.3 m s^{-1}). Storm length was initially identified as the ± 3 -day period surrounding the peak wind speed day, with day 3 designated as the storm day. Storm events were characterized using hourly measurements of wind speed, wind direction, and

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precipitation from the Météo-France Boulogne-Sur-Mer station (50.73° N, 1.59° E; <https://meteo.data.gouv.fr/>) for the period 2012–2022. The station is located 8 km from the DYPHYRAD transect. The 90th-percentile threshold of wind speed was calculated from a 25-year reference period (1 January 2000 to 30 June 2025).

Table 2. Flow cytometry phytoplankton groups vocabulary and brief descriptions of the phytoplankton groups and their Flow cytometry characteristics in the eastern English Channel DYPHYRAD transect (adapted from Hubert et al., 2026 and Thyssen et al., 2022).

Phytoplankton groups	Phytoplankton description	Flow Cytometry characteristics
OraPicoProk (< 3 µm)	<i>Synechococcus</i> spp., unicellular photosynthetic cyanobacteria	Orange-fluorescing prokaryote-picophytoplankton, rich in the pigment phycoerythrin
RedPico (< 3 µm)	Picophytoplankton	Red-only fluorescing picophytoplankton (not rich in phycoerythrin)
RedNano (≈ 3–20 µm)	Nanophytoplankton	Red-only fluorescing nanophytoplankton (not rich in phycoerythrin)
OraNano (≈ 3–20 µm)	Larger cyanobacteria (e.g., large-size <i>Crocosphaera</i> , <i>Richelia</i>) red algae and cryptophytes	Orange and red fluorescing nanophytoplankton, rich in the pigment phycoerythrin
HsNano (≈ 3–20 µm)	Coccolithophores, and some autotrophs and armoured dinoflagellates	Red-fluorescing nanophytoplankton with relatively high sideward light scattering properties
RedMicro (cells or chains > 20 µm)	Diatoms, and other microphytoplankton	Red-only fluorescing microphytoplankton

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Phytoplankton groups	Phytoplankton	Flow cytometry characteristics
OraPicoProk (< 3 µm)	<i>Synechococcus</i> -like, unicellular photosynthetic cyanobacteria	Orange-fluorescing prokaryote picophytoplankton, rich in Prokaryotes containing the pigment phycoerythrin
RedPico (< 3 µm)	Picophytoplankton Picoeukaryotes (chlorophytes, prasinophytes)	Red-only fluorescing picophytoplankton (not rich in phycoerythrin) Small red-fluorescent eukaryotes
RedNano (≈ 3–20 µm)	Nano-eukaryotes including haptophytes (and mainly different life stages of <i>Phaeocystis globosa</i> in the English Channel and North Sea)	Red-only fluorescing nanophytoplankton (not rich in phycoerythrin)
OraNano (≈ 3–20 µm)	Cryptophytes-like Larger cyanobacteria (e.g., <i>Crocosphaera</i> , <i>Richelia</i>) red algae and nano-flagellates cryptophytes	Orange and red fluorescing nanophytoplankton, rich in the pigment phycoerythrin

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HsNano ($\approx 3\text{--}20\ \mu\text{m}$)	Coccolithophores	Red fluorescing nanophytoplankton with relatively high sideward light scattering properties
RedMicro (cells or chains $> 20\ \mu\text{m}$)	Diatoms, and also possible detection of dinoflagellates and <i>Phaeocystis globosa</i> only if abundant	Red only -fluorescing microphytoplankton

2.3 Storm event identification and characterization

Storm events in this study were identified as periods when wind speeds exceeded the 90th percentile ($11.3\ \text{m s}^{-1}$), calculated from a 25-year reference period (2000-01-01 to 2025-06-30). Storm length was identified as the ± 3 -day period surrounding the peak wind speed day, with day 3 designated as the storm day. Storm events were characterized using hourly measurements of wind speed, wind direction, and precipitation from the Météo-France Boulogne-sur-Mer station ($50.73^\circ\ \text{N}$, $1.59^\circ\ \text{E}$; <https://meteo.data.gouv.fr/>), located 8 km from the DYPHYRAD transect, for the period 2012–2022.

Storm events in this study were identified as periods when wind speeds exceeded the 90th percentile (Fig. A1) ($11.3\ \text{m s}^{-1}$). Storm length was initially identified as the ± 3 -day period surrounding the peak wind speed day, with day 3 designated as the storm day. Storms were selected for analysis when phytoplankton abundance and environmental data were available for at least 10 days prior to the storm day and for 14 days following the peak storm event. Wind observations include both wind speed and direction (Fig. A1–A2). Wind observations were used to evaluate the wind stress at the sea surface (τ , N m^{-2}) computed as (Wu, 1982):

$$\tau = \rho_{\text{air}} C_d U^2, \quad (1)$$

where ρ_{air} is the air density (assumed here as ~~constant~~ $\rho_{\text{air}} = 1.225\ \text{kg m}^{-3}$) and the drag coefficient C_d was assumed to depend on the wind speed as (Wu, 1982):

$$C_d = (0.8 + 0.065U) 10^{-3} \quad (2)$$

The wind stress was derived from wind speed using a ± 3 -day window around each peak date. This approach allowed us to classify periods of low versus high wind forcing, which in turn served as an indicator of water column stability and the likelihood of wind-induced mixing.

Daily freshwater inflows were obtained from river ~~discharge-inflow~~ data for the Slack and Wimereux rivers, which border the transect (Fig. 1) (<https://www.eaufrance.fr/>; <https://www.eaufrance.fr/>). River flow rates were used as indicators of riverine inputs from the respective watershed areas. For the analysis, we used the combined inflow from both rivers to estimate the mean freshwater input during storm event. ~~We expect phytoplankton to respond rapidly to changes in nutrient availability.~~ In the study area, river plumes are transported under the influence of prevailing south–westerly winds (Brylinski et al., 1991, 1996). ~~Because of their close proximity to the transect, the Wimereux Estuary and the River Slack were used as indicators of local riverine influence on water chemistry.~~

Although the Slack lies north of the transect, strong tidal mixing, wind reversals and the NE–SW ebb-directed tidal flow (Brylinski et al., 1991) can transport its freshwater signal into the study area (Brylinski et al., 1991). ~~Consequently, the River Slack and the Wimereux estuary affect water chemistry along the transect earlier than other estuaries in the region (Fig. 1), thereby initiating changes in community structure.~~ Total accumulated

precipitation (mm) and mean river inflow ($\text{m}^3 \text{s}^{-1}$) were calculated over the ± 3 -day storm period (Fig. 3).
 240 Thresholds for total precipitation and mean river flow were derived from the combined June–July distribution
 across the 25-year period (Fig. B1), with the 80th percentiles used to define “High” and “Low” classes as indicators
 of storm impact (Fig. 3). In addition, interannual variability in the number of windy days (wind speed $> 8 \text{ m s}^{-1}$)
 and average river inflow ($\text{m}^3 \text{s}^{-1}$) from the Slack and Wimereux rivers during June and July near the DYPHYRAD
 transect was analyzed to characterize storm and freshwater input patterns (Fig. 4).

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245 2.4 Chl-a analysis and June–July baseline phytoplankton distribution

Whisker plots were constructed to evaluate post-storm changes in Chl-a and to examine variability in Chl-a relative
 to the average river discharge-inflow associated with each storm (Fig. 5). Due to the limited temporal coverage of
 Chl-a measurements in the DYPHYRAD dataset, Chl-a data from all available stations were used. These data were
 also employed to construct the seasonal climatology of Chl-a (Fig. C1c). Seasonal climatologies climatology-of
 250 phytoplankton abundances were derived from DYPHYRAD data (Fig. 6). To assess the impact of storm events on
 phytoplankton abundances, we calculated the empirical complementary cumulative distribution function (CCDF,
 (Helton, 1997)), which represents the probability of observing abundance greater than or equal to a particular
 abundance level. In order to focus on all values, from medium to extremes, the CCDF were displayed in log–log
 plots to emphasize extreme events (Derot et al., 2015), (Fig. 7). For each phytoplankton group, the CCDF ($P(X \geq$
 255 $x)$) was constructed from June–July observations from the DYPHYRAD dataset, providing a baseline
 distribution:

$$P(X \geq x) = 1 - F_X(x) \quad (3)$$

Where $F_X(x)$ is the cumulative distribution function of a phytoplankton abundances X and x denotes a specific
 abundance threshold (i.e., an observed value of phytoplankton abundance).

260 Shaded percentile bands (50–90%) were used to represent the expected June–July baseline variability, and
 values exceeding the 90th percentile falling outside this range were interpreted as extreme abundances (Fig. 7). The
 pre-storm window was limited to 10 days to ensure at least one available observation per station given the weekly
 sampling frequency, whereas the post-storm window was extended to 14 days to capture the propagation of
 storm-driven freshwater and nutrient inputs into the Strait of Dover. Phytoplankton abundances from the pre-storm
 265 (=10 days) and post-storm (up to 14 days) periods were compared with this baseline to determine whether post-
 storm conditions remained within, or exceeded, the typical seasonal range. This non-parametric approach avoids
 assumptions about underlying distributions and is particularly suitable in this context, as phytoplankton
 abundances are not normally distributed (Derot et al., 2015)(Derot et al., 2015). It also allows for a direct
 comparison of pre- and post-storm conditions relative to the seasonal climatology. Post-storm abundances were
 270 further examined using a distribution-wide Anderson–Darling (AD) test and a tail-focused exceedance test.

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3 Results

3.1 Storm duration, precipitation and river flow rate

Based on the availability of flow cytometry data, 10ten storms were retained for analysis, each showing distinct
 patterns in wind stress, precipitation, and river inflow. Wind speeds above 8 m s^{-1} generated wind stress exceeding
 275 0.1 N m^{-2} (Fig. 2), reaching more than 0.2 N m^{-2} during extreme winds ($> 11.3 \text{ m s}^{-1}$). Several storms persisted for

multiple days (e.g., 2016-07-02; Fig. A1), with the 2016-07-02 event representing the most intense episode, during which wind stress frequently surpassed 0.1 N m^{-2} (Fig. 2). Storm-associated wind stress varied considerably among events (Fig. 2). Most storms were characterized by sustained windy conditions, with median and interquartile range (IQR) values close to 0.1 N m^{-2} , whereas others were weaker, marked only by short bursts of strong winds (2016-06-20, 2020-06-06, 2022-06-06). The consistently windy storms included 2012-06-22, 2012-07-12, 2013-06-15, 2015-06-02, 2015-07-13, 2016-07-02, and 2020-07-27 (Fig. 2; Table 3). Across all events, wind speeds exceeding 8 m s^{-1} originated predominantly from south-westerly directions (Fig. A2). Wind speeds above 8 m s^{-1} generated wind stress exceeding 0.1 N m^{-2} (Fig. 2), reaching more than 0.2 N m^{-2} during extreme winds ($> 11.3 \text{ m s}^{-1}$). The storm event on 2016-07-02 exhibited the longest duration of winds above 8 m s^{-1} (86 h; Fig. A1, Appendix) and the strongest wind-stress forcing (mean = 0.12 ; SD = 0.09 N m^{-2} ; Fig. 2). Across all events, wind speeds exceeding 8 m s^{-1} originated predominantly from south-westerly directions (Fig. A2 in Appendix A).

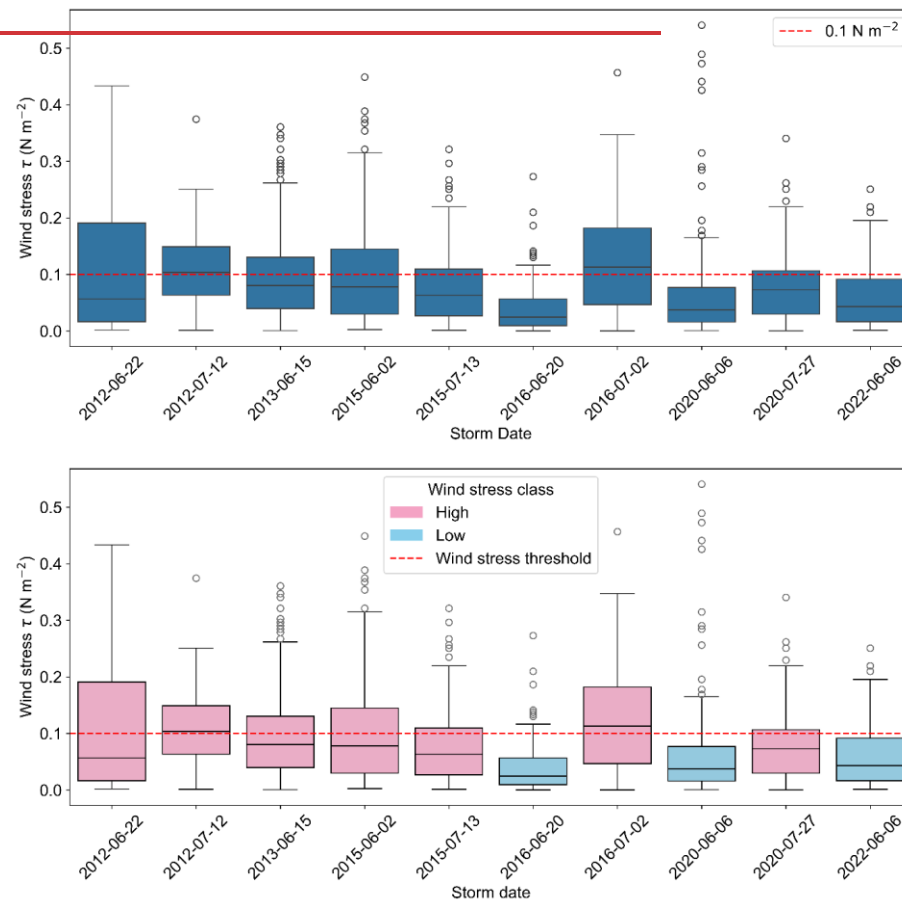


Figure 2. Boxplots of wind stress (τ ; N m^{-2}) distributions across the 10 storms, derived from wind speed measurements over ± 3 days around each storm event at Boulogne-sur-Mer (Meteo-France station). The red dashed line marks the wind-stress

threshold (0.1 N m^{-2}). Storms were classified as high (pink) or low (blue) wind stress. “High” storms are those for which the upper quartile (Q3) exceeded the set wind stress threshold of 0.1 N m^{-2} (dashed line), threshold used to categorize storms as high or low wind stress.

295 Figure 3 presents total precipitation and average flow rate during each storm event. Precipitation amounts ranged from 1 mm (2015-07-13) to 32.20 mm (2016-06-20) over the ± 3 -day window surrounding each storm (Fig. 3a). High precipitation and high inflow were defined using the 80th percentile of their respective June–July distributions, corresponding to thresholds of 16.12 mm and “High” precipitation was defined as $\geq 16.12 \text{ mm}$, and “High” inflow as $\geq 0.45 \text{ m}^3 \text{ s}^{-1}$ (Fig. B1 in Appendix B). In most cases, precipitation amounts corresponded with
300 flow rates, with high precipitation events typically producing high inflows (Fig. 3b). Exceptions included the 2020-07-27 and 2022-06-06 storms, where this relationship did not hold. Similarly, the 2016-07-02 storm showed low precipitation at Boulogne-sur-mer but was associated with elevated inflows (Fig. 3b). Across all events, discharge-inflow ranged from a minimum of $0.18 \text{ m}^3 \text{ s}^{-1}$ (2015-07-13) to a maximum of $1.98 \text{ m}^3 \text{ s}^{-1}$ (2016-06-20). River discharge-inflow strongly influenced environmental variables (Fig. C1 a–f, in Appendix C). Salinity, which
305 decreased below the climatological mean of 34.42 PSU during “High” inflow storms (Fig. C1b in Appendix C). Events in 2012, 2013, and 2016 were associated with elevated inflows and a corresponding reduction in salinity produced marked salinity reductions (33.4 – 34.0 PSU ; Table 3). The highest discharge-inflow rate ($1.976 \text{ m}^3 \text{ s}^{-1}$ on 2016-06-20) corresponded to the lowest observed salinity (33.4 PSU). In contrast, storms with “Low” inflow (2015-06-02, 2015-07-13, 2020-07-27, 2022-06-06) had little effect on salinity (post-storm salinity
310 $> 34.0 \text{ PSU}$), and in the case of 2022-06-06 (34.572 PSU) salinity (34.572) did not fall below the climatological mean (Table 3). Elevated discharge-inflow events were also linked to substantial increases in nutrient concentrations. Because pre-storm nutrient samples were limited (1 sample per station within the 10-day pre-storm window) and did not consistently capture conditions immediately before each event, we used climatological means as the reference baseline (Fig. C1 d–f in Appendix C). Summer nutrient concentrations were typically low, while
315 post-storm concentrations exceeding these baselines therefore indicated anomalous nutrient inputs. For example, the 2016-06-20 storm exhibited DIN and DiSi(OH)_4 concentrations of $3.0 \mu\text{mol L}^{-1}$, while the 2012-06-22 event, characterized by strong winds and relatively high discharge-inflow, yielded DIN concentrations of $1.52 \mu\text{mol L}^{-1}$, DIP concentrations of $0.39 \mu\text{mol L}^{-1}$, and DiSi(OH)_4 concentrations of $3.136 \mu\text{mol L}^{-1}$ (Table 3). Other events also alleviated nutrient limitation, including the 2012-07-12 and 2015-07-13 storms (Table 3).
320 However, due to the relatively low sampling frequency, some storm-related changes in salinity and nutrient concentrations (e.g., from mixing or riverine supply) may not have been captured, as in the cases of 2016-07-02 and 2013-06-15.

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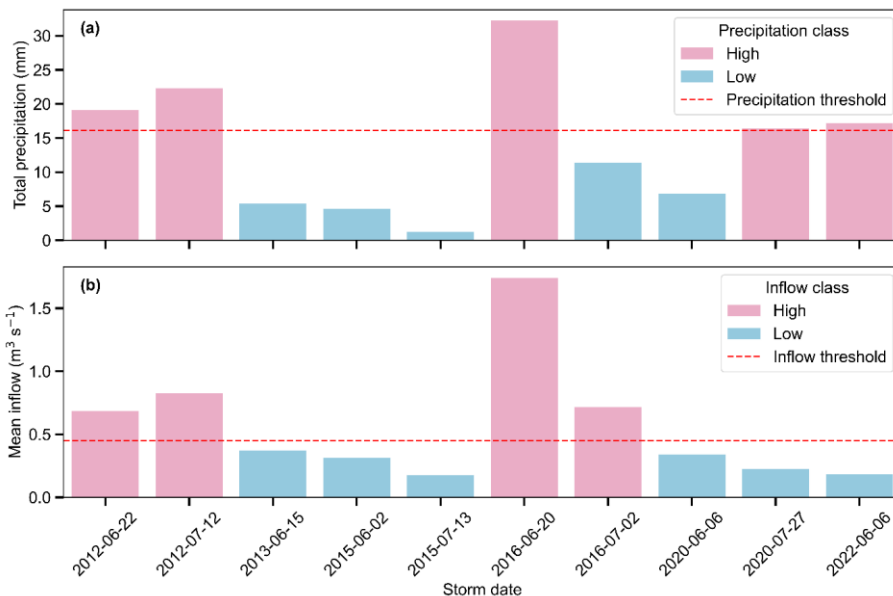
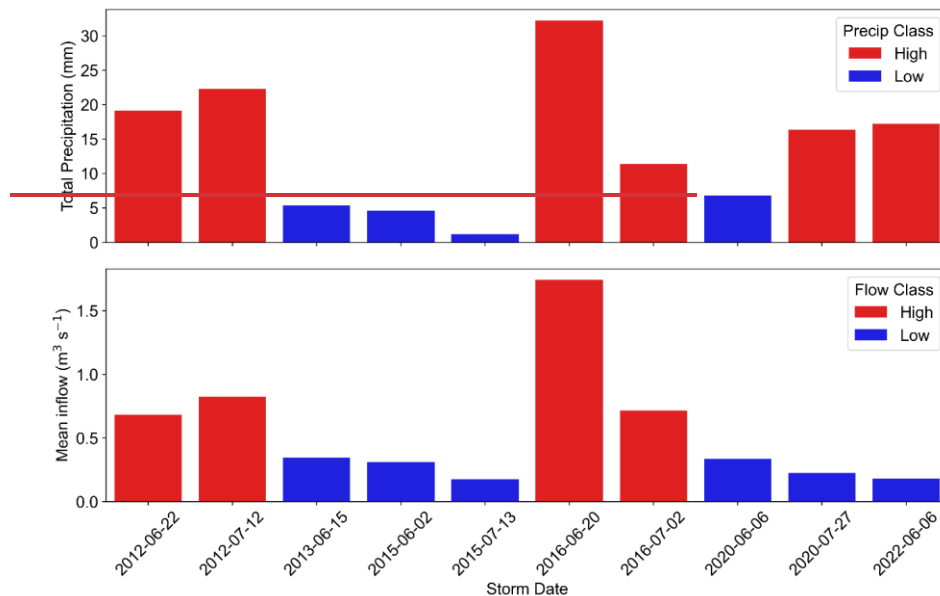


Figure 3. (a) Total precipitation (mm) over ± 3 days at Boulogne-sur-Mer (Meteo-France station) (a) and mean river inflow ($\text{m}^3 \text{s}^{-1}$) (b) from the Slack and Wimereux rivers for 10 storms, averaged over ± 3 days around each storm. Precipitation and inflow classes ("High" and "Low") were defined based on the 80th percentile of their respective June–July distributions. The corresponding threshold values are 16.12 mm for precipitation and 0.45 $\text{m}^3 \text{s}^{-1}$ for inflow. Precipitation classes ("High" and "Low") were defined from June–July rainfall distribution, with the high threshold set at 16.12 mm (80th percentile); inflow classes were defined from June–July river-flow distribution, with the high threshold set at 0.45 $\text{m}^3 \text{s}^{-1}$ (80th percentile). Blue

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bars denote “Low” class and red bars denote “High” class in both panels. Pink bars denote “High” class and blue bars denote “Low” class in both panels.

Interannual variability in the number of windy days (days with wind speed $> 8 \text{ m s}^{-1}$; at least 10 days per month) and average river inflow ($\text{m}^3 \text{ s}^{-1}$) from the Slack and Wimereux rivers during June and July near the DYPHYRAD transect was analyzed to characterize weather patterns (Fig. 4). Pronounced interannual variability was observed in June–July wind speeds and river inflows (Fig. 4). Years with high inflows (2012, 2013, 2016, 2021) exhibited June–July mean discharge/inflow above $0.35 \text{ m}^3 \text{ s}^{-1}$ (Fig. 4) and included storms such as 2012-06-22, 2012-07-12, 2013-06-15, 2016-06-20, and 2016-07-02. In contrast, periods with low monthly inflows (2014, 2015, 2017, June 2018, July 2019, 2020, 2022; Fig. 4) encompassed storms such as 2015-06-02, 2015-07-13, 2020-07-27, and 2022-06-06. Some years were characterised by notably windy days-conditions (days with wind speeds $> 8 \text{ m s}^{-1}$; at least ≥ 10 days per month) despite low inflows, including July 2014, 2015, July 2017, July 2020, and June 2022. June–July months in 2015 and July 2020 all experienced more than 24 windy days above 8 m s^{-1} , coupled with June–July average river flow below $0.35 \text{ m}^3 \text{ s}^{-1}$ (Fig. 4).

Thus, storm impacts arose either from high inflows, from strong winds alone, or from low inflows combined with short windy events (e.g., 2022-06-06). Storms were classified as consecutive when they occurred shortly after a preceding or following storm, such that the effects of the consecutive storms could have persisted. For example, the 2016-07-02 storm followed the 2016-06-20 event, suggesting that storm-driven changes in the marine environment may have been sustained between them. A similar sequence occurred in 2012, when the 2012-07-12 storm followed the 2012-06-22 event.

Table 3. Overview of selected storm events. Storm date, wind stress, precipitation and inflow are classified as High (X) or Low (O). High wind stress events correspond to those for which the event-specific upper quartile (Q3) exceeds 0.1 N m^{-2} (see Fig. 2). High precipitation and high inflow events are defined as those exceeding the 80th percentile thresholds (16.12 mm and $0.45 \text{ m}^3 \text{ s}^{-1}$, respectively; see Fig. 3a, b). Salinity and nutrients represent the lowest and highest values, respectively, available in our dataset during the post-storm period. Salinity and nutrients represent the lowest and highest values, respectively, available in our dataset after each storm event.

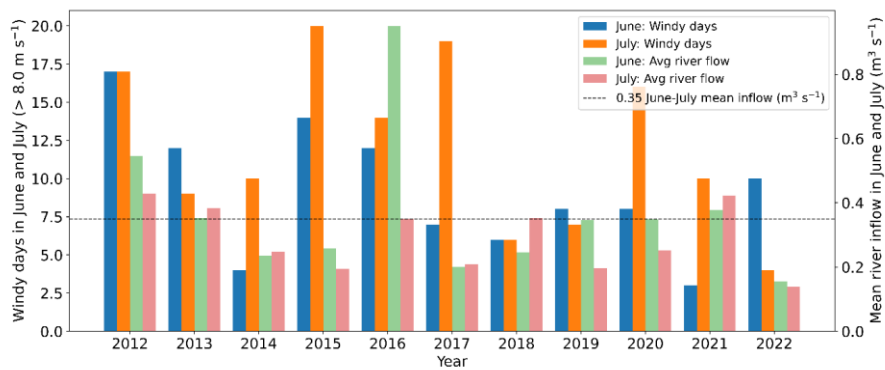
Date of storm	Most rainy	Most windy	Shortest	Least inflow	Salinity, PSU (Lowest after storm)	Nutrients, $\mu\text{mol L}^{-1}$ (Highest after storm)
2012-06-22	X	X			34.04	DIN (1.523) DIP (0.39) Si(OH) ₄ (3.136)
2012-07-12	X	X			33.6	DIN (1.517)

2013-06-15		X			33.64	DIP (0.001) Si(OH) ₄ (1.056) DIN (0.656) DIP (0.096) Si(OH) ₄ (0.031)
2015-06-02		X		X	34.2	DIN (1.124) DIP (0.079) Si(OH) ₄ (0.001)
2015-07-13		X		X	34.19	DIN (2.316) DIP (0.342) Si(OH) ₄ (0.843)
2016-06-20	X		X		33.41	DIN (3.005) DIP (0.091) Si(OH) ₄ (3.006)
2016-07-02	X	X			33.92	DIN (0.632) DIP (0.091) Si(OH) ₄ (0.001)
2020-06-06			X		33.959	DIN (0.56) DIP (0.146) Si(OH) ₄ (1.748)
2020-07-27	X	X		X	34.571	DIN (0.749) DIP (0.089) Si(OH) ₄ (0.019)
2022-06-06	X		X	X	34.572	DIN (0.732) DIP (0.065) Si(OH) ₄ (1.65)
Storm date (y-m-d)	Wind S _{stress}	Precipitation	Inflow	Salinity	Dissolved inorganic nutrients (DIN/DIP/DiSi, μmol L ⁻¹)	
2012-06-22	X	X	X	34.04	1.523	/
					0.39	/
					3.136	
2012-07-12	X	X	X	33.6	1.517	/
					0.001	/
					1.056	
2013-06-15	X	O	O	33.64	0.656	/
					0.096	/
					0.031	
2015-06-02	X	O	O	34.2	1.124	
					/	0.079

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2015-07-13	X	O	O	34.19	$\downarrow$ 0.001
					2.316
					$\downarrow$ 0.342
					$\downarrow$ 0.843
2016-06-20	O	X	X	33.41	3.005
					$\downarrow$ 0.091 $\downarrow$
					3.006
2016-07-02	X	O	X	33.92	0.632
					$\pm$ 0.091 $\pm$
					-0.001
2020-06-06	O	O	O	33.959	0.56
					$\pm$ 0.146
					$\pm$ 1.748
2020-07-27	X	X	O	34.571	0.749
					$\pm$ 0.089
					$\pm$ 0.019
2022-06-06	O	X	O	34.572	0.732
					$\pm$ 0.065
					$\pm$ 1.65



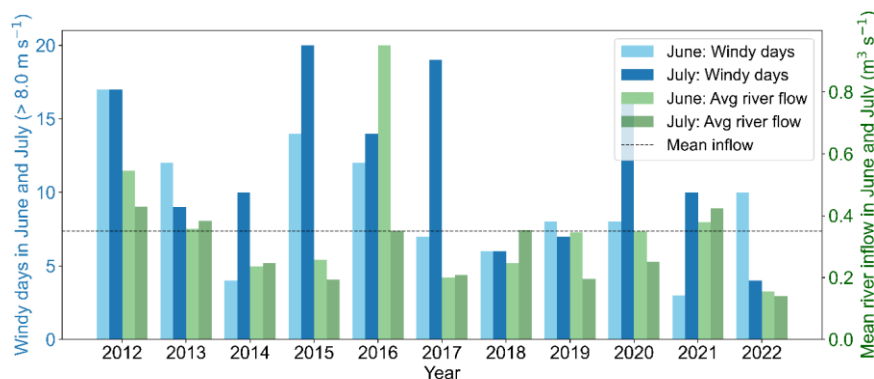
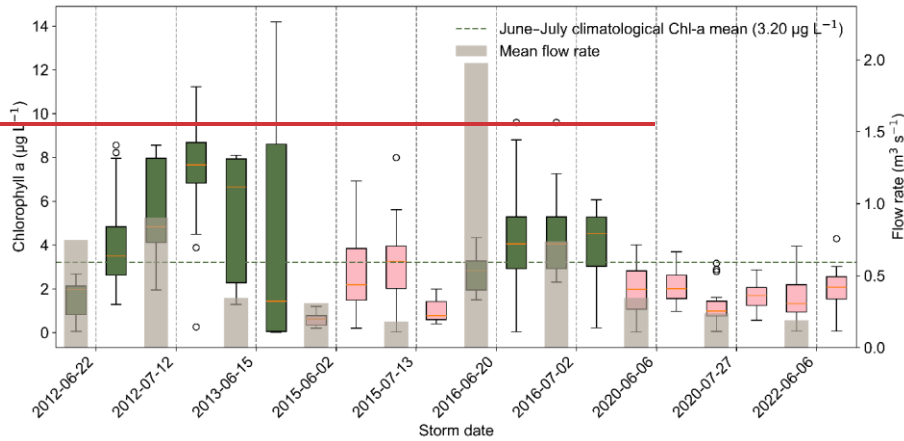


Figure 4. Number of windy days (wind speed > 8 m s⁻¹) at Boulogne-sur-Mer (Meteo-France station) and average river flow (m³ s⁻¹) from the Slack and Wimereux rivers during June and July (2012–2022). The dashed line indicates the mean June–July inflow of 0.35 m³ s⁻¹. The blue bars indicate the number of days with wind speed > 8 m s⁻¹ during June–July and the green bars indicate mean June–July inflow.

3.2 Exploring summer storm impact on Chl-a and phytoplankton communities

Storms were characterized by the biological response of Chl-a assessed through their pre- and post-storm distributions. Pre-storm mean Chl-a concentrations increased following nearly all storm events, except for those on 2013-06-15 and 2015-07-13 (Fig. 5). In high inflow storms (depicted in greenpink-shades, Fig. 5), post-storm mean increases persisted above the June–July climatological mean of 3.20 µg L⁻¹. The consecutive storm events of 2012 resulted in up to a 4-fold increase in Chl-a concentrations, whereas the consecutive events of 2016 maintained concentrations above the 3.20 µg L⁻¹. A similar persistence of elevated Chl-a was observed following the 2013-06-15 storm, despite the relatively low inflow (depicted in pink-shadeblue, Fig. 5) of 0.35 m³ s⁻¹. A subsequent event on 2013-06-22, with a mean flow rate of 0.39 m³ s⁻¹, occurred within the 14-day post-storm window and is therefore considered part of the same response as the 2013-06-15 storm. In-contrast, The lowremaining low inflow storms (depicted in pinkblue-shade, Fig. 5) did not elevate post-storm mean Chl-a concentrations above 3.20 µg L⁻¹. Post-storm responses in Chl-a distribution were more closely aligned with river inflow than with precipitation, as illustrated by the 2020-07-27 and 2022-06-06 storms (Fig. 5; Fig. E1 in Appendix

E).



390 The 15-day climatology derived from weekly to biweekly data captured spatial and temporal variations in
 phytoplankton abundances within each month and revealed that distinct groups characterize different periods of
 the year (Fig. 6a–f). RedMicro (diatoms and other microphytoplankton) reached abundances on the order of
 10^5 cells L^{-1} , increasing from late winter to late spring and declining during summer (Fig. 6a). A sharp increase in
 RedNano (10^5 cells L^{-1}) from late March to early May reflected the recurring *Phaeocystis globosa* blooms in EEC
 waters. After spring, RedNano abundances were sustained by nanophytoplankton at $\sim 10^5$ cells L^{-1} (Fig. 6b). Other
 395 nano-sized groups showed distinct seasonal peaks: HsNano (eoccolithophorids) in summer and autumn (Fig. 6c),
 and OraNano (cryptophytes), which increased steeply from June through autumn, reaching $\sim 10^5$ cells L^{-1} (Fig. 6d).

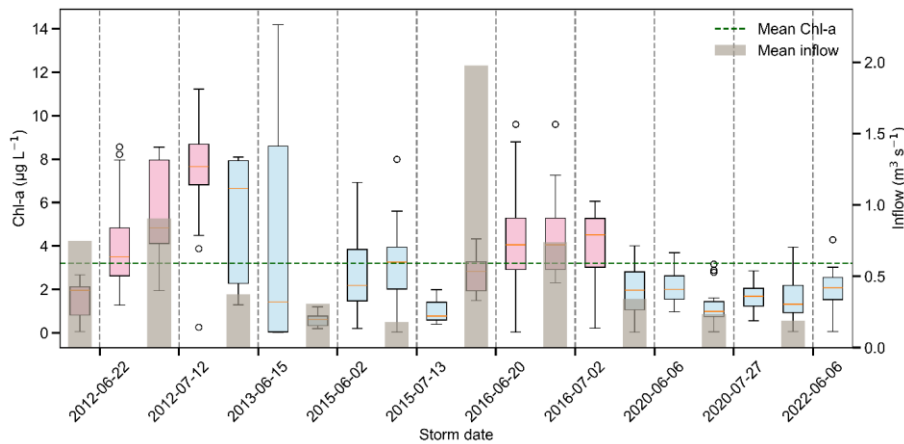
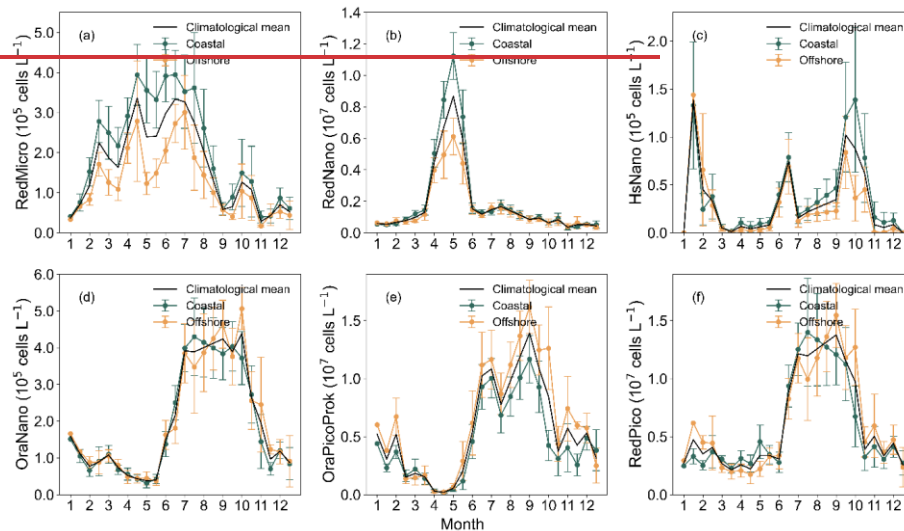


Figure 5. Boxplots of pre- and post-storm Chlorophyll a (Chl-a) distributions (compiled from DYPHYRAD and
 400 SOMLIT) concentrations for before and after the 10 storms. Vertical dashed lines indicate the day of each storm event.
 Pre-storm Chl-a distributions are shown together with mean inflow over a ± 3 -day storm period (grey bars), with river inflow
 (pink bars) and mean inflow (grey bars) overlaid. The green dashed line marks the June–July climatological mean of Chl-a
 concentration ($3.20 \mu g L^{-1}$) in the eastern English Channel EEC. Pink and blue colouring indicate “High” and “Low” inflow
 storms, respectively. Data are compiled from DYPHYRAD and SOMLIT stations. Green and pink shading indicate “High”
 405 and “Low” inflow storms, respectively.

The 15-day climatology derived from weekly to biweekly data captured spatial and temporal variations in phytoplankton abundances within each month and revealed that distinct groups characterize different periods of the year (Fig. 6a–f). RedMicro (diatoms) reached abundances on the order of 10^5 cells L^{-1} , increasing from late winter to late spring and declining during summer (Fig. 6a). A sharp increase in RedNano (10^7 cells L^{-1}) from late March to early May reflected the recurring *Phaeocystis globosa* blooms in EEC waters (Fig. 6b). After spring, RedNano abundances were sustained at $\sim 10^6$ cells L^{-1} . Other nanophytoplankton groups showed distinct seasonal peaks: HsNano (coccolithophorids) in summer and autumn (Fig. 6c), and OraNano (cryptophytes), which increased steeply from June through autumn, reaching $\sim 10^5$ cells L^{-1} (Fig. 6d). During summer, the phytoplankton community was dominated by pico-sized phytoplankton groups, with abundances on the order of 10^7 cells L^{-1} (Fig. 6e–f), including OraPicoProk (*Synechococcus*) and RedPico (picoeukaryotes). The climatology also revealed high standard errors in diatom, pico-sized phytoplankton, and cryptophyte abundances, indicating greater variability during June–July. Spatially, RedMicro were more abundant in coastal waters (Fig. 6a), whereas *Synechococcus* dominated offshore waters (Fig. 6e).



Chl-a exhibited similar seasonal and spatial patterns, increasing from late winter to late spring and declining during summer (Fig. C1e). In June and July, *Synechococcus* (OraPicoProk) and picoeukaryotes (RedPico) exhibited the highest mean (8.9×10^6 and 8.4×10^6 cells L^{-1} , respectively), while coccolithophores (HsNano) showed the lowest. Intermediate mean values were observed for nanophytoplankton (1.4×10^6 cells L^{-1}), diatoms (3.4×10^5 cells L^{-1}), and cryptophytes (2.6×10^5 cells L^{-1}) (Fig. 5). An empirical complementary cumulative distribution function (CCDF) was applied to detect shifts in phytoplankton abundances by quantifying the probability of blooms exceeding climatological ranges (Fig. 7A–D). Four storm types were considered. The first type was characterized by high inflow with low wind stress, exemplified by the storm of 2016-06-20, which was the rainiest and had the highest inflow, while showing the least impact of wind (Fig. 2–3). The second type consisted of consecutive storms, with the storm of 2016-07-02 occurring immediately after the previous storm on 2016-06-20. The third type was defined by low inflow with high wind stress, represented by the storm of 2015-07-15, which had the lowest rainfall and inflow but was marked by strong winds (Fig. 2–3). The fourth type involved low inflow with

low wind stress, illustrated by the short storm of 2022-06-06, which was classified as high in precipitation yet remained among the lowest in inflow and wind stress. To illustrate changes in community structure across these contrasting storm regimes, see Fig. 7A–D and Table G. The CCDFs of the remaining six storms are presented in the appendix with these storm characterizations (Fig. F1–6).

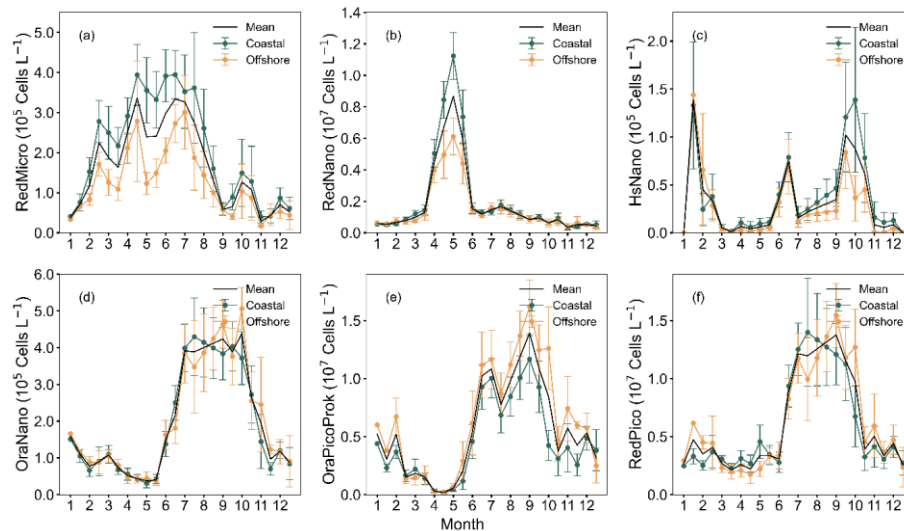


Figure 6. Climatological means and standard errors of phytoplankton abundances in the Coastal (R0–R2) and Offshore (R2'–R4) regions along the DYPRAD transect, based on 15-day means from February 2012 to December 2022. The black line represents the mean value across all stations. (a) RedMicro (diatoms), (b) RedNano (nanoeukaryotes), (c) HsNano (coccolithophorids), (d) OraNano (cryptophytes), (e) OraPicoProk (*Synechococcus*), and (f) RedPico (picoeukaryotes), respectively (see also Table 2). Seasonal and spatial variability of phytoplankton abundances in the eastern English Channel, based on 15-day climatological means from February 2012 to December 2022 estimated from DYPRAD data. Mean values (circles) and standard errors (error bars) are shown for coastal (green) and offshore (orange) stations. Subplots (a–f) represent RedMicro (diatoms), RedNano (nanophytoplankton), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes), respectively.

An empirical complementary cumulative distribution function (CCDF) was applied to detect shifts in phytoplankton abundances by quantifying the probability of blooms exceeding climatological ranges (Fig. 7A–D). Four storm types were considered. The first type was characterized by high inflow with low wind stress, exemplified by the storm of 2016-06-20, which was the rainiest and had the highest inflow, while showing the least impact of wind. The second type consisted of consecutive storms, with the storm of 2016-07-02 occurring immediately after the previous storm on 2016-06-20. The third type was defined by low inflow with high wind stress, represented by the storm of 2015-07-13, which had the lowest precipitation and inflow but was marked by strong winds. The fourth type involved low inflow with low wind stress, illustrated by the short storm of 2022-06-06, which was classified as high in precipitation yet remained among the lowest in inflow and wind stress. The CCDFs of the remaining six storms are presented in the appendices with these storm characterizations (Figs. F1–F6 in Appendix F).

3.2.1 High inflow, low wind stress storm: 2016-06-20

The storm on 2016-06-20 had contrasting impacts across phytoplankton groups and locations. In coastal waters, diatoms responded most strongly, while offshore the dominant signal came from *Synechococcus* (Fig. 7A), mirroring broader summer seasonal patterns (Fig. 6). This event was characterized by high inflow and heavy-high rainfallprecipitation, with only short-lived wind stress (Fig. 2), conditions that delivered substantial nutrient inputs to the coast. Across the DYPHYRAD transect, diatom abundances increased significantly from pre- to post-storm (Table G; Anderson–Darling test, $p = 0.001$; Table G1 in Appendix G), with a five-fold rise in the mean (Fig. 7A(a)). At the stations closer to the coast R0–R1, diatom concentrations approached the 90th percentile, and the maximum post-storm abundance was 8.0×10^5 cells L⁻¹. Note that at Point 1 BPHYTOBS Boulogne on 23 June 2016–06-23, the diatom *Leptocylindrus danicus* reached 3.0×10^6 cells L⁻¹ (Table H1 in Appendix H), representing 90% of the diatom-microphytoplankton assemblage, and was accompanied by a Chl-a concentration of $9.6 \mu\text{g L}^{-1}$.

In contrast, nanoeukaryotesphytoplankton and cryptophytes declined well below their June–July climatological means (14 and 2.6×10^5 cells L⁻¹, Fig. 6b, 6d respectively), with the sharpest decreases observed at station R0–R1 closer to the coast (Fig. 7A(b–d)). Pico-sizedphytoplankton groups, however, showed a different pattern. *Synechococcus* abundances were more than two-fold higher than the climatological mean (8.9×10^6 cells L⁻¹, Fig. 6e), reaching a post-storm mean of 1.6×10^7 cells L⁻¹ across the DYPHYRAD transect (Fig. 7A(e)). Offshore stations (R2–R3, R3–R4) exhibited the strongest response, with abundances exceeding the 90th-percentile and peaking at 2.5×10^7 cells L⁻¹. Picoeukaryotes, by contrast, showed only a slight reduction, maintaining abundances close to their climatological levels (Fig. 7A(f)).

Fig. 7A — High inflow, low wind stress storm: 2016-06-20

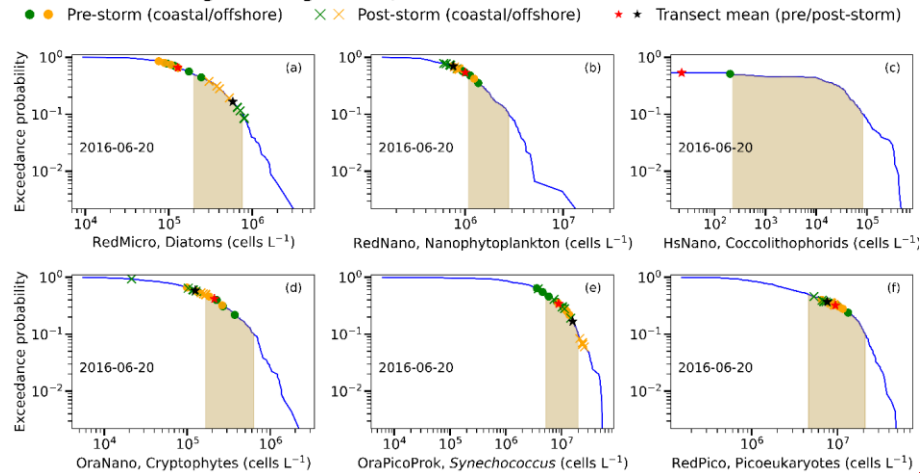


Fig. 7B — Consecutive storm: 2016-07-02 (following 2016-06-20)

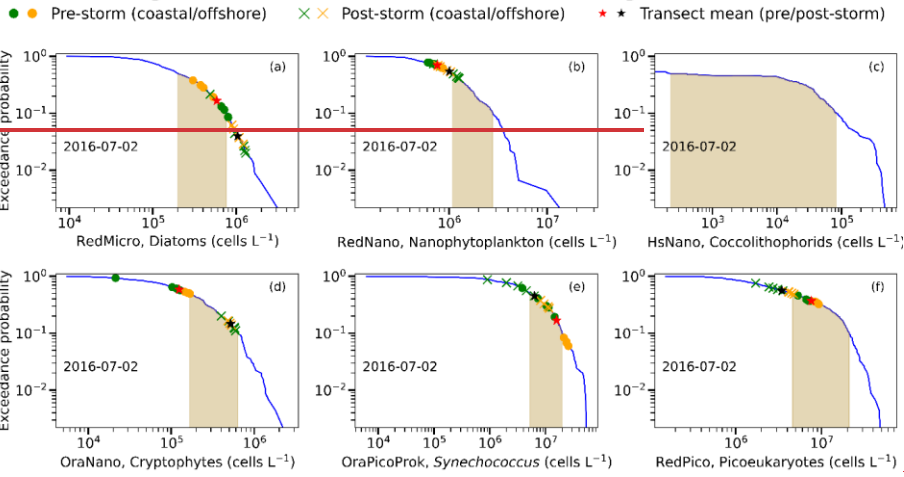


Fig. 7C — Low inflow, high wind stress storm: 2015-07-13

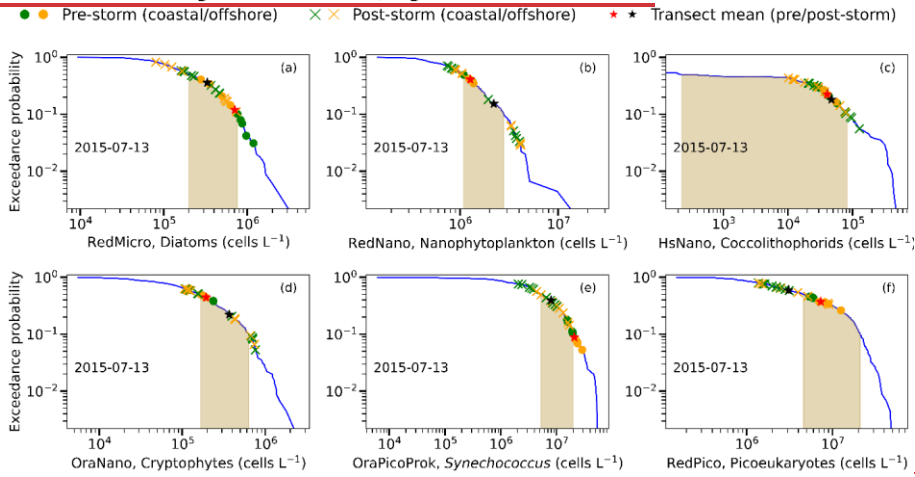


Fig. 7D — Low inflow, low wind stress storm: 2022-06-06

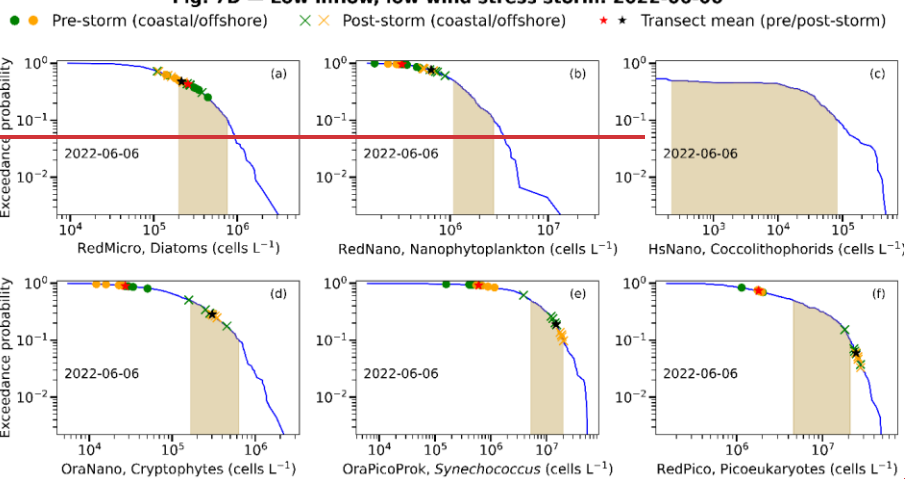


Fig. 7A

High inflow, low wind stress storm: 2016-06-20

● ● Pre-storm (coastal/offshore) ▲ ▲ Post-storm (coastal/offshore) ★ ★ Transect mean (pre/post-storm)

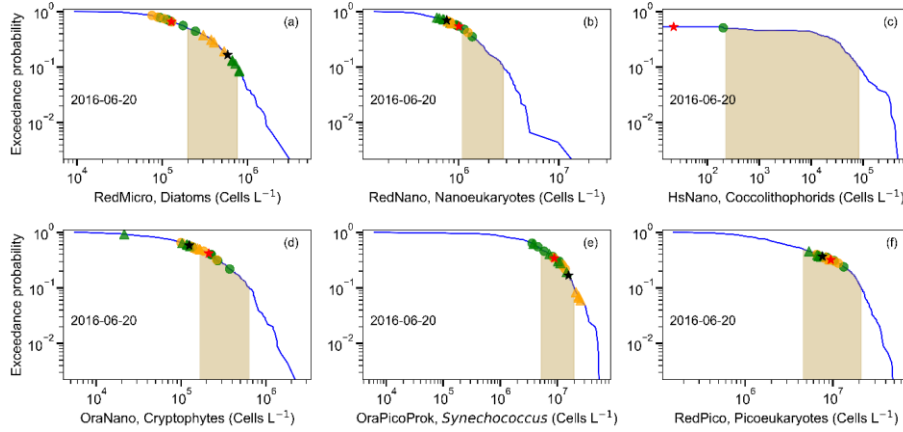


Fig. 7B

Consecutive storm: 2016-07-02 (following 2016-06-20)

● ● Pre-storm (coastal/offshore) ▲ ▲ Post-storm (coastal/offshore) ★ ★ Transect mean (pre/post-storm)

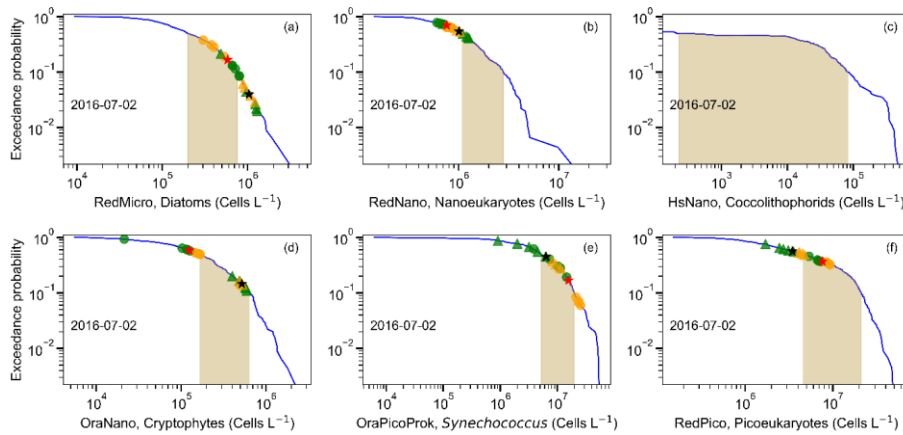


Fig. 7C

Low inflow, high wind stress storm: 2015-07-13

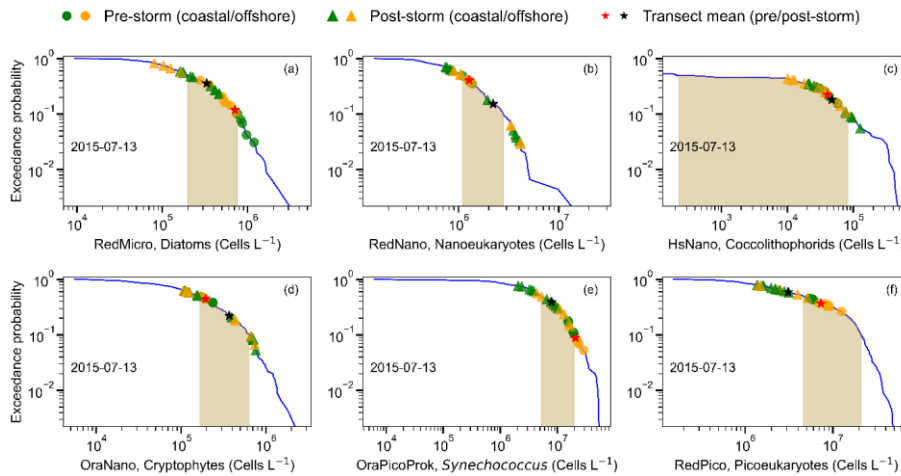


Fig. 7D

Low inflow, low wind stress storm: 2022-06-06

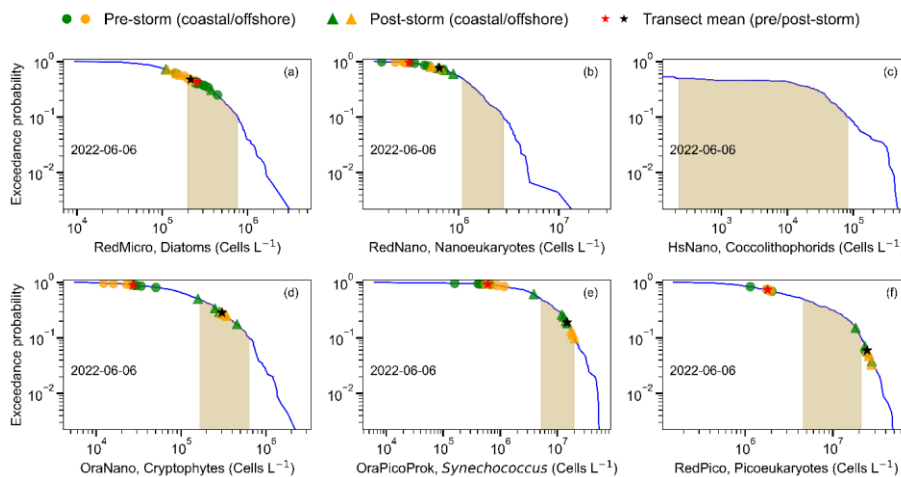


Figure 7. Exceedance probability (CCDF) distributions of six phytoplankton groups (a-f) along the DYPHYRAD transect during selected storms. Panels show: (A) 2016-06-20, (B) 2016-07-02, (C) 2015-07-13, and (D) 2022-06-06. For each panel: RedMicro (diatoms), RedNano (nanoeukaryotes), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes) are shown as subplots (a-f within each panel) presented. Blue lines represent June-July climatological distributions, with shaded areas indicating the 50th-90th-percentiles. Pre-storm (-10 days) and post-storm (+14 days) observations are plotted as green (coastal) and orange (offshore) symbols: circles for pre-storm and crosses-triangles for post-storm abundances. Red and black stars indicate the transect mean abundances before and after the storm, respectively.

3.2.2 High inflow consecutive storm: 2016-07-02

The 2-July-2016-07-02 storm was the windiest event recorded in the analysis (Fig. 2), arriving less than two weeks after the 20-June-2016-06-20 storm and forming a consecutive high inflow sequence. Before this storm, the phytoplankton community was characterized by high abundances of both diatoms and *Synechococcus* (Fig. 7A).

This back-to-back pattern illustrates how successive storms can reinforce impacts, in this case triggering a pronounced shift toward diatom dominance in the community structure (Fig. 7B). ~~Before the storm, the phytoplankton community was characterized by high abundances of both diatoms and *Synechococcus* (Fig. 7A).~~

Following the storm, diatoms surged dramatically across the DYPHYRAD transect (Fig. 7Ba), with post-storm abundances exceeding the 90th -percentile (AD test, $p = 0.0013$ and Table G, tail-exceedance test, $p < 10^{-7}$;

Anderson-Darling test, $p = 0.0013$ Table G1 in Appendix G). Diatom abundances doubled relative to pre-storm levels, reaching a mean of 1.1×10^6 cells L⁻¹, with peaks of 1.3×10^6 cells L⁻¹ at coastal stations and 1.2×10^6 cells L⁻¹ offshore (Fig. 7B(a)). ~~This bloom marked a shift in dominance from *Leptocylindrus danicus* to~~

~~*Chaetoceros socialis*.~~ At Point L-BPHYTOBS Boulogne (Fig. 1), the planktonic diatom *Chaetoceros socialis* reached 1.8×10^6 cells L⁻¹ on 4 July 2016-07-04 (Table H1 in Appendix H), accompanied by a Chl-a concentration of 7.26 µg L⁻¹. ~~This bloom marked a shift in dominance from *Leptocylindrus danicus* to *Chaetoceros socialis*.~~

Other groups responded differently. Nano-eukaryotes phytoplankton showed only slight increases (Fig. 7B(b)), while cryptophytes rose sharply with a more than a four-fold increase at all stations. (Fig. 7B(d)), with a post-storm mean of 5.2×10^5 cells L⁻¹. At Point L-SOMLIT L (Fig. 1) on 6 July 2016-07-06, cryptophyte abundance peaked at 1.2×10^6 cells L⁻¹ (Table H2 in Appendix H), indicating a pronounced offshore response.

In contrast, *Synechococcus* declined markedly, with post-storm abundances reduced nearly three-fold to a mean of 6.3×10^6 cells L⁻¹, particularly offshore (Fig. 7B(e)). Picoeukaryotes also decreased, maintaining abundances below pre-storm levels. Both *Synechococcus* and picoeukaryotes declined significantly relative to pre-storm conditions (Table G; AD tests, $p = 0.014$ and tail-exceedance test, $p = 0.001$, respectively; Table G1 in Appendix G), underscoring the contrasting trajectories of pico- and nano-sized groups compared with the strong diatom bloom).

Similar transient yet recurrent responses were observed across the summer years. *Leptocylindrus danicus* dominated June diatom blooms between 2016 and 2020, except in 2018 when *Pseudo-nitzschia* prevailed ($\sim 10^6$ cells L⁻¹; Skouroliaou et al., 2024), contributing 90% of total diatom abundance at PHYTOBS C. Comparable storm-driven diatom dominance was observed in earlier years. In June–July 2012, consecutive high-inflow storms sustained strong coastal diatom blooms, with mean abundances of 8.4×10^5 cells L⁻¹ (Fig. F2a in Appendix F) and post-storm mean Chl-a concentrations of 7.12 µg L⁻¹ (Fig. 5). Following the 2012-06-19 storm, *Leptocylindrus danicus* peaked at 7.6×10^5 cells L⁻¹ at PHYTOBS Boulogne (Table H1 in Appendix H). Similarly, in June 2013, consecutive storms (15 and 22 June) elevated diatom abundances to maxima of 1.6×10^6 cells L⁻¹ (Fig. F3a in Appendix F), with *L. danicus* reaching 5.9×10^6 cells L⁻¹ (Table H1 in Appendix H) and Chl-a concentrations of 14.19 µg L⁻¹ at PHYTOBS C on 2013-06-25. Additional evidence of storm-driven responses was observed on 2016-07-21 at PHYTOBS C, following the 2016-07-11 storm, when a bloom of *Chaetoceros socialis* reached 3.0×10^6 cells L⁻¹ (Table H1 in Appendix H).

3.2.3 Low inflow, high wind stress storm: 2015-07-13

The 13 July 2015-07-13 storm was the windiest event among the low-inflow, low-precipitation storms (Fig. 2). It generated strong turbulence in the water column without delivering additional nutrients from riverine inputs. Under these conditions, the phytoplankton community was reshaped: diatoms and pico-sized phytoplankton groups were suppressed, while nano-sized taxaphytoplankton were favoured (Fig. 7C). Diatom abundances declined sharply in

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535 nearshore-coastal stations (R0–R2), with the pre-storm mean of 6.8×10^5 cells L⁻¹ reduced by 2-fold to 3.3×10^5 cells L⁻¹ (Fig. 7C(a)).

In contrast, nano-sized phytoplankton—including nanophytoplankton, coccolithophorids, and cryptophytes—responded positively (Fig. 7C(b–d)). Nano-eukaryotes phytoplankton increased significantly relative to pre-storm conditions (Table G; AD test, $p = 0.033$; Table G1 in Appendix G), with postand post-storm abundances at all stations exceeding the 90th-percentile (Table G; tail-exceedance test, $p < 0.001$; Table G1 in Appendix G). Their distribution shifted from the 50th-to above the 90th-percentile (Fig. 7C(b)), with a post-storm mean of 2.2×10^6 cells L⁻¹ and a maximum of 4.1×10^6 cells L⁻¹. Coccolithophorids peaked at 1.2×10^5 cells L⁻¹ at the near to the coast R0' station (Fig. 7C(c)), while cryptophytes showed a strong increase (Fig. 7C(d)) moving offshore from at stations R1 to R3R3 stations (mean: 3.6×10^5 cells L⁻¹; max: 7.6×10^5 cells L⁻¹), exceeding their climatological mean of 3.0×10^5 cells L⁻¹ (Fig. 6).

By contrast, pico-sized phytoplankton groups declined markedly. *Synechococcus* abundances dropped nearly 4-fold, from a pre-storm mean of 2.1 to 8.2×10^6 cells L⁻¹, while picoeukaryotes decreased from 7.4 to 3.2×10^6 cells L⁻¹ in the DYPHYRAD transect (Fig. 7C(e–f)). Similarly, at SOMLIT Point L, the suppression was particularly striking: *Synechococcus* fell from 3.4×10^7 cells L⁻¹ to 3.6×10^6 cells L⁻¹, and picoeukaryotes from 1.1×10^7 cells L⁻¹ to 7.98×10^5 cells L⁻¹ by 15 July 2015-07-15 (Table H2 in Appendix H) with Chl-a concentrations limited to $1.39 \mu\text{g L}^{-1}$.

3.2.4 Low inflow, low wind stress storm: 2022-06-06

The 6 June 2022-06-06 storm was characterized by both low inflow and low wind stress (Figs. 2, 3), conditions that suggested-implied minimal mixing and limited nutrient supply from rivers. Yet, occurring during a marine heatwave (Simon et al., 2023), this event uniquely reshaped the phytoplankton community. Rather than stimulating diatoms, Under the prevailing warm conditions, the storm amplified pico-sized phytoplankton under the prevailing warm conditions, while diatoms were further suppressed (Fig. 7D).

Diatom abundances declined slightly, with a post-storm mean of 2.0×10^5 cells L⁻¹ (Fig. 7D(a)), remaining below the climatological mean of 3.4×10^5 cells L⁻¹ (Fig. 6a). Before the storm, populations of nano-eukaryotes phytoplankton, cryptophytes, *Synechococcus*, and picoeukaryotes were underdeveloped (Fig. 7D(b–f)). Following the storm, cryptophytes responded modestly at stations R0', R2', R3', and R4, increasing to a post-storm mean of 3.0×10^5 cells L⁻¹ (Fig. 7D(d)). In contrast, *Synechococcus* exhibited a dramatic surge at all stations (Fig. 7D(e)), increasing from a post-storm mean of 6.3×10^5 to 1.5×10^7 cells L⁻¹, with an offshore maximum of 2.0×10^7 cells L⁻¹. This increase reflected a significant distributional shift (AD test, $p = 0.001$; Table G1 in Appendix G), though without enrichment of extreme values (Fig. 7D(e)). The strongest response, however, came from picoeukaryotes. They not only shifted significantly (AD test, $p = 0.001$; Table G1 in Appendix G) but also exhibited strong enrichment at all stations—except at R0, reaching extreme abundances (Fig. 7D(f)); tail-exceedance binomial-test, $p < 10^{-7}$; Table G1 in Appendix G). Post-storm, their mean abundance rose to 2.4×10^7 cells L⁻¹, with maxima of 2.8×10^7 cells L⁻¹.

570 4 Discussion

Summer storm impacts in the EEC were highly variable between years, arising from different combinations of river inflows and wind events that were in turn modulated by large-scale atmospheric circulation (Alvarez et al.,

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2024; Crawford et al., 2023; Turki et al., 2023). These patterns ~~directly~~ support our ~~initial~~ hypothesis that ~~variations in river inflow and wind forcing drive changes in phytoplankton abundance and community composition~~ ~~different storm types exert distinct ecological impacts~~. Specifically, our findings ~~confirm~~ ~~indicate~~ that high inflow storms favoured diatoms, wind-driven mixing, low inflow summers promoted nanophytoplankton, ~~such as~~ cryptophytes and pico-sized phytoplankton (Table 4). Nutrient loading ~~through~~ ~~via~~ riverine ~~discharge~~ ~~inflow~~ and sediment resuspension can be modulated by precipitation intensity and wind-driven mixing, ~~respectively~~, resulting in variable storm impacts on ~~coastal~~ ~~temperate~~ phytoplankton community structure. High inflow ~~summer~~ storms were predominantly observed in 2012, 2013, 2016, and June 2020, while low inflow windy conditions characterized summer of 2014, 2015, 2017, and July 2020. The 2022 event exemplified a short, low inflow storm with minimal ~~extreme~~ wind duration (<1 h, ~~Table 4~~ ~~Fig. A1 in Appendix A~~). These contrasting phytoplankton dynamics are discussed below.

4.1 Summer storm induced changes in marine environment of the ~~eastern English Channel~~ ~~EEC~~

In During June–July, south-westerly winds frequently prevail, often exceeding 8 m s^{-1} (Figs. ~~A1–2, D1 in Appendix A~~). These winds enhance vertical mixing and drive the northward transport of deep and oceanic waters, replenishing nutrients in surface layers (Dulière et al., 2019). In addition, high precipitation events can produce either ~~strong~~ ~~high~~ or ~~weak~~ ~~low~~ inflow ~~rates~~ (Fig. 3). At the same time, south-westerly winds sustain a narrow coastal current, 3–4 km wide, originating from the Bay of Somme and occasionally linked to the Seine ~~e~~Estuary (Brylinski et al., 1991). This current is distinct from offshore waters, as reflected in the coastal–offshore salinity gradient, and serves as a conduit for riverine inputs from the Authie, Canche, Slack, Wimereux, and Lianne rivers. Storm impacts are reflected in the coastal water salinity climatology, which exhibits an increasing trend until late May, followed by a decline through the end of July (Fig. C1b ~~in Appendix C~~). Under south-westerly ~~storm~~ winds (Figs. ~~A2, and D1 in Appendix A and D~~), these surplus inputs can be advected northward into the study area, ultimately reaching the Strait of Dover (Brylinski et al., 1996).

For example, the Somme ~~E~~estuary delivers daily averages of $\sim 500 \text{ kmol d}^{-1}$ of silicate and nitrate during June–July (Loquet et al., 2000). Such enrichment from the Bay of Somme has long been associated with the proliferation of diatoms and *Phaeocystis globosa* in the EEC (Brunet et al., 1996).

Table 4. Summary of different storm impacts and their associated physical responses in EEC, highlighting the phytoplankton groups that benefit under each condition. Coastal flow following high-inflow storms under south-westerly winds transports surplus nutrients from the Somme, Authie and Canche estuaries toward the Strait of Dover along the EEC coast (Brylinski et al. 1991). Wind driven mixing following June–July storms also supplies regenerated nutrients (DIN, DIP) from the degradation of the spring *Phaeocystis* spp. bloom.

Storm type	Storm	Dominant physical mechanism	Physical description	Primary and secondary nutrient source and pathway	Benefiting phytoplankton (size class; taxa)
High inflow, Low-wind stress	2016-06-20 2020-06-06	Horizontal advection	South-westerly wind-driven coastal flow transports river plume northward	Riverine Si, DIN, DIP enriched water advected northward	Diatoms, Pico-sized phytoplankton
High inflow, high-wind stress	2012-06-22 2012-07-12 2013-06-15 2016-07-02	Horizontal advection Vertical Mixing	Brief mixing pulse then quick re-stratification of the water column South-westerly wind-driven coastal flow transports river plume northward Turbulent water	Regenerated DIN DIP supply from deep water and sediment Riverine Si, DIN, DIP enriched water advected northward Regenerated DIN-DIP supply from deep water and sediment resuspension	(<i>Synechococcus</i> spp. and picoeukaryotes) Diatoms, Nano-sized phytoplankton (Nanophytoplankton; cryptophytes)
Low inflow, high-wind stress	2015-06-02 2015-07-13 2020-07-27	Horizontal advection Vertical Mixing	South-westerly wind-driven coastal flow transports river plume northward Turbulent water	No surplus nutrients from the river to the DYPHYRAD transect Regenerated DIN-DIP supply from deep water and sediment resuspension	Nano-sized phytoplankton (Nanophytoplankton; cryptophytes)
Low inflow, Low-wind stress (short storm)	2022-06-06	Horizontal advection Vertical mixing followed by rapid re-stratification	South-westerly wind-driven coastal flow transports river plume northward Brief mixing pulse then quick re-stratification of the water column	No surplus nutrients from the river to the DYPHYRAD transect Regenerated DIN-DIP supply from deep water and sediment resuspension	Pico-sized phytoplankton (<i>Synechococcus</i> spp. and picoeukaryotes)

600	Table 4. Summary of storm impacts and their associated <u>nutrient and phytoplankton ecological</u> responses. See Table 2 for <u>phytoplankton group description</u> .					Formatted: Font: Not Bold
Storm type	Storm date (y-m-d)	Vertical mixing intensity	Nutrient supply (DIN, DIP, DiSi)	Benefiting phytoplankton group(size class; taxa)		
High inflow, low wind stress	2016-06-20 2020-06-06	Weak mixing followed by rapid re-stratification	Riverine inputs <u>and</u> deeper water <u>and</u> sediment resuspension	<u>Diatoms</u> <u>RedMicro</u> , <u>Synechococcus</u> <u>OraPico</u> <u>picoeukaryotes</u> <u>RedP</u>	Formatted: Font: Not Italic Formatted: Font: Not Italic	
High inflow, high wind stress	2012-06-22 2012-07-12 2013-06-15 2016-07-02	Strong vertical Mixing		<u>RedMicro</u> <u>Diatom</u> <u>Nanophytoplankton</u> <u>RedNan</u> <u>o</u> <u>cryptophytes</u> <u>OraNano</u>	Formatted Table	
Low inflow, high wind stress	2015-06-02 2015-07-13 2020-07-27	Strong vertical Mixing	Deeper water and sediment resuspension	<u>RedNano</u> <u>Nanophytoplankton</u> <u>cryptophytes</u> <u>OraNano</u> <u>HsNano</u>		
Low inflow, low wind stress	2022-06-06	Weak mixing followed by rapid re-stratification		<u>Synechococcus</u> <u>OraPico</u> <u>Prok</u> <u>picoeukaryotes</u> <u>RedPico</u>	Formatted: Font: Not Italic Formatted: Font: Not Italic	

In the English Channel and southern North Sea, summer is often associated with storm activity (Cook et al., 2015; Gronholz et al., 2017; Scholz et al., 2022). Extratropical storms generate extensive cloud cover, rainfallprecipitation, and riverine inflows, all of which can alter light availability, nutrient concentrations and, salinity, mixing, and light availability (Jennings et al., 2012; Kasprzak et al., 2017; Rees et al., 2009). The EEC summer months are typically marked by low-co-limitation-of silicate, nitrate, and phosphate concentrations (Fig. C1d-f in Appendix C). Despite these constraints,Chl-a concentrations were relatively high and showed spatial differences, with higher values in coastal waters compared with offshore waters during the summer months (Fig. C1c in Appendix C). As previously reported, phytoplankton blooms in the English Channel can persist for several weeks after summer storms-phytoplankton blooms can persist for weeks (e.g., (Rees et al., 2009; Skouroliakou et al., 2022)). For instance, Rees et al. (2009) documented three summer precipitation events that induced freshwater stratification and delivered DIN to surface waters, stimulating primary production. They proposed that storm-driven nutrient loading alleviated DIN limitation, while dissolved organic phosphate was mobilized to meet DIP demand. Such processes may generate synergistic, non-additive responses to dual nutrient enrichments, resulting in enhanced phytoplankton growth (Allgeier et al., 2011).

4.2 Storm impacts on Chl-a and phytoplankton summer communities

Interannual variability in windy days (number of days > 8 m s⁻¹) and inflow during June-July was evident (Fig. 4), with episodes of strong winds in 2015 and 2020, and enhanced riverine discharge-inflow in 2012, 2013, 2016, and 2021 (Fig. 4). Long-term records show that northern Europe has become wetter since the last century (Cook

et al., 2015), with alternating wet and dry periods driven by both climate change and natural variability. Corresponding variability was reflected in post-storm Chl-a concentrations (Fig. 5) and phytoplankton community structure (Fig. 7). Since 2012, Chl-a in the DYPHYRAD transect has declined (Hubert et al., 2025a), consistent with earlier observations of interannual shifts in the EEC, including a late-20th-century decrease followed by a rise in the early 2000s (Lefebvre et al., 2011). Similar patterns have been reported elsewhere, with summer primary production responding to rainfall-precipitation and riverine inputs in the western English Channel (Barnes et al., 2015) and to increased summer winds in the Arctic Ocean (Crawford et al., 2020). These findings suggest that interannual and multidecadal variability in Chl-a may be in part also regulated by distinct storm impacts affecting phytoplankton composition (Stockwell et al., 2020).

Previous studies have shown that large phytoplankton often dominate nutrient-rich upwelling regions of the ocean, whereas open-ocean waters are typically dominated by picophytoplankton (James et al., 2022; Ribalet et al., 2010). A similar pattern was observed in the English Channel, where riverine input represents the dominant mechanism of nutrient supply. This nutrient enrichment supports the abundance of larger phytoplankton, such as diatoms and *Phaeocystis globosa*, in coastal waters (Bonato et al., 2015; Napoléon et al., 2014). During the summer months, distinct and contrasting patterns emerged between coastal and offshore waters: diatoms were consistently more abundant in coastal zones waters (Fig. 6a), whereas while *Synechococcus* dominated offshore waters (Fig. 6e). Seasonal dynamics revealed a June–July mean increase in diatom abundance in early July, following the spring bloom (Fig. 6a). *Synechococcus* rose in late May but dipped in early July despite warming temperatures, then recovered by late July as diatoms declined. This crossover suggests that transient meteorological disturbances, including storm-related reductions in light or shifts in nutrient dynamics, temporarily favoured diatoms over *Synechococcus*. The subsequent reversal toward late July reflects a return to more stable summer conditions (Fig. 6e). Similarly, high standard errors in diatom, pico-sized phytoplankton, and cryptophyte abundances point to greater fluctuations during June–July (Fig. 6a–f) due to storm-driven disturbances.

High inflow storms and diatom (microphytoplankton) responses

In several cases, post-storm increases in Chl-a (Fig. 5) coincided with strong diatom dominance, particularly during the 2012, 2013, and 2016 storm events. These summers were characterized as windy because June and July recorded by sustained high diatom concentrations (Hubert et al., 2025), with more than 10 days of with wind speeds exceeding 8 m s⁻¹ and monthly average river flows above 0.35 m³ s⁻¹ (Fig. 4). Storms create turbulent, nutrient-rich niches that benefit diatoms (Margalef, 1978). Their large cell size allows them to store nutrients during fluctuating nutrient conditions (Litchman et al., 2009), while their ability to increase Chl-a and other pigments under variable light regimes enhances resilience to rapid changes in irradiance (Kuczynska et al., 2015; Pniewski and Piasecka-Jędrzejak, 2020). High diatom abundances in nearshore waters are therefore expected, given their reliance on riverine inputs such as silicate.

Post-storm peaks in microphytoplankton abundances were often driven by specific diatom taxa such as *Leptocylindrus danicus* and *Chaetoceros socialis*, whose abundances exceeded climatological baseline shown in Fig. 6a–f records by more than 3-fold (Table H1 in Appendix H). *Leptocylindrus danicus* dominated June diatom blooms between 2016 and 2020 (Houliez et al., 2023; Skouroliaikou et al., 2022), except in 2018 when *Pseudonitzschia* prevailed (Skouroliaikou et al., 2024), reaching ~10⁶ cells L⁻¹ and contributing 90% of total diatom abundance at SOMLIT-C and PHYTOBS-1-Boulogne stations (Fig. 1). Comparable storm-driven diatom

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dominance was observed in earlier years. In June–July 2012, consecutive high-inflow storms sustained strong coastal diatom blooms, with mean abundances of 8.4×10^5 cells L^{-1} (Fig. F2a) and post-storm Chl-a concentrations of $7.12 \mu g L^{-1}$ (Fig. 5). Following the 19 June 2012 storm, *Leptocylindrus danicus* peaked at 7.6×10^5 cells L^{-1} at Point 1-B (Table H1). Similarly, in June 2013, consecutive storms (15 and 22 June) elevated diatom abundances to maxima of 1.6×10^6 cells L^{-1} (Fig. F3a), with *L. danicus* reaching 5.9×10^6 cells L^{-1} (Table H1) and Chl-a concentrations of $14.19 \mu g L^{-1}$ at SOMLIT Point C. Additional evidence of storm-driven responses was observed on 21 July 2016 at SOMLIT Point C near the Lianne River (Fig. 1), following the 11 July storm, when a bloom of *Chaetoceros socialis* reached 3.0×10^6 cells L^{-1} (Table H1). These responses reflect ecological drift, where enhanced growth and reduced competition allow a single taxon to dominate briefly before the community resets (Skouroliaikou et al., 2022). The recurrence of these post-storm diatom blooms across multiple years (Table 4; 2012, 2013, 2016–, 2020) indicates that they are not isolated anomalies but rather a consistent feature of coastal phytoplankton dynamics (Houliez et al., 2023; Skouroliaikou et al., 2022). High inflow storms in 2012, 2013, 2016, and June 2020 were consistently associated with significant increases in diatom abundances (AD test, $p < 0.05$; Fig. 7A–B, Figs. F3a, F5a in Appendix F), particularly in nearshore-coastal waters (R0–R2, Fig. 1), as summarized in Table 4. In a previous study, Rees et al. (2009) reported a monospecific post-storm bloom of *Chaetoceros debilis* associated with increased Chl-a following enhanced river inflow, supporting our observation that such blooms are recurrent in the region. Higher summer silicate concentrations ($\sim 1.8 \mu mol L^{-1}$) at the coastal station R0 (Hubert et al., 2025a) likely favour diatom growth in coastal waters.

Periods of consecutive rainy storms at the end of June may explain the convergence of coastal and offshore diatom climatology in early July (Fig. 6a) (Hubert et al., 2025a; Skouroliaikou et al., 2022). In addition, consecutive storms often ensure that this-the nutrient-rich coastal flow reaches the Strait of Dover, consistent with the high diatom abundances (Fig. 7A–B, Figs. F1–, 3, 5 in Appendix F) observed in the nearshore-coastal (R0–R2) and frontal zone (R20–R3'). In contrast, the 6 June 2022-06-06 storm, characterized by low inflow and weak wind stress (Fig. 7D), did not enhance diatom abundances across the transect. Instead, elevated Chl-a concentrations were detected at Point 1-B-PHYTOBS Boulogne and PHYTOBS Point C (Table H1; 4.29 and $4.7 \mu g L^{-1}$, respectively; Table H1 in Appendix H), accompanied by a bloom of *Leptocylindrus danicus* (2.27×10^6 cells L^{-1} at Point 1-B-PHYTOBS Boulogne). These responses suggest that the impact of low wind stress on coastal flow was largely confined to the south till Boulogne-sur-mer-Mer, while limited inflows from smaller rivers such as the Slack and Wimereux did not enhance diatom growth in the transect (Fig. 7D). Under weak winds, reduced advection creates strong spatial patchiness in the EEC (Bonato et al., 2015). Consequently, it was appropriate that our analysis did not incorporate flow rates from rivers such as the Canche and Liane, as their influence on the transect would have been minimal under these conditions.

This study highlights that certain diatom genera and species are able to dominate storm-driven summer blooms; specifically, *Leptocylindrus danicus* in June and *Chaetoceros socialis* in July. Such dominance suggests that these taxa are well adapted to post-storm conditions associated with riverine nutrient supply under the well-lit conditions of summer (Polimene et al., 2014; Widdicombe et al., 2010). Moreover, while diatoms in offshore waters during the summer are generally confined to subsurface layers (20–30 m; Barnett et al., 2019), riverine nutrient inputs and mixing can promote their proliferation in surface waters across the transect (e.g., Fig. 7Ba and F3a in Appendix F).

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700 High wind stress, low inflow storms and nano-sized phytoplankton responses

June–July periods in 2015 and 2020 have consistently recorded more windy days than high-inflow days, with summer 2015 standing out for its 34 windy days, particularly in July (Fig. 4). Under such conditions, pico- and nano-sized phytoplankton flourished across the EEC (Hubert et al., 2025; Skouroliaikou et al., 2022). Summer stratification of the English Channel (Barnett et al., 2024; Schmitt et al., 2024) provides the backdrop for these dynamics. Wind speeds of $\sim 8 \text{ m s}^{-1}$ are sufficient to disrupt stratification (Barnett et al., 2019), mixing the water column and transporting remineralized nutrients from deeper layers to the surface (Table 4) (Williams et al., 2013). Nutrients released–remineralized from *Phaeocystis globosa* organic matter (Lamy et al., 2009) along the EEC coast can be transported northward by south-westerly winds (Brylinski et al., 1996). Turbulence in the frontal zone (R2–R3') (Brylinski et al., 1991) explains both the lack of spatial differences in nano-eukaryotes phytoplankton climatology (Fig. 6b) and their accumulation in frontal zones (Gieskes et al., 2007; Hubert et al., 2025a), as turbulent conditions favour nutrient consumption. With low inflows limiting silicate supply, diatom growth was constrained, leaving space for nanophytoplankton and cryptophytes nanophytoplankton to expand by exploiting available DIN and DIP (Margalef, 1978). Windy events illustrate this dynamic clearly. On 2015-07-13 (Fig. 7C), 2015-06-02 (Fig. F4), 2016-07-02 (Fig. 7B), and 2020-07-27 (Fig. F6), pico-sized phytoplankton declined post-storm, replaced by nanophytoplankton. Dry and windy summers such as 2015 and 2020 produced significant increases in nanophytoplankton (Hubert et al., 2026) (Hubert et al., 2025e) (Fig. 7B, D; Fig. F4b in Appendix F; AD test, $p < 0.05$; Table G1 in Appendix G Fig. 7B, D; Fig. F4b). According to Metabarcoding, small eukaryotic phytoplankton analyses have shown that pico- and nano-sized phytoplankton communities were composed dominated of by the *Synechococcus*, coccolithophorid *Emiliania* and the nanoplanktonic diatom *Minidiscus*, while cryptophyte peaks — dominated by *Plagioselmis* — were observed in July 2016, 2018, and 2020 (Skouroliaikou et al., 2022).

Low wind stress storms and pico-sized phytoplankton responses

By contrast, the 2022-06-06 storm produced a different outcome. This short-lived event generated only weak wind forcing. With only a brief one-hour windy period, and the post-storm community was dominated by pico-sized phytoplankton (Table 4), with only marginal increases in nanophytoplankton (Fig. 7D). This event unfolded during concurrent marine and atmospheric heatwaves (Guinaldo et al., 2023; Simon et al., 2023), which elevated sea surface temperatures and reduced cloud cover and wind speeds, creating favourable conditions for pico-sized taxaphytoplankton (Levasseur et al., 2025). Their high surface-to-volume ratio confers a competitive advantage under oligotrophic conditions, enabling efficient nutrient uptake even when concentrations are low (Raven, 1984). Then, the EEC remained stratified until a new short windy event disrupted the stratification on 2022-06-19 (not shown here). By late June, *Synechococcus* and picoeukaryotes reached exceptional abundances offshore (1.0×10^8 and $2.3 \times 10^8 \text{ cells L}^{-1}$ at Point L-SOMLIT L; Table H2 in Appendix H) and at the coast (4.8×10^7 and $1.8 \times 10^7 \text{ cells L}^{-1}$ at Point C-SOMLIT C; Table H2 in Appendix H). Similar low-wind storm in June 2016 also favoured picophytoplankton. Low wind-stress storms (e.g., 2016-06-20 and 2022-06-06) were associated with significant increases in *Synechococcus* and picoeukaryotes, respectively, with no significant decrease in picoeukaryotes during the 2016-06-20 event (AD test, $p < 0.05$; Table G1, Appendix G). Nanophytoplankton and picophytoplankton are well adapted to low nutrient concentrations, efficiently acquiring resources and sustaining growth under windy, low-inflow conditions (Table 4). Wind-driven mixing maintains sufficient nutrient levels in

surface waters without fully replenishing them, favouring pico-sized taxa during most summers (Fig. 6e–f; Hubert et al., 2025a).

The higher frequency and intensity of storms in recent years (Wasko et al., 2021) causes increasing disturbances to the water column by changing turbidity, salinity and nutrients. Storms repeatedly disrupted seasonal succession, generating short-lived but pronounced shifts in community structure, including transient monospecific peaks. Such disturbance-driven variability aligns with the broader understanding that biological responses under fluctuating conditions can be governed by stochastic processes such as ecological drift and dispersal (Jurburg et al., 2017). Although we did not explicitly quantify stochasticity in this study, our results suggest that storms acted as environmental disturbances capable of supporting stochastic phytoplankton growth, consistent with the finding that stochastic processes explained 69% of summer community turnover in the EEC (Skouroliaou et al., 2022).

While previous research in this region attributed summer phytoplankton blooms and community turnover primarily to stochastic processes (69%; Skouroliaou et al., 2022), the underlying drivers of these disturbances remained unclear. The present study elucidates these patterns by identifying weather-induced nutrient suppletion as a key mechanism in an otherwise nutrient-depleted environment after the spring bloom. We found that recurrent storms disrupted seasonal succession, triggering short-lived but pronounced community shifts characterized by transient monospecific peaks such as *Leptocylindrus danicus* and *Chaetoceros socialis* observed in our study. Such disturbance-driven conditions may facilitate the emergence of unpredictable blooms, including monospecific events such as *Leptocylindrus danicus*. Similar storm-related shifts have been documented in other aquatic systems—for example, the post-storm dominance of cryptomonads in a temperate lake (Jacobsen and Simonsen, 1993) and reduced phytoplankton diversity linked to stochastic processes in the Yangtze River estuary (Xian et al., 2024)—highlighting the wider relevance of our observations i.e., post-storm high abundance of certain phytoplankton groups.

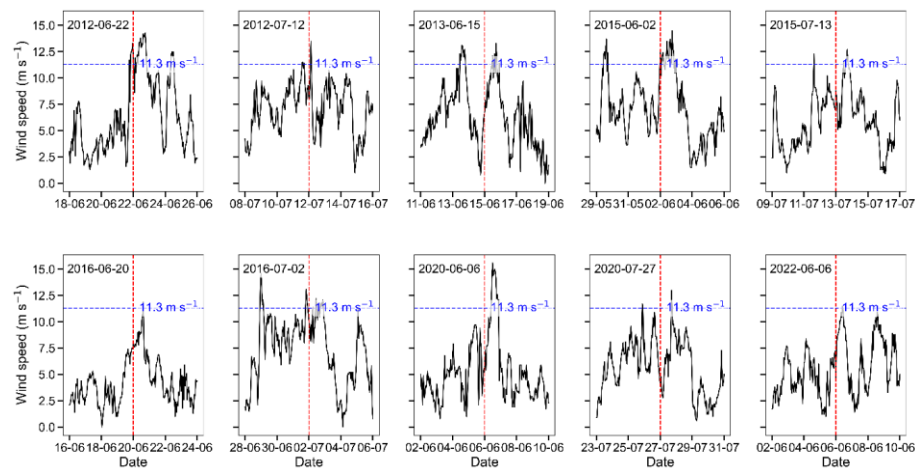
5-Concluding remarks

The higher frequency and intensity of storms in recent years (Wasko et al., 2021) causes increasing disturbances to the water column by changing turbidity, salinity and nutrients. The present study revealed that summer phytoplankton dynamics were strongly shaped by the interplay of stratification, turbulence, and riverine inputs due to storms. Summer storm impacts in the EEC were highly variable between years, arising from different combinations of river inflows and wind storms that are themselves modulated by large-scale atmospheric circulation. Storms repeatedly disrupted seasonal succession, generating short-lived but pronounced shifts in community structure, including transient monospecific peaks. Such disturbance-driven variability aligns with the broader understanding that biological responses under fluctuating conditions can be governed by stochastic processes such as ecological drift and dispersal (Jurburg et al., 2017). Although we did not explicitly quantify stochasticity in this study, our results suggest that storms acted as environmental disturbances capable of supporting stochastic phytoplankton growth, consistent with the finding that stochastic processes explained 69% of summer community turnover in the EEC (Skouroliaou et al., 2022). Such disturbance-driven conditions may facilitate the emergence of unpredictable blooms, including monospecific events such as *Leptocylindrus danicus*. Similar storm-related shifts have been documented in other aquatic systems—for example, the post-storm dominance of cryptomonads in a temperate lake (Jacobsen and Simonsen, 1993) and reduced phytoplankton diversity linked to stochastic processes in the Yangtze River estuary (Xian et al., 2024)—highlighting the wider

relevance of our observations i.e., post-storm high abundance of certain phytoplankton groups. Finally, our study highlighted how disturbances such as storms act as environmental drivers that foster stochastic growth, a mechanism that should be considered into models to better predict ecosystem responses under increasing frequency of extreme events. In conclusion, interannual variability in storm impacts (wind and riverine forcing) was reflected in phytoplankton community composition. Higher riverine inputs favoured diatoms through enhanced silicate availability, leading to increased Chl-a concentrations in coastal waters. In contrast, in the absence of strong riverine inputs, wind-driven mixing events favoured nanophytoplankton, whereas strong wind-driven mixing suppressed picophytoplankton.

Appendix A: Wind speed and direction during storms

The wind speed and direction during the 10 storms is shown in Fig. A1–A2 respectively. The dataset consists of hourly wind measurements, which capture the high variability in wind speed. The longest storm occurred on 2016-07-02, when wind speeds never dropped below 8 m s^{-1} during the ± 3 -day period around the peak. In contrast, the shortest storms were on 2016-06-20 and 2022-06-06, when extreme wind speeds ($\geq 11.3 \text{ m s}^{-1}$) lasted for no more than 1 hour within the ± 3 -day window. As mentioned previously, the ± 3 -day period was used to calculate wind stress (Fig. 2) at the sea surface. Across all events, the strongest winds during the ± 3 -day periods were consistently directed from the south-west. Unfortunately, subsurface current data are not available, preventing us from showing the corresponding direction of the coastal flow.



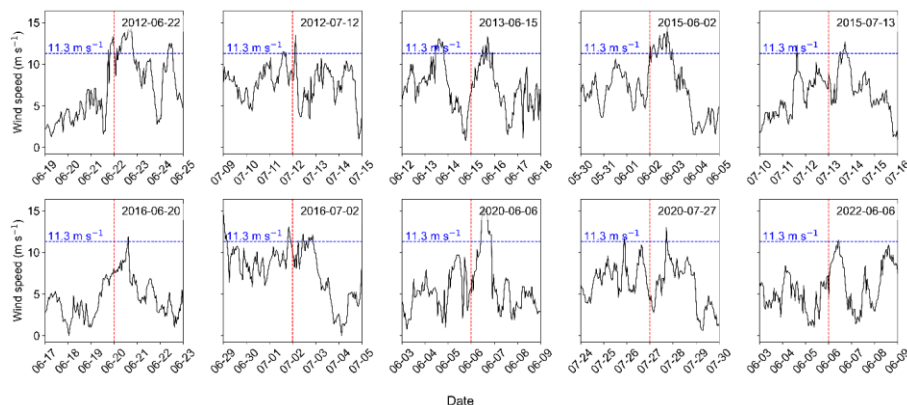


Figure A1. Hourly wind speed time series centred on each storm event at Boulogne-sur-Mer (Meteo-France station). The red dashed line marks the central storm day, and all analyses use a ± 3 -day window around this reference point. The longest event occurred on 2016-07-02, when wind speeds remained above 8 m s^{-1} throughout the ± 3 -day period. In contrast, the 2016-06-20 and 2022-06-06 storms exhibited short-lived peaks ($>11.3 \text{ m s}^{-1}$) lasting no more than one hour within the ± 3 -day window. Wind speed time series during storm events (± 4 days). The red dashed line indicates the selected central storm day, with analyses conducted over a ± 3 -day window around this reference point.

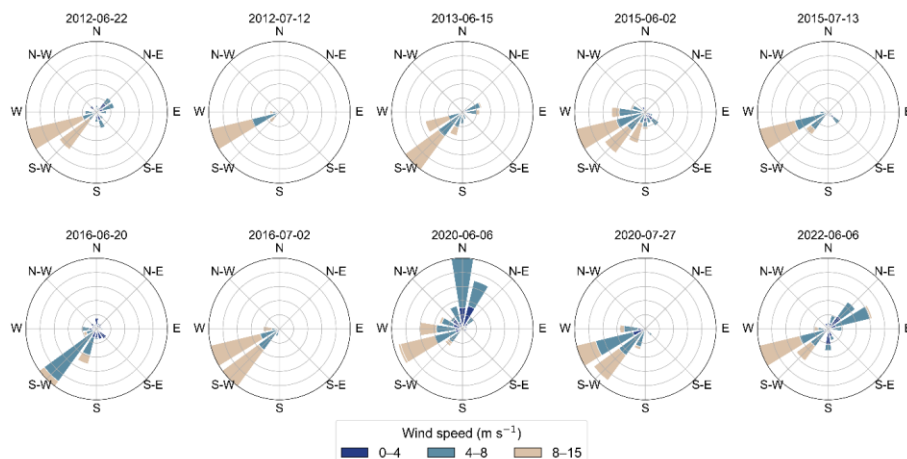


Figure A2. Hourly wind direction time series centred on each storm event at Boulogne-sur-Mer (Meteo-France station). Across all storms, the strongest winds during the ± 3 -day analytical windows were consistently from the south-west. Subsurface current data were not available, preventing comparison with coastal flow direction. Wind direction and speed during storm events (± 3 -day) at the Boulogne-Sur-Mer meteorological station. Polar plots show the frequency of winds by compass sector, with colours indicating wind-speed categories.

Appendix B: Frequency distributions of June–July precipitation and river inflow

Frequency distributions of June–July precipitation and river inflow were visualized using bar plots of storm totals and means within ± 3 days of identified storm dates (Fig. B1). The 80th percentile of these aggregates was used to classify storm intensity: 16.12 mm for precipitation and $0.45 \text{ m}^3 \text{ s}^{-1}$ for river inflow. Storm periods were then categorized as “High” or “Low” relative to these thresholds, and precipitation totals and mean inflows were compared against them to assess storm intensity (Fig. 3).

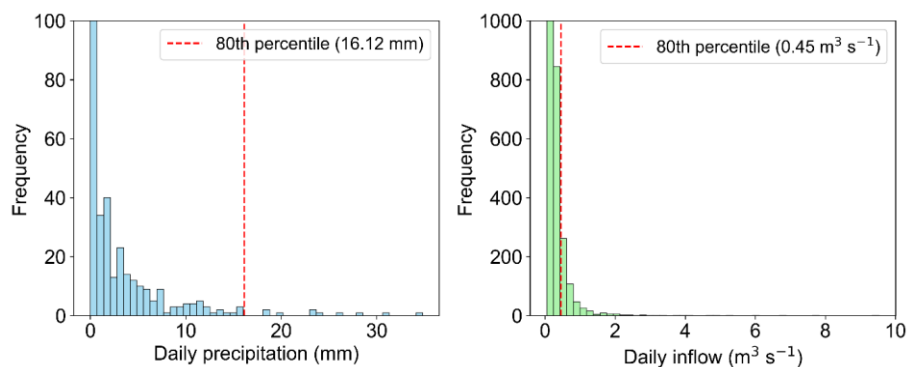
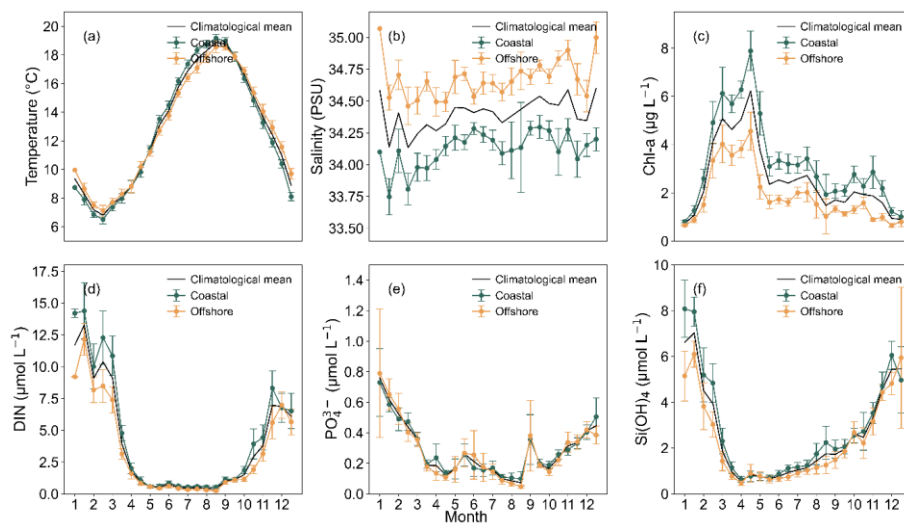


Figure B1. Frequency distributions of June–July precipitation (left) and river inflow (right) at the study site Boulogne-sur-Mer (Meteo-France station). Red dashed lines indicate the 80th-percentile thresholds (16.12 mm for precipitation; 0.45 m³ s⁻¹ for inflow), calculated from normalized ± 3 -day total accumulated precipitation and mean inflow values. These thresholds were used to identify storm impacts as “High” or “Low” classes precipitation and river discharge inflow.

820 Appendix C: Seasonal and spatial variability of environmental variables

Seasonal and spatial variability indicates that nearshore stations (R0–R2) are more strongly affected by seasonal progression, particularly reflected in salinity (Fig. C1b) and chlorophyll-a (Fig. C1c). Spatial difference in salinity and Chl-a suggests that EEC waters are strongly influenced by riverine inputs along the coast. Two peaks are observed during spring: the first dominated by diatoms, and the second in April by *Phaeocystis globosa*. A third chlorophyll-a peak occurs in June–July, followed by a fourth, smaller peak in autumn. Even though nutrient limitation was strongest in June and July, Chl-a levels were nevertheless sustained during this period.



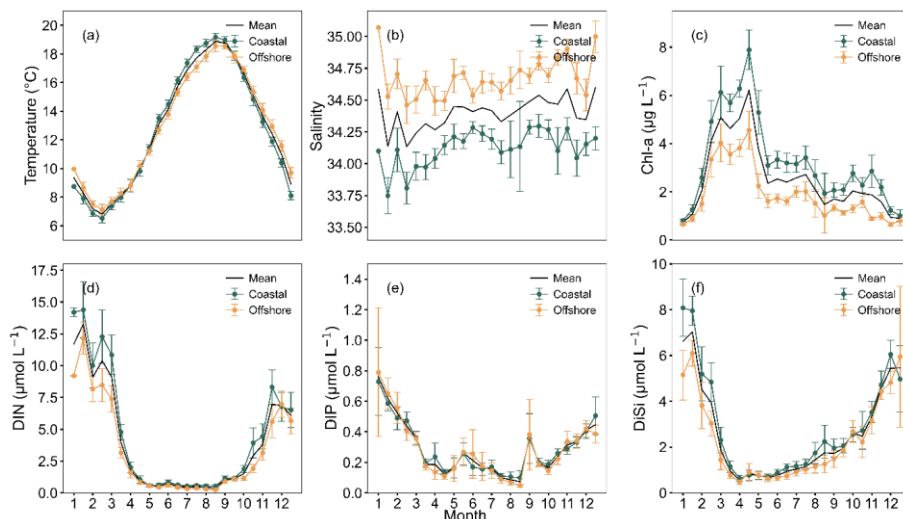


Figure C1. Climatological means and standard errors for Coastal (R0–R2 + SOMLIT C) and Offshore (R2'–R4 + SOMLIT L) regions of the EEC, based on 15-day means from February 2012 to December 2022. The black line represents the mean value across all stations. Seasonal and spatial variability of environmental variables; panels show: (a) sea surface temperature (°C), (b) salinity (PSU), (c) Chl-a ($\mu\text{g L}^{-1}$), (d) dissolved inorganic nitrogen (DIN, $\mu\text{mol L}^{-1}$), (e) dissolved inorganic phosphorus (DIP, $\mu\text{mol L}^{-1}$), and (f) dissolved inorganic silicate (DiSi, $\mu\text{mol L}^{-1}$). Data are based on 15-day climatological means from February 2012 to December 2022 using observations from DYPHYRAD, SNO-SOMLIT, and SNO-Phytobs. Mean values (circles) and standard errors of the mean (SEM; error bars) are shown for coastal (green) and offshore (orange) stations. Coastal stations (R0–R2 + SOMLIT C) show stronger seasonal variability than offshore stations (R2'–R4 + SOMLIT L), particularly in salinity and Chl-a, reflecting coastal riverine influence. Chl-a exhibits two spring peaks (the first associated with diatoms and the second in April with *P. globosa*), followed by a summer peak in June–July and a smaller autumn peak. Despite strongest nutrient limitation in June–July, Chl-a concentration remained elevated.

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Appendix D: Climatology of wind speed and direction

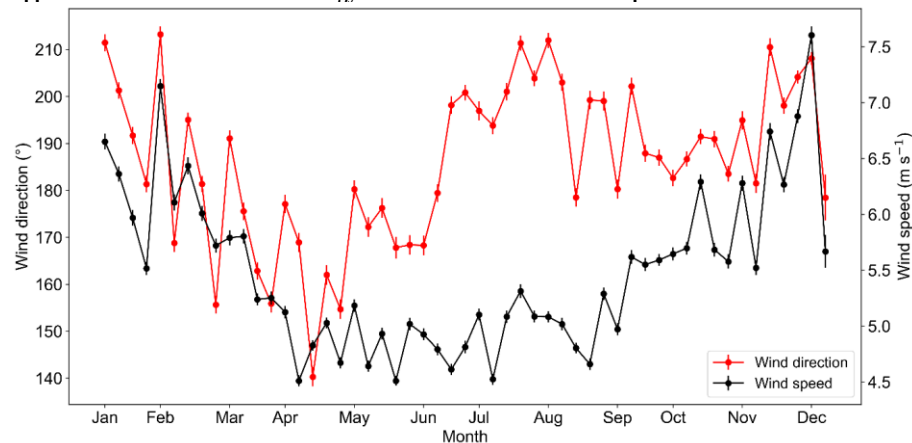


Figure D1 shows the climatology of wind speed and direction across the year. During spring, wind direction is predominantly north-easterly, whereas from June onward it is dominated by south-westerly winds for the remainder of the year.

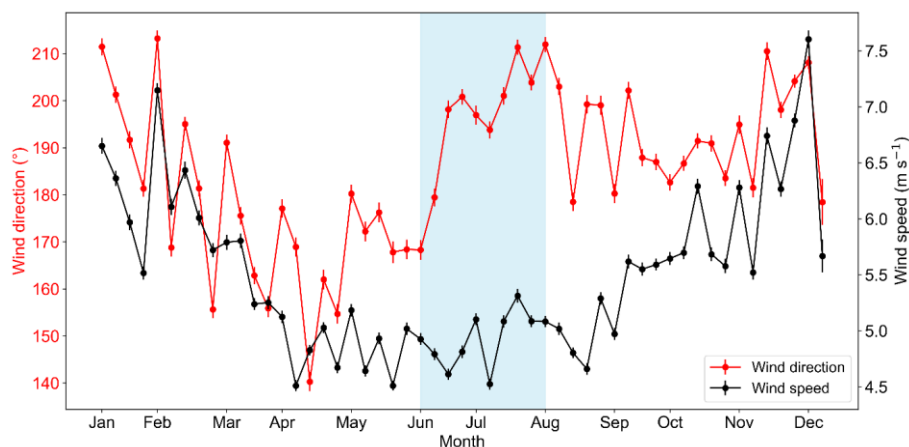


Figure D1. 15-day climatology of wind speed (black line, mean $\pm$ SEM) and wind direction (red line, mean $\pm$ SEM) at the study site Boulogne-sur-Mer (Meteo-France station), based on hourly measurements for 2010–2025. The shaded area highlights the June–July period used for the summer analysis, during which south-westerly winds dominate. The June–July period is characterized by a clear predominance of south-westerly winds, coinciding with the summer storm season.

Appendix E: Variability of Chl-a concentrations in relation to storms and precipitation

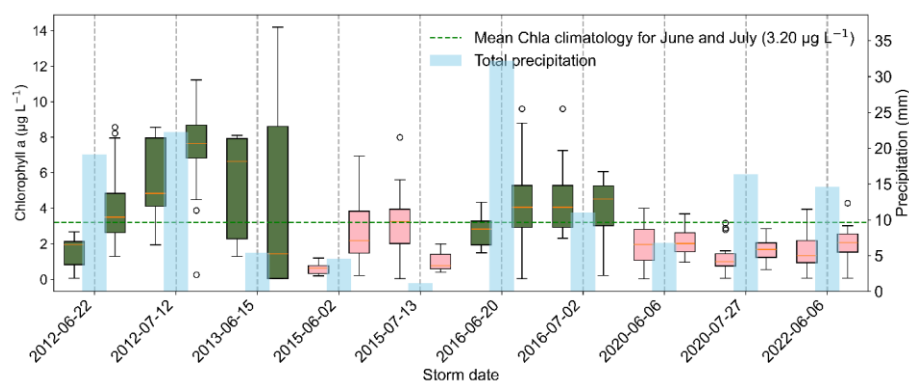


Figure E1 shows the pre- and post-storm distributions relative to precipitation occurring within ± 3 days. Precipitation and post-storm chlorophyll a did not exhibit a linear relationship across storms.

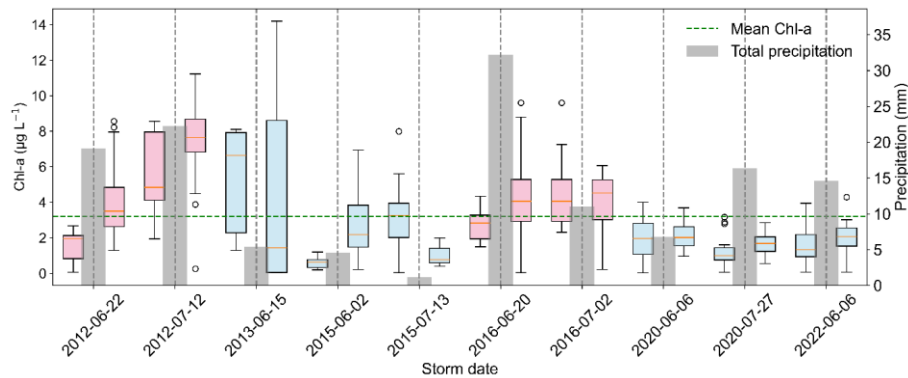


Figure E1. Boxplots of pre- and post-storm Chl-a distributions (compiled from DYPHYRAD and SOMLIT) for the 10 storms. Vertical dashed lines indicate the timing of each storm event. Pink and blue boxplots denote “high” and “low” inflow storms, respectively, corresponding to increased and decreased Chl-a responses. Pre-storm Chl-a distributions are shown together with total accumulated precipitation over a ± 3 -day storm period (dark grey bars). Total precipitation and post-storm Chl-a did not exhibit a linear relationship for the storms on 2013-06-15, 2020-07-27 and 2022-06-06. The green dashed line indicates the June–July climatological mean Chl-a concentration ($3.20 \mu\text{g L}^{-1}$) in the EEC.

Appendix F: Phytoplankton CCDFs during the storm events

The CCDFs of the remaining six storms are shown in Fig. F1–F6. Storms on 2012-06-22, 2012-07-12, and 2013-06-15 were characterized by high inflow and high wind stress, with post-storm distributions dominated by diatoms. In the latter two storms, elevated diatom abundances persisted until mid-July, replacing nanophytoplankton (Fig. F2–3). The storm of 2015-06-02 was marked by low inflow but high wind stress in early June, supporting a nanophytoplankton bloom that was subsequently overtaken by high abundances of *Phaeocystis globosa* (Fig. F4(b)). The storm of 2020-06-06 received additional precipitation and inflow on 2020-06-16 (not shown here), supporting diatoms and pico-sized phytoplankton (Fig. F5) under low wind stress (Fig. 2). Finally, the storm of 2020-07-27, characterized by high wind stress and low inflow, resulted in increased nanophytoplankton and replacement of picoeukaryotes in nearshore waters (Fig. F6).

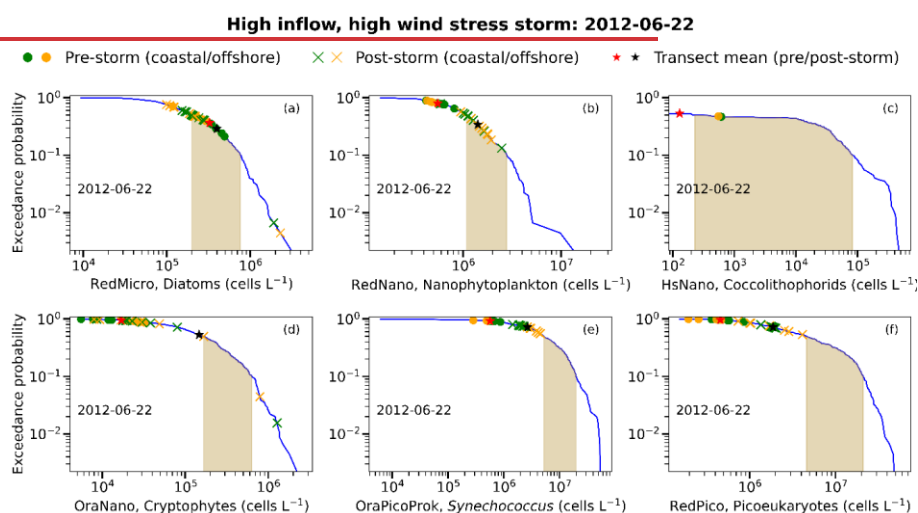
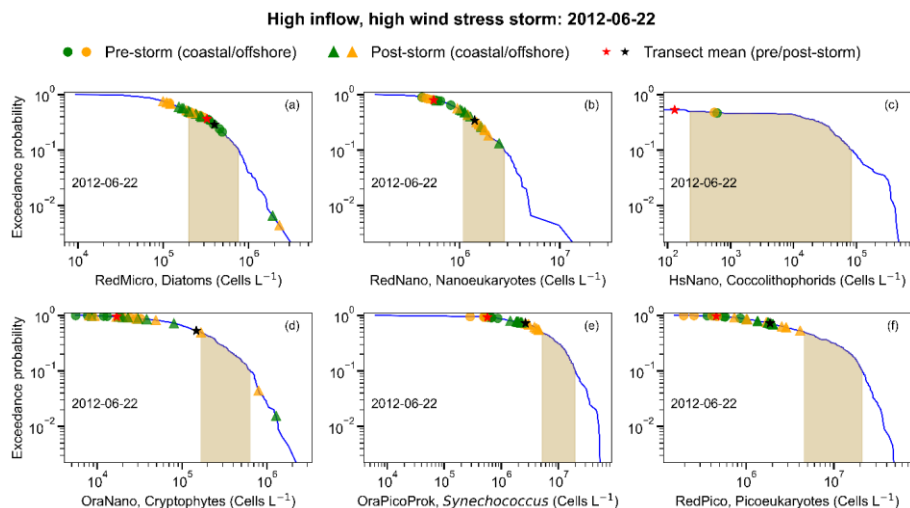
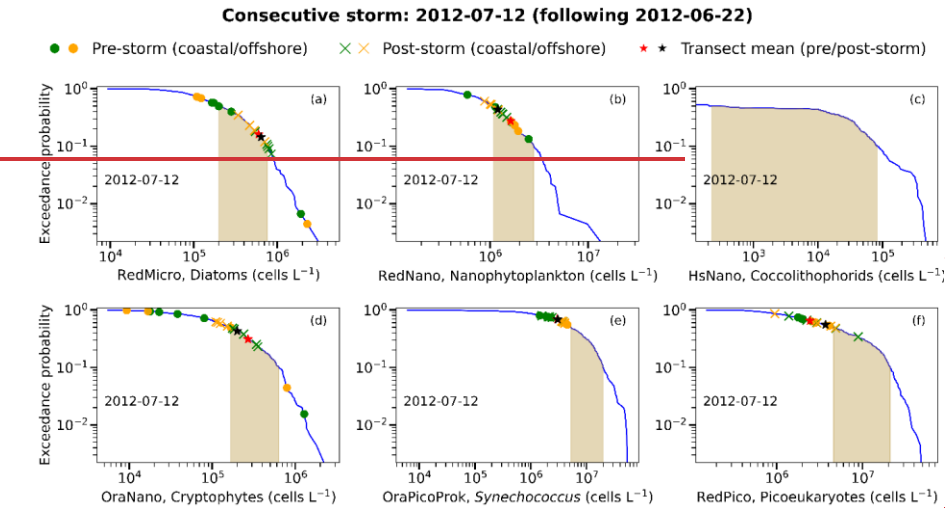
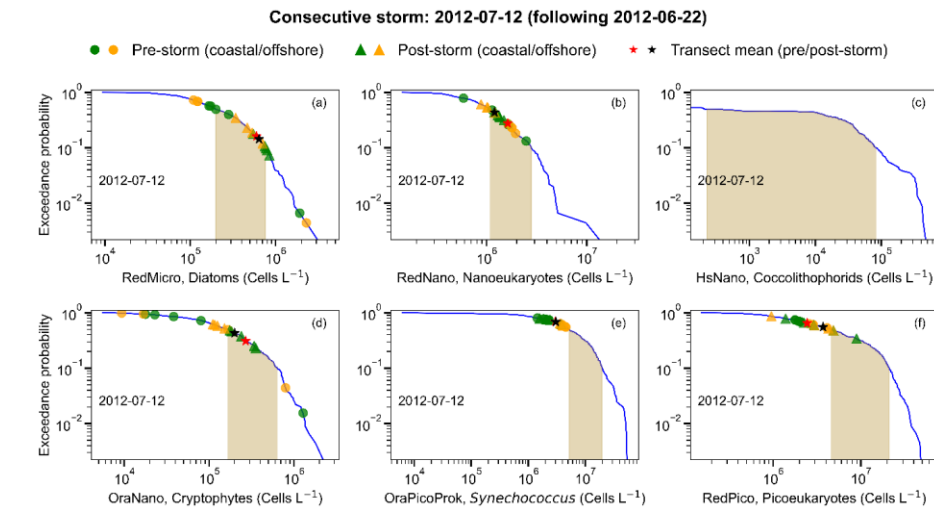


Figure F1. Exceedance probability (CCDF) distributions of six phytoplankton groups (a–f) along the DYPHYRAD transect during the storm of 2012-06-22. For each panel, RedMicro (diatoms), RedNano (nanoeukaryotes), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes) are presented shown as subplots (a–f). Blue lines represent June–July climatological distributions, with shaded areas indicating the 50th–90th percentiles. Pre-storm (–10 days) and post-storm (+14 days) observations are shown as green (coastal) and orange (offshore) symbols, with circles indicating pre-storm and triangles indicating post-storm abundances. Red and black stars indicate transect-mean abundances before and after the storm, respectively. Post-storm communities were dominated by diatoms and nanophytoplankton.



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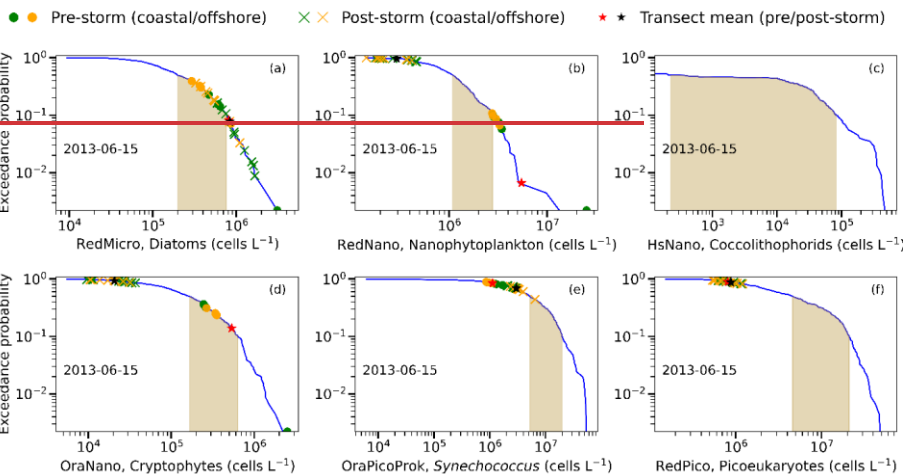


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Figure F2. Exceedance probability (CCDF) distributions of six phytoplankton groups (a–f) along the DYPHYRAD transect during the storm of 2012-07-12. For each panel, RedMicro (diatoms), RedNano (nanoeukaryotes), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes) are shown as subplots (a–f) presented. Blue lines represent June–July climatological distributions, with shaded areas indicating the 50th–90th percentiles. Pre-storm (–10 days) and post-storm (+14 days) observations are shown as green (coastal) and orange (offshore) symbols, with circles indicating pre-storm and triangles indicating post-storm abundances. Red and black stars indicate transect-mean abundances

before and after the storm, respectively. Post-storm communities were dominated by diatoms and cryptophytes.

Consecutive storm: 2013-06-15 (preceding 2013-06-22)



Consecutive storm: 2013-06-15 (preceding 2013-06-22)

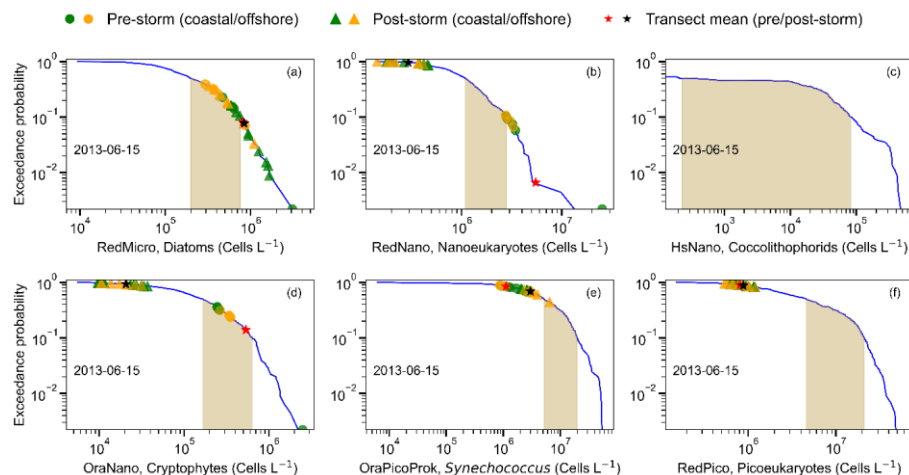


Figure F3. Exceedance probability (CCDF) distributions of six phytoplankton groups (a–f) along the DYPHYRAD transect during the storm of 2013-06-15. For each panel, RedMicro (diatoms), RedNano (nanoeukaryotes), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes) are presented shown as subplots (a–f). Blue lines represent June–July climatological distributions, with shaded areas indicating the 50th–90th percentiles. Pre-storm (–10 days) and post-storm (+14 days) observations are shown as green (coastal) and orange (offshore) symbols, with circles indicating pre-storm and triangles indicating post-storm abundances. Red and black stars indicate transect-mean abundances before and after the storm, respectively. Post-storm communities were dominated by diatoms.

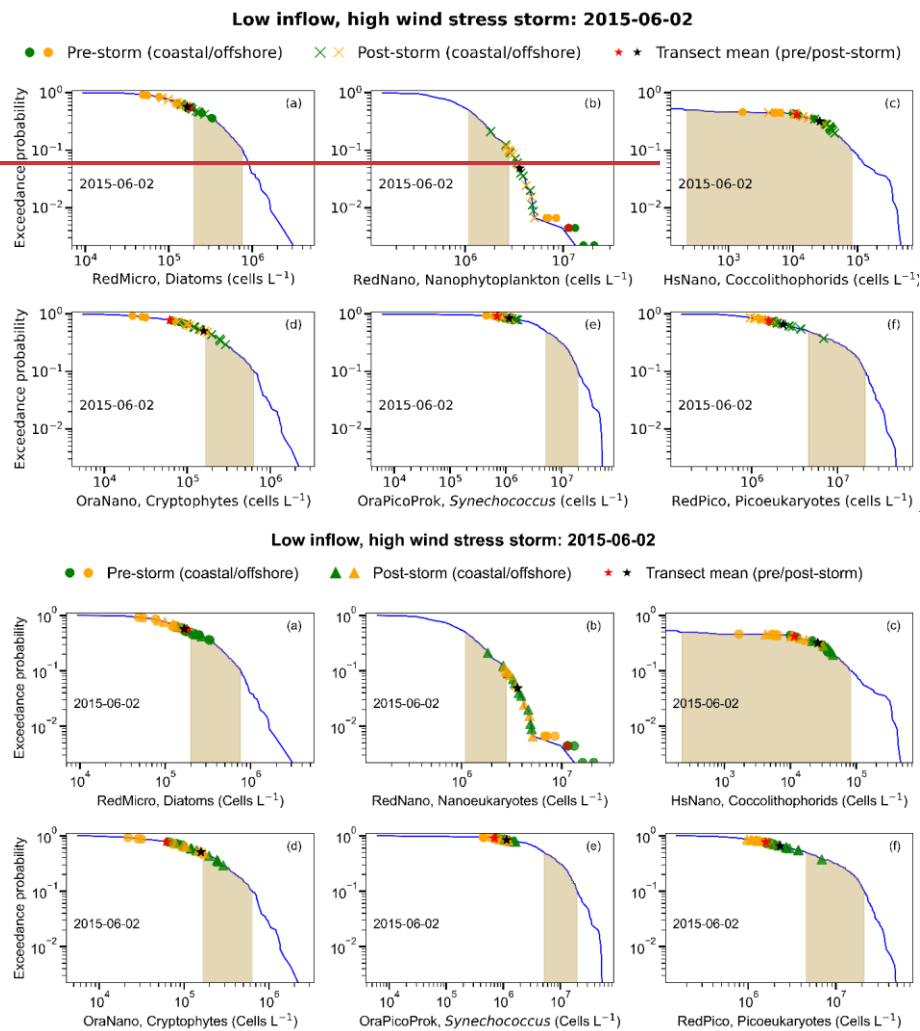


Figure F4. Exceedance probability (CCDF) distributions of six phytoplankton groups (a–f) along the DYPHYRAD transect during the storm of 2015-06-02. For each panel, RedMicro (diatoms), RedNano (nanoeukaryotes), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes) are presented shown as subplots (a–f). Blue lines represent June–July climatological distributions, with shaded areas indicating the 50th–90th percentiles. Pre-storm (–10 days) and post-storm (+14 days) observations are shown as green (coastal) and orange (offshore) symbols, with circles indicating pre-storm and triangles indicating post-storm abundances. Red and black stars indicate transect-mean abundances before and after the storm, respectively. Post-storm communities were initially dominated by *Phaeocystis globosa*, before being

replaced

by

nanophytoplankton.

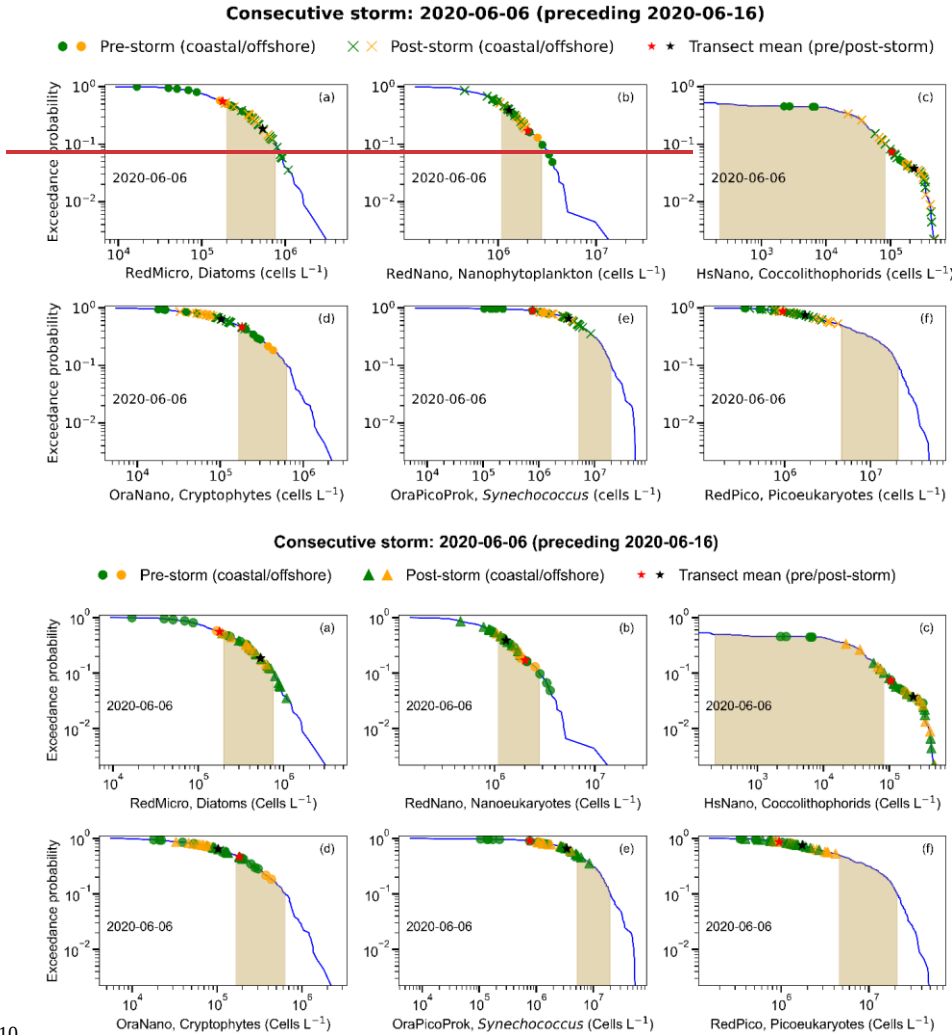
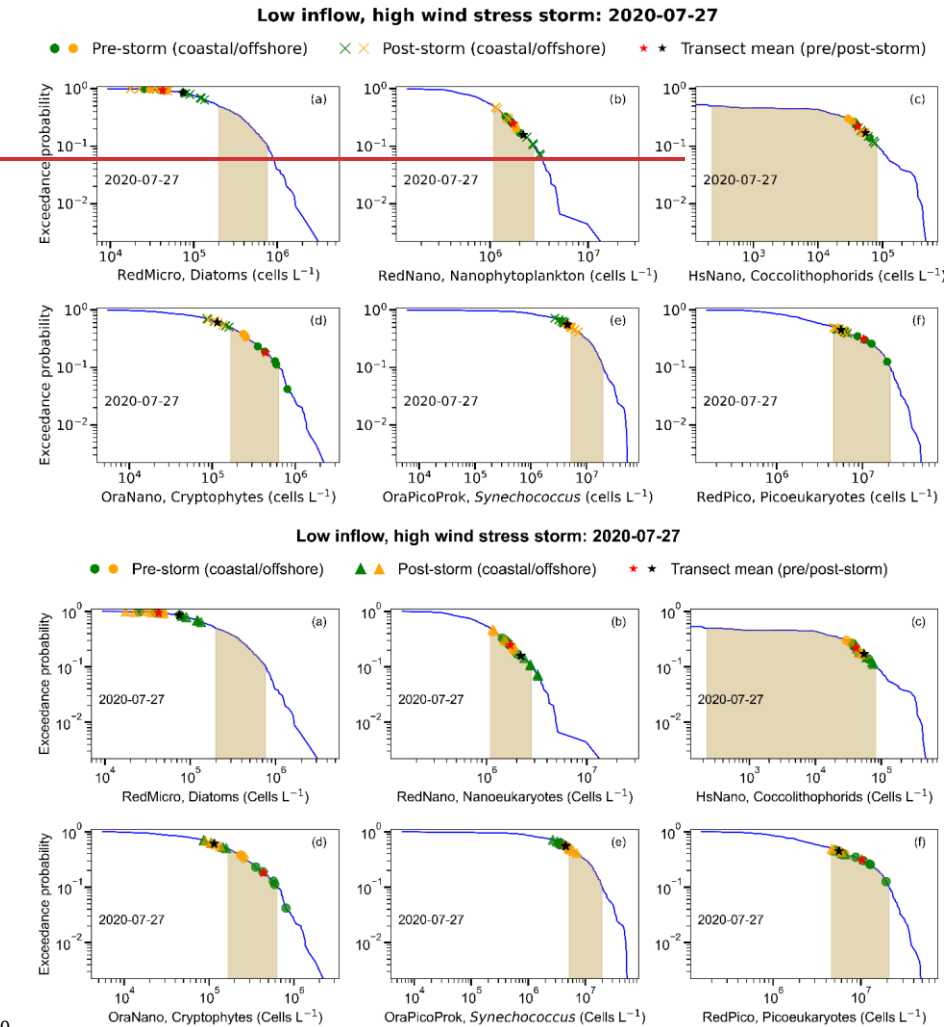


Figure F5. Exceedance probability (CCDF) distributions of six phytoplankton groups (a-f) along the DYPHYRAD transect during the storm of 2020-06-06. For each panel, RedMicro (diatoms), RedNano (nanophytoplankton), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes) are shown as subplots (a-f) presented. Blue lines represent June–July climatological distributions, with shaded areas indicating the 50th–90th percentiles. Pre-storm (–10 days) and post-storm (+14 days) observations are shown as green (coastal) and orange (offshore) symbols, with circles indicating pre-storm and triangles indicating post-storm abundances. Red and black stars indicate transect-mean abundances before and after the storm, respectively. The 2020-06-06 storm received additional precipitation and inflow on 2020-06-16 (not shown), supporting diatoms.



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Figure F6. Exceedance probability (CCDF) distributions of six phytoplankton groups (a–f) along the DYPHYRAD transect during the storm of 2020-07-27. For each panel, RedMicro (diatoms), RedNano (nanoeukaryotes), HsNano (coccolithophorids), OraNano (cryptophytes), OraPicoProk (*Synechococcus*), and RedPico (picoeukaryotes) are shown as subplots (a–f) presented. Blue lines represent June–July climatological distributions, with shaded areas indicating the 50th–90th percentiles. Pre-storm (–10 days) and post-storm (+14 days) observations are shown as green (coastal) and orange (offshore) symbols, with circles indicating pre-storm and triangles indicating post-storm abundances. Red and black stars indicate transect-mean abundances before and after the storm, respectively. Post-storm communities showed increased nanoeukaryotes and a replacement of cryptophytes and picoeukaryotes in coastal waters.

Appendix G: Abundance responses to storms: Anderson–Darling and Tail-exceedance test results

Table G1. Results of distribution-wide (Anderson–Darling) and tail-exceedance tests used to characterize phytoplankton responses to storm events in the EEC. The Anderson–Darling test detects overall shifts in abundance distributions between pre-

935 and post-storm samples, while the tail-exceedance test evaluates whether the frequency of extreme post-storm abundances (above the 90th percentile climatology) differs significantly from expectation (i.e., 90th percentile). Significant *p*-values (*p* < 0.05) in bold indicate either a distributional shift or enrichment of extreme values.

Storm date (y-m-d)	Phytoplankton group	Pre-storm samples (n)	Post-storm samples (n)	Anderson–Darling (AD) statistic	AD <i>p</i> -value	Tail-exceedance test <i>p</i> -value
2012-06-22	RedMicro	9	18	3.25	0.015	0.55
	RedNano	9	18	11.28	0.001	1
	HsNano	9	18			1
	OraNano	9	18	1.76	0.060	0.55
	OraPicoProk	9	18	12.47	0.001	1
	RedPico	9	18	12.04	0.001	1
2012-07-12	RedMicro	9	9	3.77	0.01	0.05
	RedNano	9	9	3.76	0.01	1
	HsNano	9	9			1
	OraNano	9	9	2.45	0.03	1
	OraPicoProk	9	9	−0.30	0.25	1
	RedPico	9	9	1.67	0.06	1
2013-06-15	RedMicro	9	18	−0.003	0.25	0.0001
	RedNano	9	18	12.47	0.001	1
	HsNano	9	18			1
	OraNano	9	18	12.47	0.001	1
	OraPicoProk	9	18	12.47	0.001	1
	RedPico	9	18	0.85	0.14	1
2015-06-02	RedMicro	9	18	1.43	0.08	1
	RedNano	9	18	12.47	0.001	7.85×10^{-13}
	HsNano	9	18	3.99	0.008	1
	OraNano	9	18	11.25	0.001	1
	OraPicoProk	9	18	8.37	0.001	1
	RedPico	9	18	1.00	0.12	1
2015-07-13	RedMicro	9	18	5.84	0.001	1
	RedNano	9	18	2.40	0.03	0.0001
	HsNano	9	18	1.75	0.06	0.27
	OraNano	9	18	2.41	0.03	0.006
	OraPicoProk	9	18	10.90	0.001	1
	RedPico	9	18	7.77	0.001	1
2016-06-20	RedMicro	9	9	8.83	0.001	0.23
	RedNano	9	9	3.95	0.008	1
	HsNano	9	9			1
	OraNano	9	9	2.77	0.02	1
	OraPicoProk	9	9	1.41	0.08	0.008

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	RedPico	9	9	1.37	0.08	1
2016-07-02	RedMicro	9	9	6.19	0.001	9.41×10^{-8}
	RedNano	9	9	2.74	0.02	1
	HsNano	9	9			1
	OraNano	9	9	8.83	0.001	1
	OraPicoProk	9	9	3.36	0.01	1
	RedPico	9	9	8.83	0.001	1
2020-06-06	RedMicro	12	27	12.18	0.001	0.13
	RedNano	12	27	4.21	0.006	1
	HsNano	12	27	3.95	0.008	6.1×10^{-15}
	OraNano	12	27	5.18	0.002	1
	OraPicoProk	12	27	13.70	0.001	1
	RedPico	12	27	3.14	0.01	1
2020-07-27	RedMicro	8	9	1.51	0.07	1
	RedNano	8	9	1.00	0.12	0.23
	HsNano	8	9	3.64	0.01	1
	OraNano	8	9	8.30	0.001	1
	OraPicoProk	8	9	1.07	0.11	1
	RedPico	8	9	4.43	0.005	1
2022-06-06	RedMicro	9	9	-0.50	0.25	1
	RedNano	9	9	8.83	0.001	1
	HsNano	9	9			1
	OraNano	9	9	8.83	0.001	1
	OraPicoProk	9	9	8.83	0.001	0.61
	RedPico	9	9	8.83	0.001	9.4×10^{-8}

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Appendix H: Phytoplankton taxa and functional group observations

Table H1. Dominant phytoplankton taxa identified in the EEC between 20 May and 10 August during storm years (2012, 2013, 2015, 2016, 2020, 2022). For each sampling date, the phytoplankton taxa with the highest cell abundance (Cells L⁻¹) were selected from the PHYTOBS Boulogne and PHYTOBS C databases.

Station	Date (y-m-d)	Phytoplankton taxa	Abundance (Cells L ⁻¹)	Chl-a (µg L ⁻¹)
PHYTOBS	2012-05-24	<i>Guinardia delicatula</i>	2.7×10^5	7.34
Boulogne	2012-06-05	<i>Leptocylindrus danicus</i>	3.9×10^5	3.32
	2012-06-19	<i>Leptocylindrus danicus</i>	7.6×10^5	2.22
	2012-07-25	<i>Leptocylindrus danicus</i>	2.4×10^5	11.23
	2013-05-30	<i>Phaeocystis globosa</i>	4.2×10^5	4.04
	2013-06-20	<i>Leptocylindrus danicus</i>	2.8×10^6	9.86
	2013-06-26	<i>Leptocylindrus danicus</i>	3.0×10^6	12.96
	2013-07-23	Cryptophyceae	1.0×10^5	2.53
	2013-08-05	<i>Rhizosolenia imbricata</i> + <i>styliiformis</i>	3.7×10^5	3.8
	2015-06-15	<i>Leptocylindrus danicus</i>	8.4×10^4	3.61
	2015-06-26	<i>Leptocylindrus danicus</i>	2.6×10^6	7.71
	2015-07-16	Cryptophyceae	3.1×10^4	1.39
	2016-05-24	<i>Phaeocystis globosa</i>	2.7×10^6	1.94
	2016-06-08	<i>Phaeocystis globosa</i>	4.8×10^5	1.57
	2016-06-23	<i>Leptocylindrus danicus</i>	3.1×10^6	9.6
	2016-07-04	<i>Chaetoceros socialis</i> + <i>socialis f. radians</i>	1.8×10^6	7.26
	2016-07-18	<i>Chaetoceros socialis f. radians</i>	1.0×10^6	8.75
	2020-05-26	Gymnodiniales	7.5×10^4	1.65
	2020-06-09	Cryptophyceae	4.9×10^4	2.66
	2020-06-24	Cryptophyceae	4.2×10^4	4.14
	2020-07-10	<i>Chaetoceros socialis f. radians</i>	5.4×10^4	1.34
	2020-07-20	<i>Chaetoceros socialis</i> + <i>socialis f. radians</i>	1.4×10^6	2.88
	2020-08-04	<i>Rhizosolenia imbricata</i> + <i>styliiformis</i>	3.7×10^4	1.55
	2022-06-01	<i>Chaetoceros socialis</i> + <i>socialis f. radians</i>	2.4×10^5	4.59
	2022-06-14	<i>Chaetoceros socialis</i> + <i>socialis f. radians</i>	2.2×10^6	4.7
	2022-06-27	<i>Chaetoceros socialis</i> + <i>socialis f. radians</i>	6.1×10^5	5.02
	2022-07-11	Cryptophyceae	1.4×10^5	3.46
	2022-07-26	<i>Chaetoceros</i>	7.4×10^4	1.6
	2022-08-10	Cryptophyceae	2.2×10^5	2.88
PHYTOBS C	2012-05-23	<i>Guinardia delicatula</i>	3.1×10^5	3.73
	2012-06-05	<i>Leptocylindrus (autres)</i>	3.4×10^5	2.12
	2012-06-21	<i>Leptocylindrus (autres)</i>	3.6×10^5	0.5
	2012-07-04	<i>Rhizosolenia imbricata</i> + <i>styliiformis</i>	1.4×10^5	7.96
	2012-07-23	<i>Leptocylindrus (autres)</i>	3.2×10^5	7.87
	2013-05-27	<i>Phaeocystis globosa</i>	1.2×10^6	1.94
	2013-06-10	<i>Leptocylindrus (autres)</i>	1.0×10^6	8.08
	2013-06-25	<i>Leptocylindrus (autres)</i>	5.9×10^6	14.19
	2013-07-09	<i>Leptocylindrus (autres)</i>	3.7×10^6	5.21

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	2013-07-22	<i>Leptocylindrus (autres)</i>	2.2×10^6	2.07
	2015-06-04	<i>Chaetoceros (autres)</i>	5.6×10^4	4.64
	2015-06-18	<i>Leptocylindrus (autres)</i>	2.3×10^5	2.85
	2015-07-03	<i>Rhizosolenia imbricata + styliiformis</i>	6.1×10^4	7.99
	2015-07-15	<i>Rhizosolenia imbricata + styliiformis</i>	3.2×10^4	1.33
	2016-05-23	<i>Phaeocystis globosa</i>	4.0×10^6	1.92
	2016-06-06	<i>Asterionellopsis</i>	1.2×10^5	9.64
	2016-06-21	<i>Gymnodiniales</i>	3.2×10^4	8.8
	2016-07-06	<i>Chaetoceros (autres)</i>	3.3×10^5	5.38
	2016-07-21	<i>Chaetoceros socialis + radians</i>	3.0×10^6	8.48
	2020-05-25	<i>Leptocylindrus (autres)</i>	3.5×10^4	1.53
	2020-06-03	<i>Leptocylindrus (autres)</i>	1.3×10^5	4.01
	2020-06-23	<i>Leptocylindrus (autres)</i>	1.9×10^5	4.01
	2020-07-07	<i>Chaetoceros socialis + radians</i>	1.8×10^4	1.54
	2020-07-22	<i>Chaetoceros socialis + radians</i>	8.7×10^4	3.17
	2022-05-30	<i>Leptocylindrus (autres)</i>	9.9×10^5	3.95
	2022-06-15	<i>Leptocylindrus (autres)</i>	2.9×10^5	4.29
	2022-06-29	<i>Leptocylindrus (autres)</i>	2.9×10^5	4.23
	2022-07-13	<i>Chaetoceros curvisetus + debilis + pseudocurvisetus</i>	1.1×10^5	4.31

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Table H2. SOMLIT observations of phytoplankton functional groups at SOMLIT C and SOMLIT L between 20 May and 10 August. Data include *Synechococcus*, picoeukaryotes, cryptophytes, and nanoeukaryotes abundances (Cells L⁻¹).

Station	Date	<i>Synechococcus</i>	Picoeukaryotes	Cryptophytes	Nanoeukaryotes
	(y-m-d)	(Cells L ⁻¹)	(Cells L ⁻¹)	(Cells L ⁻¹)	(Cells L ⁻¹)

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SOMLIT C	2012-05-23	2.9×10^5	4.0×10^5		9.3×10^5
	2012-06-21	6.1×10^6	3.3×10^5	2.5×10^3	1.4×10^6
	2012-07-04	2.2×10^6	4.4×10^5		6.2×10^5
	2012-07-23	2.4×10^6	4.2×10^5	3.0×10^4	5.5×10^5
	2013-05-27	7.9×10^4	3.3×10^4	8.9×10^4	5.6×10^4
	2013-06-10	1.3×10^6	1.8×10^5	2.5×10^4	1.9×10^5
	2013-06-25	6.2×10^5	4.0×10^5	2.5×10^4	6.0×10^4
	2013-07-06	9.2×10^5	2.5×10^5	5.4×10^4	2.7×10^5
	2013-07-22	1.5×10^6	5.8×10^4	1.5×10^4	1.3×10^5
	2015-06-04	8.6×10^5		2.1×10^4	9.3×10^5
	2015-06-18	1.3×10^6		2.0×10^4	1.2×10^6
	2015-07-03	1.0×10^7		6.7×10^4	2.2×10^6
	2015-07-15	3.6×10^6	1.4×10^6	6.7×10^4	1.1×10^6
	2016-05-23	2.2×10^6		1.1×10^5	1.4×10^7
	2016-06-06	9.0×10^6	1.4×10^6	1.1×10^5	1.1×10^6
	2016-06-21	9.9×10^6	1.5×10^6	6.7×10^4	9.6×10^5
	2016-07-06	8.6×10^6	1.2×10^6	3.4×10^6	7.7×10^5
	2016-07-21	5.8×10^6	2.3×10^6	4.2×10^6	2.3×10^6
	2020-05-25	6.9×10^6	4.8×10^6	1.5×10^5	1.7×10^6
	2020-06-03	2.5×10^5	3.0×10^5	6.1×10^4	2.0×10^6
	2020-06-23	3.8×10^6	6.5×10^5	1.7×10^5	2.2×10^6
	2020-07-07	2.4×10^7	5.0×10^6	1.6×10^5	4.9×10^6
	2020-07-22	3.4×10^7	1.6×10^7	7.3×10^5	2.1×10^6
	2022-05-17	3.5×10^4	1.8×10^7	3.5×10^5	1.4×10^6
	2022-06-29	4.9×10^7	5.7×10^6	2.5×10^5	4.2×10^6
	2022-07-13	1.4×10^7		2.2×10^5	3.8×10^6
SOMLIT L	2012-05-23	8.9×10^5	6.2×10^5	2.8×10^4	7.8×10^5
	2012-06-21	1.7×10^6	3.4×10^5	7.6×10^3	6.6×10^5
	2012-07-04	8.8×10^6	1.4×10^6	5.0×10^3	6.5×10^5
	2012-07-23	5.4×10^6	6.6×10^5	2.3×10^4	5.5×10^5
	2013-05-27	4.4×10^5	1.3×10^6	3.6×10^5	3.0×10^5
	2013-06-10	1.2×10^6	1.7×10^5	2.3×10^4	1.9×10^5
	2013-06-25	8.4×10^6	2.9×10^5	2.5×10^4	1.3×10^5
	2013-07-22	7.3×10^6	5.5×10^5	1.7×10^4	2.3×10^5
	2015-06-04	3.7×10^5		3.3×10^3	1.5×10^6
	2015-06-18	8.1×10^5	3.0×10^5	8.2×10^3	1.6×10^6
	2015-07-03	3.4×10^7	1.1×10^7	1.3×10^5	2.6×10^6
	2015-07-15	3.6×10^6	7.9×10^5	6.1×10^4	1.0×10^6
	2016-05-23	1.4×10^7	3.6×10^6	1.7×10^5	2.6×10^6
	2016-06-06	2.1×10^7	1.8×10^6	1.8×10^5	1.4×10^6

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▲	2016-07-06	1.8×10^7	4.5×10^6	1.3×10^6	1.3×10^6
▲	2020-06-03	9.5×10^5	1.0×10^6	7.9×10^4	2.8×10^6
▲	2020-07-22	8.3×10^6	4.0×10^6	3.6×10^5	2.8×10^6
▲	2022-05-17	2.3×10^5	2.4×10^7	4.0×10^3	4.8×10^6
▲	2022-06-29	1.0×10^8	7.8×10^6	5.1×10^4	2.4×10^6
▲	2022-07-13	1.8×10^7		1.0×10^5	2.1×10^6

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Data availability.

965 The cytometric and environmental datasets (Hubert et al., 2025b), as well as phytoplankton abundance data from the SOMLIT (Savoie et al., 2026) and PHYTOBS (PHYTOBS, 2025) stations, are available through the SEANOE data repository. Meteorological data (wind speed, precipitation and direction) are provided by Météo-France and available at <https://meteo.data.gouv.fr/>. Hydrological data on freshwater inflow are accessible from Eau France at <https://www.eaufrance.fr/>.

970 *Author contributions.*

This work was conceptualized by FGS, UC, and HC. LFA provided DYPHYRAD data HC performed the analysis and interpreted the results with input from FGS and UC. HC wrote the first draft with the help of UC and FGS. FGS and UC secured funding and supervised HC.

Competing interests.

975 The contact author has declared that none of the authors has any competing interests.

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