Multiscale phytoplankton dynamics in a coastal system of the Eastern English Channel: the Boulogne-sur-Mer coastal area

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Abstract. To study changes in phytoplankton community composition at different time scales, an automated flow cytometer (Cytosub, Cytobuoy b.v.) was deployed on the MAREL Carnot automated monitoring station in Boulogne-sur-Mer (Eastern English Channel, France) during spring (2021, 2022) and summer (2022), following an Eulerian approach. Phytoplankton dynamics were recorded every 2 hours, distinguishing 11 Phytoplankton Functional Groups (PFGs) based on optical and fluorescence properties. This enabled detailed characterization of PFG successions, including MicroRED (mostly diatoms) and NanoRED (mostly haptophytes of the ~~genus~~ species *Phaeocystis globosa*) transitions in spring, as well as a summer dominance by PicoORG (pico-cyanobacteria, mostly of the genus *Synechococcus*) and PicoRED. Four extreme events, including a salinity drop (April 2021), ~~high~~ strong winds (May 2021 and April 2022), and a marine heatwave (July 2022), caused rapid shifts in phytoplankton community ~~composition~~ assemblage. Empirical Mode Decomposition (EMD) and Lomb-Scargle Periodogram (LSP) analyses revealed that 85 ± 10 % of variability in total phytoplankton abundance, red fluorescence (proxy of chlorophyll *a*), and Shannon diversity occurred at relatively short timescales (9 hours to 11 days) for time series of several months, highlighting the value of high frequency monitoring in capturing ecological dynamics under macrotidal conditions in the Eastern English Channel.

1 Introduction

Phytoplankton, comprising unicellular autotrophic organisms suspended in the water column, are key primary producers in marine ecosystems, driving carbon fixation and supporting heterotrophic organisms (Falkowski et al., 2003; Pal and Choudhury, 2014). They play a central role in marine food webs including microbial food web (Legendre and Rassoulzadegan, 1995),

biogeochemical cycles, and the carbon biological pump. Despite constituting less than 0.1 % of global biomass, phytoplankton contribute to approximately half of the world's annual net primary production (Falkowski et al., 1998; Field et al., 1998; Bar-On et al., 2018; Bar-On and Milo, 2019).

Coastal zones, defined as transitional areas between marine and terrestrial environments which cover 12 % of the Earth's surface and accommodate between 23 % and 50 % of the global population (Crossland et al., 2005), are highly dynamic environments with significant ecological and socio-economic importance. These regions support 90 % of global fishing activity and exhibit high primary production driven by nutrient enrichment (Crossland et al., 2005; Cloern et al., 2014). Monitoring phytoplankton in these zones provides valuable insights into ecosystem health, helps us to better understand local ecosystems and offers indirect socio-economic benefits (Holland et al., 2023; Louchart et al., 2023). Coastal waters are characterized by high spatio-temporal variability influenced by natural and anthropogenic factors, making them ideal for high frequency studies, which can capture rapid phenomena occurring within hours (Dubelaar et al., 2004; Kbaier Ben Ismail et al., 2016) and elucidating the strong spatio-temporal variability linked to meso and sub-meso scales processes (Rantajärvi et al., 1998; Bonato et al., 2015). These studies are especially valuable for understanding processes like Harmful Algal Blooms (HABs; Serre-Fredj et al., 2021) and multi-scale phytoplankton dynamics in connection to multi-scale changes in coastal waters state (Hynes et al., 2024).

Phytoplankton dynamics respond rapidly to environmental changes driven by abiotic factors (e.g., light, turbulence, nutrients, temperature, salinity) and biotic factors (e.g., competition, predation, parasitism Smith and Lancelot, 2004; Menge and Weitz, 2009; Wyatt, 2014; Chiswell et al., 2015). Understanding these responses requires monitoring approaches that capture temporal variability. Eulerian and Lagrangian frameworks are often employed, but interpreting time series data can be challenging due to the interplay between spatial and temporal changes.

In this study, we deployed an automated submersible "pulse shape-recording" flow cytometer, associated with physico-chemical parameters, on a coastal monitoring station in the Eastern English Channel (EEC). This instrument performs optical single-cell measurements every 2 hours, capturing phytoplankton dynamics from picophytoplankton (1 μm) to microphytoplankton (800 μm width; Olson et al., 2003; Dubelaar et al., 2004; Pomati et al., 2013; Fontana and Pomati, 2014; Pereira et al., 2017; Fragoso et al., 2019; Louchart et al., 2020). High frequency cytometry measurements has previously revealed insights into growth rates, physiological responses to extreme events, and community variability (Sosik et al., 2010; Dugenne et al., 2014; Thyssen et al., 2014). By deploying the automated flow cytometry in an Eulerian framework in a highly dynamic system submitted to anthropogenic pressure, we aimed to track phytoplankton variability across multiple timescales, capturing both periodic (e.g., tidal cycles) and non-periodic (e.g., extreme events) changes in functional groups and community ~~composition~~ assemblage. This approach allowed us to explore phytoplankton dynamics over hours to months, enhancing our understanding of EEC coastal ecosystem variability.
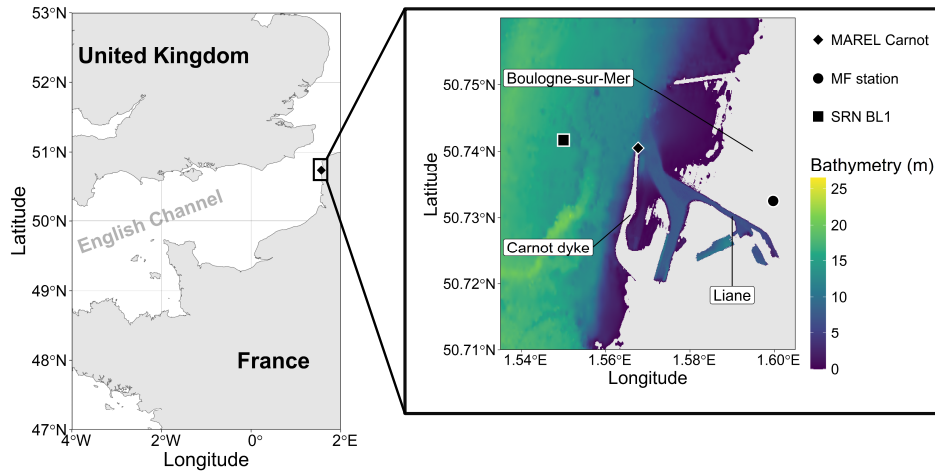
Figure 1. Map of the study area showing the location of the MAREL buoy on the Carnot dyke in Boulogne-sur-Mer. The bathymetry data, with an approximate resolution of 10 meters, were developed as part of the TANDEM project (SHOM, 2015). Only regions with bathymetric depths more than 0 m are displayed. The MAREL Carnot, the Météo France (MF; 2.43 km from MAREL Carnot) and the SRN 'Boulogne 1' (BL1; 1.25 km from MAREL Carnot) stations are indicated.

2 Materials and methods

2.1 MAREL Carnot station

The MAREL Carnot station is an automated measurement platform, part of the National Observation Service and integrated into the COAST-HF network (https://coast-hf.fr; last accessed: 12th December 2024) integrated to the French National Structure for Littoral and Coastal Observation IR ILICO infrastructure (https://www.ir-ilico.fr; last accessed: 12th December 2024) dedicated to high frequency monitoring of French coastal environments (Halawi Ghosn et al., 2023; MAREL Carnot, 2024). The station is situated at the end of the 2-km-long Carnot dike (50°44'25.8" N, 1°34'3.72" E), near the lighthouse at the entrance of Boulogne-sur-Mer harbor (Pas-de-Calais, France), at the mouth of the Liane estuary (Fig. 1). The depth of this area ranges between 5 and 16 m, with a mean depth of approximately 10 m (Halawi Ghosn et al., 2023). This coastal area is subject to significant anthropogenic pressures, including those from harbor activities but also agricultural runoff entering the river (Lheureux et al., 2023). This station continuously monitors subsurface (1.5 m depth) physico-chemical parameters at 20-minute intervals, including Sea Surface Temperature (SST), salinity, turbidity, dissolved oxygen, wind direction and speed, and fluorescence with a multiparameter sensor (NKE MP6) and a static weather station (AirMAR 200WX). A comprehensive description of these parameters is provided in Halawi Ghosn et al. (2023). As a fixed monitoring platform, it enables Eulerian observation of the marine environment by continuously recording temporal variations at a single location.
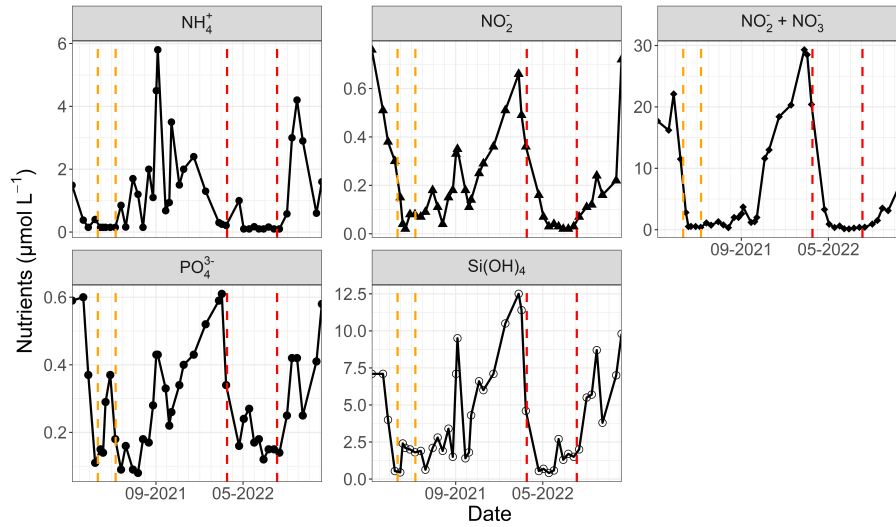
Figure 2. SRN nutrients data (Lefebvre et al., 2024) at the 'Boulogne 1' station for 2021 and 2022. The two study periods are highlighted in by the dashed lines (orange for 2021 and red for 2022).

Wind data for 2021 were sourced from Météo France (50°43'57" N, 1°35'59" E) due to a lack of available data from the MAREL CARNOT station during that period. Additionally, water height data for 2021 and 2022 were obtained from the 'Réseaux marégraphiques français' (REFMAR) data of the 'Service Hydrographique et Océanographique de la Marine' (SHOM, France). Furthermore, low-frequency nutrient data (ammonium, nitrite, nitrate, phosphate, and silicate) from the 'Suivi Régional des Nutriments' (SRN) program were utilized at the Boulogne 1 SRN-station (50°43'90 N, 1°33'00 E) off Boulogne-sur-Mer coastal area (the nearest low frequency monitoring station with fortnightly 0.5 to 1 m depth sampling), as these parameters were not monitored by the MAREL Carnot station (Lefebvre et al., 2024). The 2021 and 2022 data are presented in Fig. 2.

The complex currents and the presence of multiple estuaries in the EEC (from the Somme estuary in Picardy, including the Liane estuary in Boulogne-sur-Mer, until the Slack estuary near the Strait of Dover, in addition to remote influence by the Seine estuary) contribute to the formation of the 'coastal flow' (Brylinski et al., 1991). This Region Of Freshwater Influence (ROFI) affects physico-chemical parameters, such as nutrients and salinity, which are influenced by freshwater discharge from local or remote estuaries and land-based streams entering the sea. Along a coastal strip spanning 3 to 5 nautical miles, brackish waters are observed, separated from the open sea by an interface similar to a desalination and tidal front (Brylinski et al., 1991). These conditions significantly shape phytoplankton dynamics, particularly during recurrent seasonal events such as the spring bloom, which is dominated in this region by an alternance of diatom and haptophyte (*Phaeocystis globosa*; Breton et al., 2000; Lefebvre et al., 2011; Breton et al., 2022). The coastal waters off Boulogne-sur-Mer are characterized by a macrotidal regime (tidal range > 4 m) and occasionally border on megatidal conditions (tidal range > 8 m; Levoy et al., 2000). The tides are semi-diurnal, completing a full cycle approximately every 12.4 hours (Lazure and Desmare, 2012). During ebb tide, the current in

the EEC flows southwestward, while flood tide results in a northeastward flow, causing a reversal in currents during tidal shifts. However, wind dynamics can significantly alter this circulation pattern, adding to the complexity of the hydrodynamics of the EEC at various spatio-temporal scales (Lazure and Desmare, 2012; Bertin et al., 2024). The current patterns within the harbor are also influenced by factors such as freshwater inflows and tidal phases, with an eddy typically forming during rising tide (Jouanneau et al., 2013; Sentchev and Yaremchuk, 2016). Current speeds inside the harbor are generally lower than offshore but remain substantial due to tidal influence, typically ranging between 0.1 m s^{-1} and 0.3 m s^{-1} (Sentchev and Yaremchuk, 2016). These speeds ensure that the water column remains well-mixed.

These hydrological characteristics play a crucial role in influencing phytoplankton dynamics across different timescales, as plankton, by definition, is transported by currents.

2.2 Automated flow cytometer

A CytoSub (Cytobuoy b.v., Netherlands) was deployed in the MAREL Carnot station between March 23rd and May 12th 2021 then between March 17th and August 3rd 2022. This automated flow cytometer uses a 488 nm-laser (blue) to digitize the optical features and pulse profile of particles. The interaction of each particle with the laser beam produces forward scatter (FWS), which relates to particle size (Cunningham and Buonnacorsi, 1992), and side scatter (SWS), which provides information about the internal and external complexity of the particles (Dubelaar et al., 2004; Fontana and Pomati, 2014; Fragoso et al., 2019). It also measures three types of fluorescence (red, orange, yellow; FLR, FLO, FLY) corresponding to pigment composition: chlorophyll *a*, phycoerythrin and phycocyanin, and phaeopigments or degraded pigments, respectively (Dubelaar and Gerritzen, 2000; Dubelaar and Jonker, 2000). The digitized profile yields different features such as the area under the curve, maximum, and minimum, which are used to create 2-dimensional plots (cytograms). In these plots, particles are positioned according to their optical properties, allowing for clustering (gating) of similar particles, as shown in Fig. 3.

Three cytometry protocols were used in this study, each optimized for specific size ranges. The "Pico" protocol targets particles below 5 μm, while the "Micro" protocol captures particles above 5 μm. A third protocol, the "Micro-Photos", mirrors the "Micro" protocol but uses a lower sample flow rate to acquire precise images of particles that compose the different nano- and micro- Phytoplankton Functional Groups (PFGs; Thyssen et al., 2022). While not allowing for a definitive taxonomic identification at the species or complex level, these images can suggest a possible composition of dominant groups—particularly for micro- and nano- PFGs clusters. This visual information is further supported by the analysis of pulse shapes, which provide an *in silico* image of cells and colonies across all clusters. In 2021, a single threshold (or trigger level) based on a minimum of FLR was applied for both protocols. In 2022, two detection thresholds were used during *in situ* measurements by MAREL Carnot with the CytoSub, using both SWS and FLR signals to capture the longer pulse-shape. This adjustment does not affect measures of PFGs abundance or total phytoplankton abundance.

During this study, 11 PFGs were defined through manual clustering using CytoClus 4 software. The bibliographic context of the study area involving the use of automated flow cytometry (Guiselin, 2010; Bonato et al., 2015; Louchart et al., 2020, 2024), sometimes in combination with complementary methods such as microscopy, and the "Micro-Photos" protocol (based on photo identification) enabled to interpret PFGs in term of probable taxonomic equivalents, which where additionally related
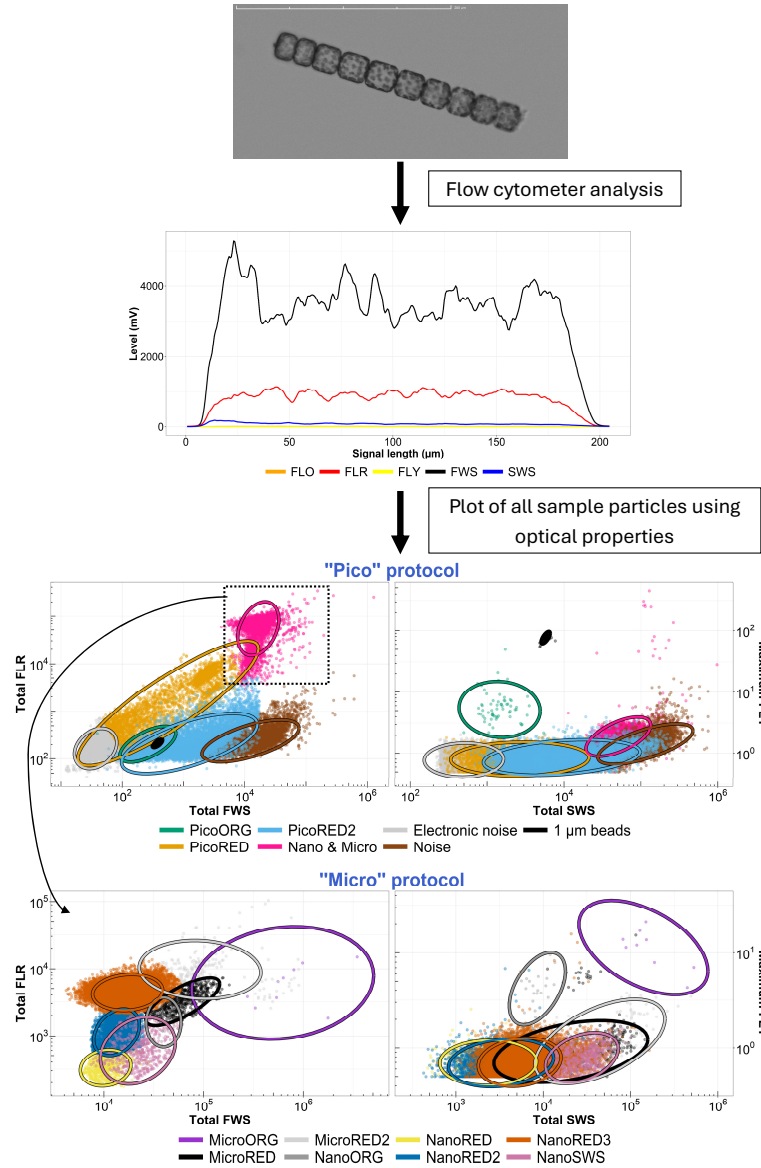
Figure 3. Diagram of the principle of the automated pulse shape-recording flow cytometer, from particles to cytograms. The top figure shows an example of picture of a colonial diatom (*Lauderia sp.*) taken by the CytoSub. Its associated optical spectrum is shown below. The cytograms shown at the bottom of the figure are based on the properties of the optical features of all the cells and colonies analyzed for a single sample, calculated from the optical signals recorded and assigned to a single cluster using an exclusive set function. The coloured scatter points and ellipses (*t* distribution confidence interval of 95 %) are shown as a gating example for these particles.

to the novel consensual nomenclature published in Thyssen et al. (2022), as detailed in Table 1. Yet, as our method was particularly atoxonomic for the smallest size classes where no photographs can be taken by the "Micro-Photos" protocol, it

Table 1. Detailed glossary of characterized PFGs. The taxonomical/optical interpretation of each group is based on determination by images and literature. A particle belonging to a given group therefore has optical properties similar to those of the proposed optical equivalent even though it is uncertain that the observed particle corresponded to the given taxa (or attributed taxa). Thyssen et al. (2022) optical group common vocabulary equivalents and associated size range are also provided.

Optical group	Example of taxonomical correspondence	Difference from similarly named groups	Size range	Standardised vocabulary
PicoRED	Autotrophic picoeukaryotes	Lower FWS	< 3 μm	RedPico
PicoRED2	Autotrophic picoeukaryotes	Higher FWS	< 3 μm	RedPico
PicoORG	Pico-cyanobacteria (mainly *Synechococcus* spp.)	-	< 3 μm	OraPicoProk
NanoRED	Eukaryotic nano autotroph (mainly *P. globosa*, flagellated cells)	Lower FLR	3 to 20 μm	RedNano
NanoRED2	Eukaryotic nano autotroph (mainly *P. globosa*, flagellated cells)	Medium FLR	3 to 20 μm	RedNano
NanoRED3	Eukaryotic nano autotroph (mainly *P. globosa*, free colonial cells)	Higher FLR	3 to 20 μm	RedNano
NanoORG	Eukaryotic nano autotrophs with phycoerythrin (mainly *Cryptophyceae sp.*)	-	3 to 20 μm	OraNano
NanoSWS	High side-ward scatter eukaryotic nano autotrophs (mainly *Coccosphaerales sp.*)	-	3 to 20 μm	HsNano
MicroRED	Eukaryotic micro autotrophs (mainly *Pseudo-Nitzschia* complex)	Lower FLR	> 20 μm	RedMicro
MicroRED2	Eukaryotic micro autotrophs (mainly free and colonial diatoms)	Higher FLR	> 20 μm	RedMicro
MicroORG	Eukaryotic micro autotrophs with phycoerythrin (mainly *Cryptophyceae sp.*)	-	> 20 μm	OraMicro

was not possible to provide definitive taxonomic identifications for the PicoRED groups. However, based on size ($< 3~\mu$m) and fluorescence characteristics, the PicoRED groups likely includes small picoeukaryotes such as *Micromonas* spp. or other similar prasinophytes (Not et al., 2004; Masquelier et al., 2011).

To facilitate comparisons between the two study years, ~~Julian days (J_d)~~ Ordinal days (O_d) were standardized to the UTC +01:00 time zone (see Sect. 3.1).
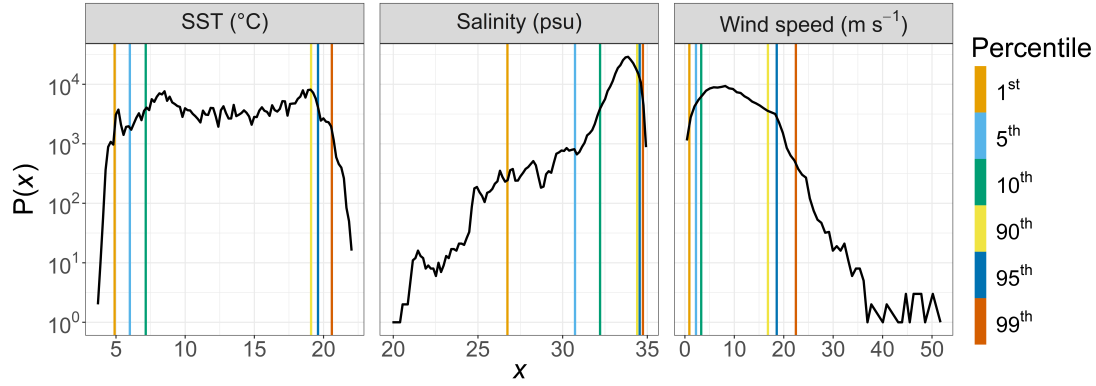
Figure 4. Probability density functions of MAREL Carnot SST (°C), salinity (psu), and wind speed (m s⁻¹) data recorded between 2004 and 2023. The colored dashed lines indicate the estimated percentiles for each time series.

2.3 Statistical analysis

2.3.1 Climatological baseline and definition of extreme events

To assess the occurrence and intensity of extreme environmental events (e.g., marine heatwave, desalination, high wind storm), we used a long-term baseline derived from high-frequency MAREL Carnot surface measurements collected between 2004 and 2023. The probability density functions of the used parameters are shown in Fig. 4. Percentile thresholds (e.g., 90th, 95th and 99th percentiles) were computed from this 20-year dataset and used to identify values considered anomalously high, as commonly done for time series extreme event detection (e.g., Camuffo et al., 2020; Jamous and Marsooli, 2023; Hemming et al., 2024). This method provides a robust site-specific context for interpreting "rare" events.

2.3.2 Emirical Mode Decomposition and Lomb-Scargle Periodogram analysis (EMD-LSP)

The Empirical Mode Decomposition (EMD) was used to charatarize the multi-scale phytoplankton dynamics. This algorithm decomposes a time series $X(t)$ into n Intrinsic Mode Functions (IMFs) $C_i(t)$ as described by Huang et al. (1998):

$$X(t) = \sum_{i=1}^{n} C_i(t) + r_n(t) \tag{1}$$

EMD works by first constructing upper and lower envelopes that connect the local maxima and minima of the time series, respectively. The mean of these envelopes defines the first zero-mean IMF $C_1(t)$. This IMF is then subtracted from the original time series, and the process is repeated n times until a monotonic function $r_n(t)$, representing the trend of the series, is obtained (Huang et al., 1998). This decomposition method allows a time series to be expressed as a sum of oscillating modes, each with a distinct characteristic scale, alongside a trend. EMD has been previously used, for instance, to used to analyze phytoplankton dynamics in Lake Geneva (France-Swiss border) by Schmitt et al. (2013), where it was applied to study multi-scale variability.

To determine the mean period of each IMF, we applied the Lomb-Scargle Periodogram (LSP), a technique originally developed for analyzing irregular astronomical time series (Lomb, 1976; Scargle, 1982) but applicable to biological time series (Ruf, 1999). The LSP evaluates various periodic patterns by fitting sine or cosine waves of different frequencies, amplitudes, and phases to the observed data. The most appropriate pattern, including its phase and amplitude, is identified by determining the frequency of the sinusoidal waveform that best describes the observed data. Only frequencies above $2f_{min}$ were retained based on the Nyquist-Shannon theorem. The mean period $\overline{T_i}$ for each IMF was calculated using:

$$\overline{T_i} = \left(\frac{\int_0^\infty f L^s{}_i(f) \mathrm{d}f}{\int_0^\infty L^s{}_i(f) \mathrm{d}f} \right)^{-1}, \tag{2}$$

where f is the frequency and $L^s{}_i$ is the Lomb-Scargle spectrum of $C_i(t)$. This method provides an energy-weighted calculation of the mean period (Huang et al., 1998, 2009). Additionally, the period of the maximum peak in the periodogram, $T_{\max}$, was extracted.

To assess the contribution of each IMF to the total signal, we calculated their relative variance $V_i = V(C_i)$. The variance lost V_i^{lost} after removing the IMFs C_1 to C_i from the original signal was estimated using:

$$V_i^{\text{lost}} = 100 \cdot \frac{\sum_{k=1}^i V_k}{\sum_{k=1}^n V_k + V(r_n)}, \tag{3}$$

where n is the total number of IMFs found for $X(t)$. This calculation provides an estimate of the cumulative information loss across different timescales based on the periods of the different IMFs.

2.3.3 Shannon diversity index H'

We applied the EMD-LSP method to the exponential value of the Shannon diversity index H' (Shannon, 1948) based on the cytometric optical communities:

$$H' = -\sum_{i=1}^S p_i \log_2(p_i), \tag{4}$$

where $\log_2$ is the binary logarithm, S is the number of communities and p_i is the proportion of the community i in the entire ecosystem. The Shannon diversity index is widely used to characterize community diversity by considering both the richness (number of functional groups) and their relative abundances (or relative FLR in our case) in a sample. It serves as an indicator of ecosystem health and can signal disturbance (Hill, 1973; Li, 1997, 2002). We examined the dynamics of its exponential form, known as Hill's diversity number of order one (Hill, 1973). This cytometric diversity index provides information about the non-taxonomic entropy of community assemblages and reflects the level of organization (in thermodynamic terms) of the ecosystem. The Shannon index dynamics capture how quickly the functional structure of a part of the ecosystem can change, as cytometric groups can be considered functional groups based on optical features as proxys of size, granulosity and pigment content (Le Quéré et al., 2005; Fontana and Pomati, 2014; Fragoso et al., 2019; Fuchs et al., 2022; Louchart et al., 2024).

Shannon entropy is fundamental in phytoplankton ecology as it determines the community structure and thereby can be linked to the environmental conditions. It has been previously applied to functional groups in other studies (e.g., Sun and

Wang, 2021). The binary logarithm was used in Eq. (4) to express the measure in bits and to ensure comparability with previous ecological studies based on functional traits (e.g., Sun and Wang, 2021).

Here, we applied the EMD-LSP analysis to the time series of $\exp(H')$ to explore the variability in the arrangement of communities over multiple timescales. The aim was to account for its multi-scale dynamics, spanning from hours to days, and to understand the dynamic shifts in community ~~composition~~ assemblage.

3 Results

3.1 Phytoplankton phenologies

The abundance and FLR data (both total and per optically-defined PFG) are shown in absolute values in Fig. 5 and in relative values in Fig. 6. First, it is important to note that these time series are incomplete. This results from technical failures that occurred during the deployments.

3.1.1 2021 deployment

The dynamics of the 2021 spring bloom on a seasonal scale can be divided into three distinct phases. At the start of the measurement series ($\cancel{J_d}\ O_d = 82$), the PicoRED2 group dominated, increasing from 8 % to 63 % of the total abundance between March 24th and March 26th ($\cancel{J_d}\ O_d = 83$ and $\cancel{J_d}\ O_d = 85$). During this period ($J_d \in [82; 96]$), total abundance ranged from $0.12 \cdot 10^4$ to $4.1 \cdot 10^4$ cells mL^{-1} (Fig. 5a). The second phase began on April 7th ($\cancel{J_d}\ O_d = 97$), marked by the predominance of the NanoREDs groups. These groups, initially dominant at the start of the study period, became the majority again, with a mean contribution of 58.5 ± 11.3 % for $J_d \in [97; 121]$. Total abundance during this phase ranged from $0.47 \cdot 10^4$ to $11.87 \cdot 10^4$ cells mL^{-1} (Fig. 5a). ~~This phase corresponded to the onset of the *P. globosa* bloom, a phenomenon typical of the EEC (Breton et al. 2022) and frequently monitored due to its classification as a HAB (Lefebvre and Dezécache, 2020).~~ Notably, the contribution of this group to total phytoplankton abundance fluctuated, with periods of high relative abundance coinciding with local maxima in total abundance, followed by brief declines. Hourly fluctuations were also observed, driven by extreme events in early May, which will be discussed in Sect. 3.2. Towards the end of the time series, the contribution of the NanoRED2 group to total abundance increased (12.8 % above the average for its associated PFG time series), while that of the NanoRED3 group decreased (5.9 % below its average).

In terms of FLR (a proxy for chlorophyll *a* biomass), a clear seasonal dynamic was observed. The MicroRED2 group was well-represented at the start of the bloom, spanning from approximately March 23rd to March 27th($\cancel{J_d}\ O_d = 82$ to $\cancel{J_d}\ O_d = 86$). Its contribution gradually declined through the beginning of April. This pattern may correspond to the initial diatom bloom, where the high FLR values reflect the metabolic activity of these cells. These high FLR per cell values may also reflect photo-acclimation to low light at the beginning of the blooming period (Houliez et al., 2013). As the season progressed, the NanoRED2 and NanoRED3 groups dominated the FLR time series, with rapid alternations in their relative importance, signaling shifts in both community assemblage and physiological state. The peak in FLR was recorded on April 24th ($\cancel{J_d}\ O_d = 114$),

Figure 5. Phytoplankton data recorded with the automated flow cytometer (CytoSub) for each sampled ~~Julian day~~ Ordinal day: (a) phyto-plankton abundance and (b) phytoplanktonic red fluorescence (proxy of the chlorophyll *a* expressed in Arbitrary Units per mL; AU). These data are represented in total values and per optically-discriminated PFG. The black line and dots represent 2021 data and the green line and dots represent 2022 data. The purple vertical lines indicate the start of each month.

coinciding with the core of the NanoREDs bloom. This period, traditionally dominated by ~~*P. globosa*~~ *Phaeocystis globosa*, saw significant representation of the NanoRED2 and NanoRED3 groups, and the associated increase in FLR indicates higher physiological activity during this phase. Towards the end of the bloom, starting on May 7th (~~J_d~~ O_d = 127), the NanoRED2 group became increasingly prominent in contributing to total fluorescence. This pattern aligns with abundance data, where NanoRED2 accounted for 28.8 ± 6.0 % of cumulative total abundance, peaking at 51.4 % on May 8th. The rise in FLR from NanoRED2 suggests enhanced metabolic processes and productivity in this group.

Figure 6. Phytoplankton data recorded for each group with the automated flow cytometer (CytoSub) for each sampled ~~Julian day~~ Ordinal day: (a) PFGs relative abundance and (b) PFGs relative red fluorescence (proxy of the chlorophyll *a*). The relative values of each group are computed as the ratio of the group's value to the total sum across all groups. The black line and dots represent 2021 data and the green line and dots represent 2022 data. The purple vertical lines indicate the start of each month. Another representation of these results is proposed in Appendix C.

3.1.2 2022 deployment

210   The dynamics of the 2022 spring bloom can be divided into several phases. The first phase was dominated by the PicoREDs groups, which accounted for 83.4 ± 7.7 % of the total abundance during $J_d \in [76; 100)$, with a peak of $12 \cdot 10^4$ cells mL^{-1} recorded on April 9th ($\cancel{J_d}\ O_d = 99$). ~~The PicoORG group also contributed an average of 7 % between March 23rd and March 27th (J_d = 82 and 86).~~ In addition, the PicoORG group contributed on average with 7 % between March 23rd and March 27th (O_d = 82 and 86) to the total abundance. From April 10th ($\cancel{J_d}\ O_d = 100$), an increase in the NanoREDs groups' total and relative

215   abundances likely marked the onset of the *P. globosa* bloom. Between May 5th and May 27th ($\cancel{J_d}\ O_d = 125$ to $\cancel{J_d}\ O_d = 147$), their

relative abundance averaged 45.8 ± 10.0 %, with absolute values ranging from $0.6 \cdot 10^4$ to $8.0 \cdot 10^4$ cells mL^{-1}. A succession was observed: NanoRED3 dominated between May 6th and May 16th ($J_d\,O_d$ = 126 to $J_d\,O_d$ = 136), followed by NanoRED2 from May 17th to May 26th ($J_d\,O_d$ = 137 to $J_d\,O_d$ = 146). Finally, from June 10th ($J_d\,O_d$ = 161), blooms of PicoRED, PicoORG (*Synechococcus* spp.), NanoORG (*Cryptophyceae*), and NanoSWS (*Coccolithophoridae*) marked the last phase. After July 10th ($J_d\,O_d$ = 191), the abundance of the PicoRED2 group also increased.

The dynamics of FLR in 2022 exhibited a distinct phenology compared to the 2021 bloom. Initially, the phytoplankton community was progressively dominated by the MicroRED2 group (mainly diatoms, as autotrophic dinoflagellates occur at very low abundance in the EEC during this period; Gómez and Souissi, 2007; Schapira et al., 2008; Lefebvre et al., 2011; Hubert et al., 2025), which accounted for approximately 65 % of the total fluorescence on March 23rd ($J_d\,O_d$ = 82; Fig. 6b). This dominance persisted until April 12th ($J_d\,O_d$ = 102). Subsequently, the NanoRED3 group became predominant, culminating in the peak FLR of the bloom on May 10th ($J_d\,O_d$ = 130). This period coincided with the delayed *P. globosa* spring bloom, which occurred later than in 2021. From May 6th ($J_d\,O_d$ = 126), the NanoRED2 group gained prominence, ultimately becoming the most fluorescent group alongside the MicroRED2 group by May 21st ($J_d\,O_d$ = 141). A notable increase in the MicroRED2 group's contribution to total fluorescence was observed through May 26th ($J_d\,O_d$ = 146). In the final phase, starting from June 10th ($J_d\,O_d$ = 161), the NanoSWS and NanoORG groups showed increased contributions to total fluorescence, although this occurred during a period of very low overall FLR values (Fig. 5b).

3.2 Extreme events recorded

Four extreme events were recorded during these two sampling periods: two with sharp wind increases, a desalination event (brackish water inputs), and a heatwave (Fig. 7).

The desalination event occurred between April 1st and April 4th 2021 (Fig. 7a,b), with salinity values falling below the 5th percentile (30.73 psu) of the MAREL Carnot salinity dataset (from 2004 to 2023, $n = 325,699$ observations). During the initial phase of this event, total phytoplankton abundance decreased, driven primarily by declines in the PicoRED2 and NanoRED3 groups. Subsequently, salinity values dropped even further (< 28 psu), coinciding with peaks in the abundances of the PicoREDs, NanoREDs, and MicroRED groups. Notably, the NanoRED3 group exhibited a more rapid change in abundance compared to PicoRED2 during the salinity decline.

The second event observed in 2021 was a breeze with wind (coming from the south-west, with a direction between 200° and 260° relative to true north; see Appendix D) speeds ranging from 8 to 20 m s^{-1} (Fig. 7c,d), exceeding the 90th percentile of MAREL Carnot wind data (16.8 m s^{-1}; from 2004 to 2023, $n = 151,663$ observations). During this event, total phytoplankton abundance decreased sharply, particularly during the initial rise in wind speed on May 3rd, and remained low through the larger peak on May 4th. All groups followed the trend of total abundance decline, except for PicoRED2 and MicroRED, which dominated both total abundance and fluorescence during this period. After the main wind episode, abundance of NanoRED2 and NanoRED3 increased, accompanied by high chlorophyll fluorescence, with MicroRED representing more than 60 % of total fluorescence (Fig. 6b), although overall fluorescence remained low (between $0.5 \cdot 10^9$ and $0.6 \cdot 10^9$ AU mL^{-1} on May 3rd).
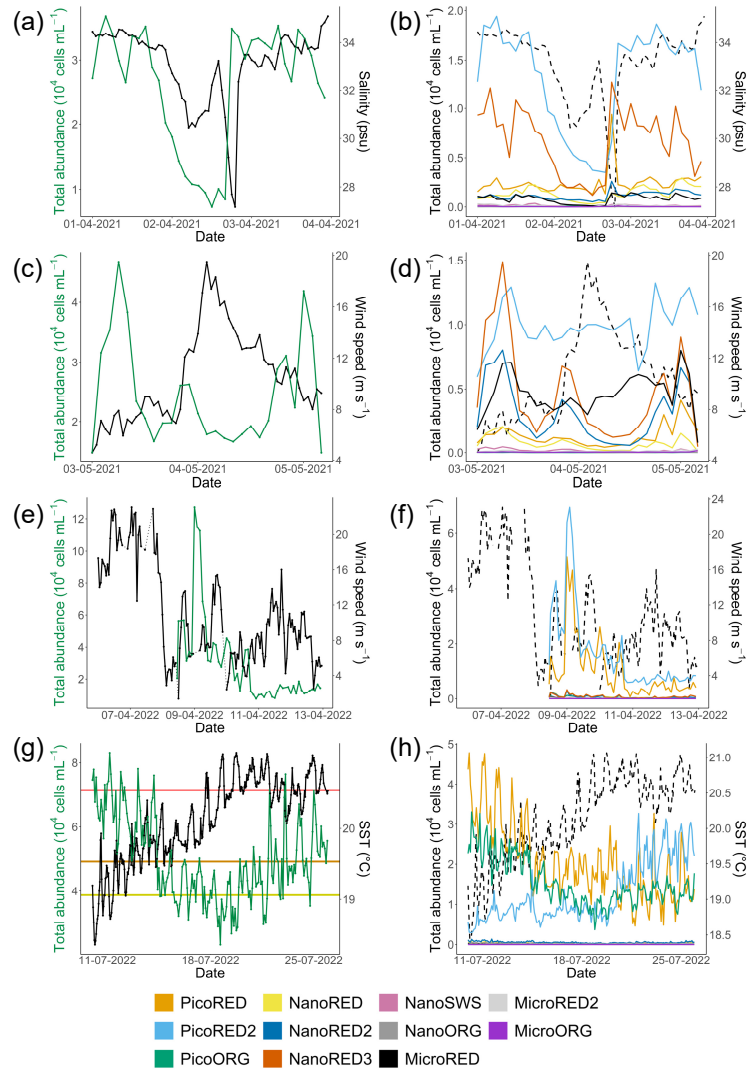
Figure 7. Examples of extreme events recorded on MAREL Carnot station during the study: (a,b) a desalination event in April 2021, (c,d) a high wind speed period in May 2021, (e,f) a strong wind period in April 2022 and (g,h) a high SST event (heatwave) in July 2022. Each of the corresponding parameters is shown on the second y-axis (right axis) as a solid black line in the (a,c,e,g) left-hand figures and as a dotted line in the (b,d,f,h) right-hand figures. The absolute total abundance are given in the left-column (a,c,e,g; green line) and the absolute abundance for each phytoplankton group are given in the right-column (b,d,f,h; colored lines). The three horizontal lines of the figure (g) represent the 90 % (yellow), 95 % (orange) and 99 % (red) percentile of the SST observations of the MAREL Carnot station between March 24th 2004 and September 30th 2023. The abiotic data (salinity, SST, wind speed) presented here comes from (a,b,e,f,g,h) MAREL Carnot station and (c,d) Météo France (Boulogne-sur-Mer station).

The third event, a high wind storm (the storm "Diego") in April 2022 (Fig. 7e,f), was marked by a peak in phytoplankton abundance on April 9th. Unfortunately, wind data for this peak were unavailable due to a power outage caused by extreme weather conditions. However, the data recorded before and after the cutoff show a change in wind direction at the peak, with winds shifting from south-western to north-eastern direction for about one day (see Appendix D). The PicoRED groups were particularly affected during this event, with observed peaks in their abundance that seemed linked to the wind speeds. In terms of fluorescence, this event appeared to favor the NanoORG group, which reached a relative fluorescence of 15 % (Fig. 6b) during a fluorescence peak, with absolute values close to $1.2 \cdot 10^9$ AU mL^{-1} (Fig. 5b).

The final event was a marine heatwave (Fig. 7g,h), marked by warm water and high air temperatures in Boulogne-sur-Mer between July 15th and July 20th 2022, with the highest air temperature recorded on July 19th (temperature in a Stevenson screen equal to 39.8 °C according to Météo France data). This event qualifies as a marine heatwave, as the SST reached the 90th percentile (estimated from MAREL Carnot data from 2004 to 2023, $n = 339,137$ observations) for at least five days (Hobday et al., 2016). We did not have 30 years of data as recommended to define the marine heatwave threshold, but this event qualification was supported by other studies in the same study location showing an intense activity of marine heatwaves during summer 2022 in the English Channel (Simon et al., 2023). During this period, phytoplankton abundances decreased as the SST increased, from the 90th (19.06 °C) to the 95th (19.53 °C) and 99th (20.54 °C) percentiles recorded since 2004. This decline was particularly evident in PicoRED and PicoORG groups, which were among the most dominant during this period. PicoORG abundance, for example, halved during the event, and its dynamics showed a strong negative correlation with SST (Pearson $r = -0.78$, p value $< 2.2 \cdot 10^{-16}$) between July 10th and July 20th. After July 21st, both PicoORG and PicoRED stabilized as SST plateaued. In contrast, PicoRED2 abundance increased during and after the SST peak.

3.3 EMD-LSP

3.3.1 A first example: 2021 abundance time series

The results obtained with EMD-LSP analysis of the 2021 abundance time series ~~was analyzed in detail, considering abundance, FLR, and Shannon index data~~ were here arbitrary chosen to be presented in detail, to provide an example of the EMD-LSP analysis results interpretation. Nevertheless, all results for the other time series are presented in Table 2.

~~Seven~~ For this case, seven IMFs were identified, with peak periods ranging from approximately 12.48 hours to 18.9 days (Fig. 8). These periods ($T_{\max}$, see Table 2) corresponded to the highest peaks in their respective LSP. The mean periods of these IMFs ranged from 10.6 hours to 6.1 days (Fig. 9a). The first IMF, C_1, had a mean period of 10.6 hours, with a peak at 12.4 hours, and an additional peak at around 6 hours. This IMF likely corresponds to the current inversion during tides (Jouanneau et al., 2013). The second IMF represents the tidal mode with a mean period of 14.9 hours and a peak near 12.4 hours. The third IMF, C_3, corresponds to two tidal cycles ($\overline{T_3} = 1.07$ days), while the fourth and fifth IMFs, C_4 and C_5, are likely related to tidal cycle impacts at different timescales ($\overline{T_4} = 2.09$ days and $\overline{T_5} = 4.40$ days). The final two IMFs, C_6 and C_7, align with the periodicity of the neap-spring tide cycle, with periods near the semi-lunar cycle ($T_{\max} = 13.2$ and 18.9 days, respectively).
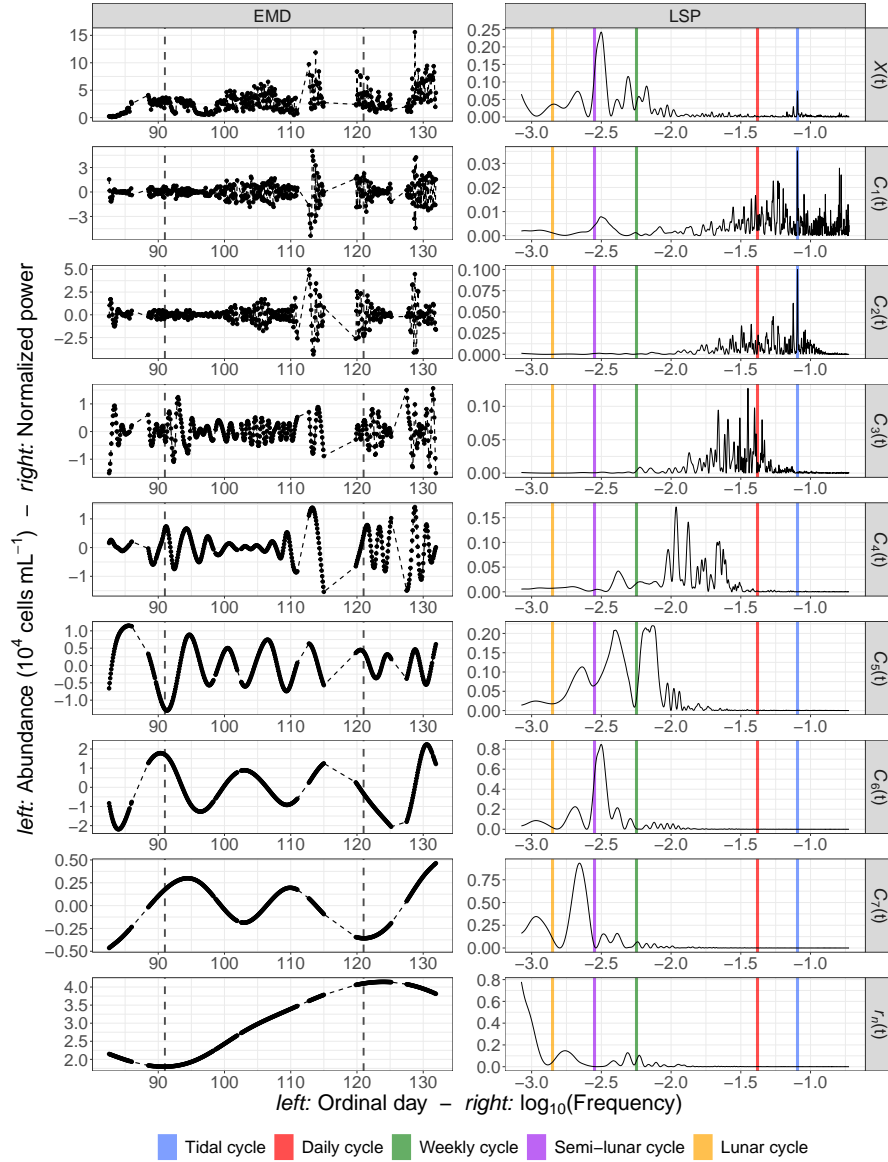
Figure 8. Decomposition of the 2021 total phytoplankton abundance data using the Empirical Mode Decomposition (EMD; left part) and the associated Lomb-Scargle Periodograms (LSP; right part) for the raw time series $X(t)$, for each IMF $C_i(t)$ and for the ~~residue~~ residual $r_n(t)$. The EMD x-axis represents the ~~Julian days~~ Ordinal days and the y-axis represents the abundance values (10^4 cells mL^{-1}). The LSP x-axis represents the decimal logarithm ($\log_{10}$) of the frequency (in h^{-1}) and the y-axis represents the normalized power. The gray dashed lines (left column) represent the beginning of April and May 2021.

The residual dynamics showed an overall increase in total phytoplankton abundance during the bloom period, with fluctuations following the lunar cycle. Peaks in abundance corresponded to spring tides, while troughs aligned with neap tides.
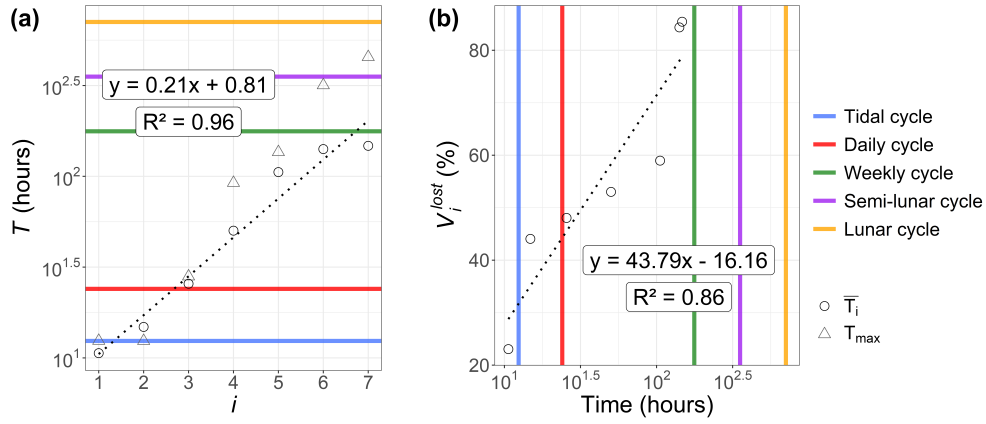
Figure 9. Results obtained from the EMD-LSP analysis for the 2021 phytoplankton abundance time series: (a) the mean period ($\overline{T_i}$) and maximum peak period (T_max) of each IMF $C_i(t)$ and (b) the percentage of variance explained for different timescales based on the mean periods of these IMFs. The black dashed lines represent the ~~estimated~~ linear regressions ~~estimated~~. The associated formula and coefficient of determination R^2 are displayed on the respective figure.

Notably, the periods of the different IMFs follow a power law: $\overline{T_i} \sim \gamma^i$. The exponent γ was found to be 1.62, which is lower than the value of 2 typically observed for fractional Gaussian noise (Flandrin et al., 2004; Flandrin and Gonçalvès, 2004) or turbulent time series (Huang et al., 2008). This indicates that the period of each mode is approximately 1.62 times longer than that of the preceding mode. The loss of variance, V_i^lost, is shown in Fig. 9b for the first example, illustrating the loss of information after removing each IMF from the raw abundance signal. The explained variance decreases with the removal of each IMF, with the loss following a logarithmic pattern: $V_i^\text{lost} \sim 43.79 \cdot \log_{10}(\overline{T_i})$.

3.3.2 Abundance and FLR

The EMD-LSP results for all the studied abundance and FLR time series ~~(abundance, FLR, Shannon index)~~ are summarized in Table 2. Each abundance and FLR time series exhibited between 7 and 10 distinct IMFs with mean periods ranging from approximately 9 hours and 11 days. Notably, the variance loss increased sharply with the different modes, particularly for the 2021 abundance and FLR time series, where tidal modes accounted for at least ~~62~~ 44 % of the total variance. The 2022 tidal modes were less important in the total variance of the time series, with values ranging between 5 and 17 %. The γ values ranged from 1.45 to 1.62, lower than the value of 2 typically found in turbulent and Gaussian time series, indicating the presence of many high frequency modes.

Overall, a significant proportion of the variability was lost quickly, with at least 72 % of the variance disappearing for time series without modes with mean periods between 4 and 11 days. This suggests that most phytoplankton variability occurred at low timescales. Additionally, according to the Nyquist-Shannon theorem, fluctuations at frequencies f_e cannot be captured by sampling frequencies lower than $2/f_e$. Thus, a time resolution of at least 5 hours is necessary to avoid losing this high frequency modal variability.

Table 2. Indicators estimated from EMD-LSP for each IMF $C_i(t)$ of the abundance, red fluorescence (FLR) and Shannon index H' time series of 2021 and 2022: the period of the maximum peak of the LSP T_{max} (days), the mean period $\overline{T_i}$ (days), the loss of explained variance in the time series after removing the i first IMFs V_i^{lost} (%) and the γ value for which $\overline{T_i} \sim \gamma^i$.

Year				2021						2022		
Time series (Units)	i	T_{max} (d)	$\overline{T_i}$ (d)	V_i^{lost} (%)	γ	Time series (Units)	i	T_{max} (d)	$\overline{T_i}$ (d)	V_i^{lost} (%)	γ
Abundance	1	0.52	0.44	23.05	1.62	Abundance	1	0.52	0.49	2.06	1.45
(cell mL^{-1})	2	0.52	0.62	44.06		(cell mL^{-1})	2	1.00	0.69	5.34	
	3	1.17	1.07	48.05			3	1.00	1.09	7.57	
	4	3.83	2.09	53.02			4	3.54	2.52	8.80	
	5	5.66	4.40	58.97			5	10.96	4.07	10.19	
	6	13.23	5.89	84.36			6	15.62	10.53	17.07	
	7	18.90	6.13	85.44			7	65.57	6.19	61.14	
	-	-	-	-			8	63.47	7.46	71.62	
	-	-	-	-			9	42.64	5.96	90.18	
FLR	1	0.48	0.77	33.08	1.51	FLR	1	0.52	0.44	9.03	1.55
(AU mL^{-1})	2	0.52	0.65	62.32		(AU mL^{-1})	2	0.52	0.57	16.53	
	3	1.50	1.15	66.54			3	1.93	1.31	22.26	
	4	3.22	1.93	70.74			4	2.13	2.12	25.25	
	5	6.59	3.97	74.89			5	16.22	3.48	28.66	
	6	13.02	5.48	89.69			6	26.63	8.82	55.34	
	7	6.05	3.34	93.28			7	57.20	6.11	66.94	
	-	-	-	-			8	55.16	6.86	72.14	
$\exp(H'_{abundance})$	1	0.60	0.38	10.44	1.55	$\exp(H'_{abundance})$	1	0.26	0.45	0.17	1.32
	2	0.52	0.62	18.67			2	0.53	0.69	0.31	
	3	1.07	1.10	22.37			3	1.59	1.07	0.39	
	4	2.48	1.96	24.62			4	5.17	2.10	0.46	
	5	3.29	2.58	30.75			5	10.24	4.74	0.84	
	6	12.52	5.04	35.15			6	42.64	5.75	1.57	
	7	24.30	9.20	50.44			7	69.50	5.07	23.80	
	8	15.56	5.18	80.09			8	45.28	3.49	70.36	
	-	-	-	-			9	39.83	5.60	75.74	
	-	-	-	-			10	41.49	4.30	91.36	
$\exp(H'_{FLR})$	1	0.53	0.46	20.29	1.35	$\exp(H'_{FLR})$	1	0.26	0.44	6.51	1.45
	2	0.94	0.63	32.41			2	0.52	0.67	11.34	
	3	2.36	1.24	38.54			3	1.00	1.09	14.08	
	4	1.72	2.32	43.32			4	2.64	2.13	16.41	
	5	5.03	4.24	49.13			5	4.97	3.04	18.64	
	6	10.39	5.44	51.96			6	11.75	4.96	24.45	
	7	10.61	5.57	56.44			7	28.72	10.67	48.87	
	8	22.02	6.23	64.61			8	29.14	6.95	78.79	
	9	6.01	3.10	65.79			9	39.71	7.53	84.34	
	-	-	-	-			10	42.90	9.48	86.22	
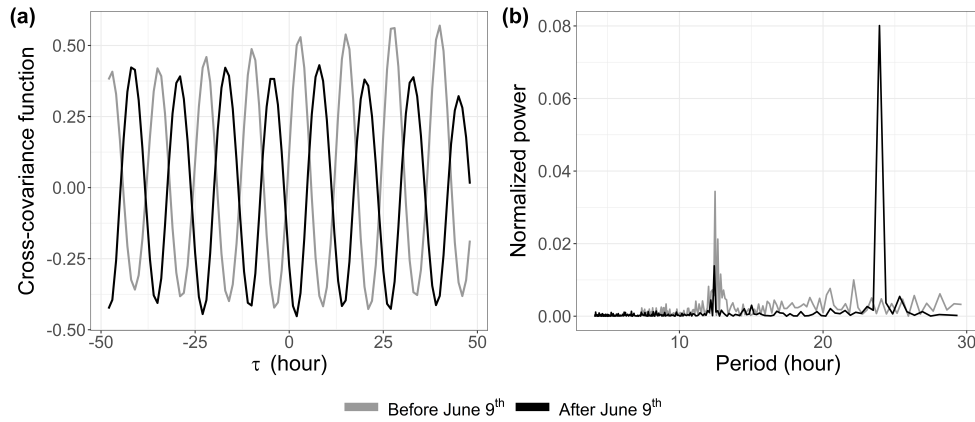
Figure 10. Short timescales observations for the 2022 phytoplankton abundance data before and after June 9th: (a) cross-covariance functions between the water height data (REFMAR data; SHOM, 2024) and the abundance data and (b) Lomb-Scargle Periodograms of the abundance data.

3.3.3 Link between phytoplankton dynamics and tidal forcing

A link between phytoplankton dynamics (abundance, FLR) and the tidal cycle was highlighted with EMD-LSP analysis (mostly for 2021 time series). This link was ~~observed~~ further investigated through cross-correlation with the water height time series. This analysis revealed a shift in the short timescale dynamics of phytoplankton abundance in 2022, occurring after June 9th (Fig. 10a). For the 2021 data (not shown here) and the early part of the 2022 data, phytoplankton abundance (and FLR, see Appendix B) showed a positive correlation with water height. However, after June 9th in 2022, the relationship became negative. Furthermore, the LSP revealed a shift in dynamics before and after June 9th. A high peak was observed at 12 hours before June 9th, which persisted but with reduced power after this date. A new peak appeared at 24 hours, highlighting the changing temporal variability of the environmental forcing on phytoplankton communities (Fig. 10b). This illustrate the emergence or variation in the intensity of forcing effects on the time series of abundance and FLR, highlighting the nonlinearity of phytoplankton dynamics over time.

3.3.4 Shannon diversity index H'

A difference was observed in the dynamics of the diversity index, $\exp(H')$, when calculated from abundance ($H'_{\text{abundance}}$; Fig. 11a) versus FLR (H'_{FLR}; Fig. 11b). In 2022, the diversity index based on abundance decreased after ~~J_d~~ $O_d = 160$ (June 9th), while the FLR-based index increased during the same period (Fig. 11c). This shift can be attributed to the dominance of pico-organisms during the summer bloom, which have a lower chlorophyll a content and, therefore, contribute less to the total FLR. In contrast, $H'_{\text{abundance}}$ peaked during the ~~*P. globosa*~~ NanoREDs bloom (Fig. 11a), while H'_{FLR} showed an opposite trend (Fig. 11b).
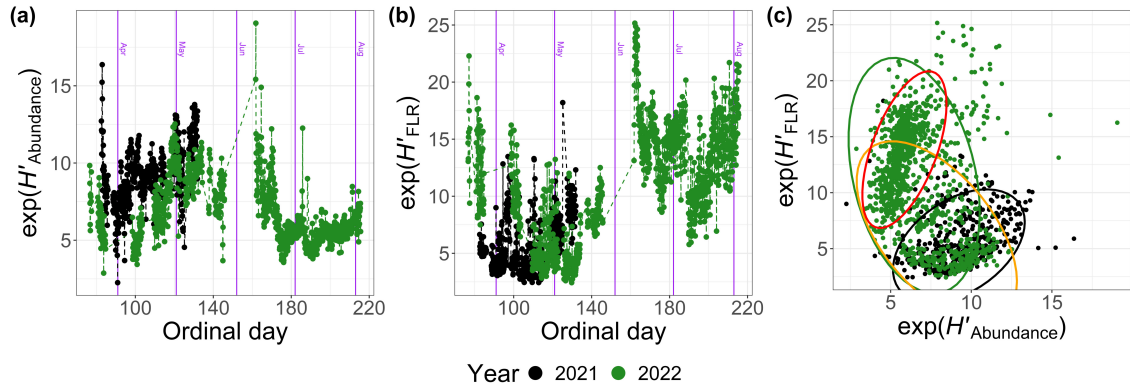
Figure 11. Exponential values of Shannon index H' calculated for 2021 and 2022 based on (a) the abundance ($H'_{\text{Abundance}}$) and (b) the FLR (H'_{FLR}) in function of the ~~Julian day~~ Ordinal day and (c) comparison of these two quantities. The ellipses represent the t distributions with a 95 % confidence interval. The orange ellipse take into account 2022 data before June 9th and the red one takes into account that after June 9th.
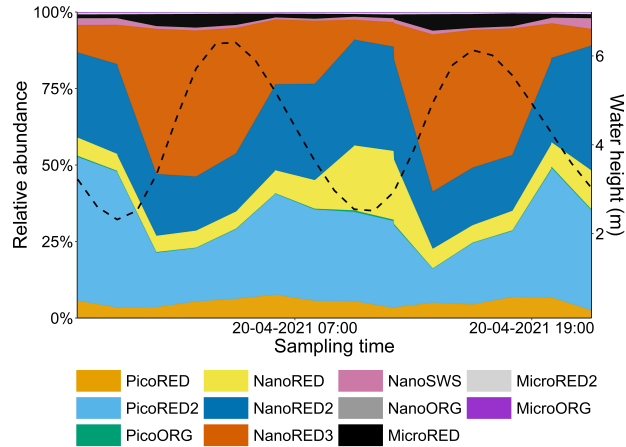
Figure 12. Relative abundance of each PFG (colored area) and water height (black dashed line; SHOM, 2024) between April 19th and 21st, 2021.

320   The Shannon index time series exhibited similar IMFs to those observed for abundance and FLR, with notable high frequency variations and the presence of tidal modes ($T_{\text{max}} \simeq 0.52$ day). These tidal modes likely reflect the varying responses of different PFGs to tidal forces, with community ~~composition~~ assemblage evolving during each tidal cycle (Fig. 12). The γ values ranged from 1.32 to 1.55 (Table 2), indicating the dominance of high frequency modes at short timescales, which accounted for at least 65 % of the variability. These findings underscore the multi-scale dynamics of the system, with high frequency variations

325   playing a significant role in shaping phytoplankton community assemblages.
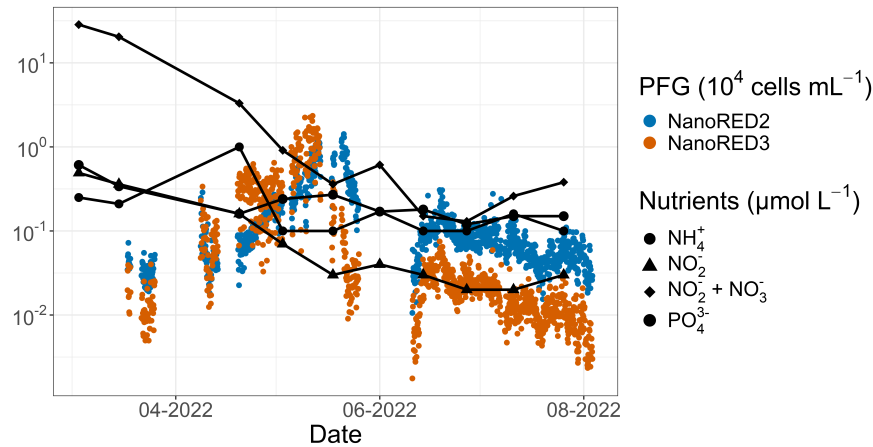
Figure 13. SRN nutrients data (Lefebvre et al., 2024) for the 2022 study period. The NanoRED2 and NanoRED3 2022 abundance data are represented in by the colored dots. The logarithmic scale for the y axis was chosen for visualization purposes.

4   Discussion

In this study, an automated flow cytometer was deployed at the MAREL Carnot fixed automated measuring station to monitor phytoplankton at high frequency. The goal was to observe and describe the variations in phytoplankton time series across several timescales, ranging from hourly events (e.g., extreme events, tidal forcing) to monthly events (e.g., phenologies). It was hypothesized that these multi-scale events influence phytoplankton communities.

4.1   Weekly-scale dynamics

In spring 2021, a significant bloom of NanoRED groups was observed, emerging phenologically in an environment where MicroRED2 (large diatoms and colonies) and PicoREDs (picoeukaryotes) dominated in terms of FLR and abundance, respectively. The increasing abundance of NanoRED groups was mostly due to the haptophyte *P. globosa*, which could be characterized through imaging (using the "Micro-Photos" protocol) and corroborated by previous studies (Rutten et al., 2005; Guiselin, 2010; Bonato et al., 2015). This phase corresponded to the onset of the *P. globosa* bloom, a phenomenon typical of the EEC (Breton et al., 2000, 2021, 2022) and frequently monitored due to its classification as a HAB (Lefebvre and Dezécache, 2020). This phenological shift, with a transition from diatoms (MicroRED2) to *P. globosa* (NanoREDs), was also observed in 2022 and has been previously documented in the study area (Breton et al., 2000; Guiselin, 2010; Grattepanche et al., 2011; Lefebvre et al., 2011; Hernández-Fariñas et al., 2014; Genitsaris et al., 2015; Lefebvre and Dezécache, 2020; Houliez et al., 2023). The *P. globosa* spring bloom is known to occur when abiotic conditions ~~are~~ become favorable, such as nutrient availability and light conditions according to the literature (e.g., Gentilhomme and Lizon, 1997; Lancelot et al., 2011; Lefebvre et al., 2011; Lefebvre and Dezécache, 2020; Breton et al., 2022). More specifically, *P. globosa* became predominant following the depletion

of $Si(OH)_4$ and PO_4^{3-} (Fig. 2), which were consumed during the diatom bloom, as observed in other studies (Karasiewicz et al., 2018).

The abundance of the MicroRED group was also notably high during the spring bloom of 2021. This group, composed of pennate diatoms optically similar to the *Pseudo-Nitzschia* complex (~~likely~~ e.g., *P. delicatissima*, *P. pungens*, and *P. seriata* in this season; Delegrange et al., 2018), was confirmed through the "Micro-Photos" protocol. The presence of MicroREDs could be linked to the high abundance of *P. globosa*, as a commensal symbiotic relationship between these two species has been described (epibiosis; Sazhin et al., 2007).

A similar spring bloom of NanoREDs was observed in 2022, although it was less pronounced in terms of FLR compared to 2021. This difference in bloom intensity is also reflected in the post-bloom phase, with higher ammonium concentrations in 2021 suggesting more intense remineralisation compared to 2022. This could be attributed to the longer persistence of nano- and microplankton cells in 2021, which may have been facilitated by higher PO_4^{3-} concentrations during that year (Fig. 2). Moreover, limiting nutrients (PO_4^{3-}, $Si(OH)_4$, NO_3^-, and NO_2^-), were rapidly depleted at the onset of the bloom, consistent with the growth of diatoms (MicroRED2) and haptophytes (NanoREDs).

In 2022, the decline of the NanoREDs bloom was evident, unlike in 2021, when measurements were ended earlier than in 2022. As the NanoREDs bloom faded, other groups began to increase, including coccolithophorids (NanoSWS), cryptophytes (NanoORG), diatoms (MicroRED2) in terms of FLR, and particularly cyanobacteria (PicoORG) and chlorophyll picoeukaryotes (PicoREDs) in terms of abundance. The dominance of these smaller cells following the spring bloom can be explained by their higher competitiveness in nutrient-poor environments (Litchman et al., 2007). Similar successions have been observed in the region and are partly explained by the physico-chemical conditions of the ecosystem (Bonato et al., 2016).

Furthermore, a succession between the NanoRED3 and NanoRED2 groups was also apparent at the end of the spring bloom (Fig. 13). As the abundance of NanoRED3 declined, NanoRED2 became more dominant for a period. This phenomenon, also observed at the end of the 2021 data recording (although less clearly), may reflect competition between different life stages of *P. globosa* (see Figs. 5 and 6). The flagellated form of *P. globosa* (NanoRED2) is more competitive in nutrient-limited environments compared to its colonial cell form (NanoRED3; Rousseau et al., 1994; Peperzak et al., 2000). As nutrients were consumed, the abundant form of this haptophyte shifted, revealing a long-term phenology driven by the gradual depletion of nutrient stocks during the spring and early summer (visible in Fig. 2; Gentilhomme and Lizon, 1997; Lancelot et al., 2011; Lefebvre et al., 2011).

4.2 Extreme events

High frequency studies enable the detection of rapid and intense events that cannot be captured with low-frequency sampling typical of long-term monitoring networks. These events can have significant ecological impacts, as different phytoplankton communities respond differently to environmental changes. This was evident during two high-wind-speed events, which had contrasting effects on phytoplankton abundance.

In one instance, a strong wind event between May 3rd and 6th 2021, promoted the dominance of the MicroRED PFG (comprising the *Pseudo-Nitzschia* complex). During this period, all NanoRED groups decreased, while MicroRED groups increased.

This shift could be explained by the resuspension of cells that had previously settled, supported by the observed increase in turbidity during this time (based on MAREL Carnot data, not shown here). Additionally, the breakdown of *P. globosa* colonies,

380   possibly due to their commensal relationship with MicroREDs (Sazhin et al., 2007), could have contributed to this increase.

Following the wind event, NanoRED groups went up, likely due to the release of *P. globosa* colonial forms. Interestingly, pico-organisms (PicoRED and PicoRED2) did not appear to be significantly affected by this storm. In contrast, a high-wind-speed event in 2022 triggered a peak in the abundance of PicoRED groups. The difference in the effects of the two events may be attributed to the wind direction: during the 2021 event, the wind was blowing from 225° (South-West), while during the

385   2022 event, the wind came from 350° (North-North-West) shortly before the PicoREDs abundance peak (as the weather station data ceased on April 9th). Wind direction is an important factor for particle transport in the harbor, and this shift could explain the contrasting responses of the phytoplankton groups (Jouanneau et al., 2013).

Additionally, the marine heatwave and low-salinity events highlighted in Sect. 3.2 also induced different responses among phytoplankton communities, with significant shifts in the assemblages occurring over just a few hours. For instance, the Pi-

390   coRED2 PFG appeared to be favored during the marine heatwave compared to other pico-plankton groups. During the 2021 low-salinity event, two distinct peaks of low salinity were observed on the same day, yet the communities responded differently at each peak. These observations underscore the complexity and non-linearity of phytoplankton community responses to extreme events, even within the same area. Further high-frequency observations are crucial to fully understanding the effects of such events on pelagic phytoplankton ecosystems, as emphasized by previous studies (e.g., Barrillon et al., 2023; Röthig

395   et al., 2023).

4.3   High-frequency multi-scale dynamics

The time series analyzed revealed a multi-scale dynamics, ranging from hours to several days, with high-frequency fluctuations (9 hours to 11 days) explaining at least 65 % of the total phytoplankton variance. Notably, tidal modes contributed significantly to phytoplankton dynamics, as observed in other regions for chlorophyll *a* (Blauw et al., 2012). The high tidal range in our

400   study area, along with temporal heterogeneity and patchiness of phytoplankton, likely drives this variability in total abundance and total FLR (Seuront et al., 1996; Seuront, 2005). Additionally, the neap-spring tidal cycle influenced the data, with increased tidal range during spring tides amplifying phytoplankton variability. This effect is linked to the coastal river's structure, where a vertical front during spring tides limits exchanges between coastal and offshore waters, isolating phytoplankton blooms near the coast, especially in westerly winds regime.

405   High-frequency dynamics also impacted community ~~composition~~ assemblage, with shifts observable in the Shannon diversity index (estimated for communities), reflecting changes at multiple ecological scales. The tidal mode influenced this index, representing up to 20 % of the total variability, highlighting the diverse influence of hydrological forcing on different PFGs. This indicates that multi-scale dynamics and high-frequency fluctuations affect phytoplankton ecology at the community level.

Furthermore, high-frequency forcing effects were not stable over time. After June 9th, 2022, a shift was observed in the

410   relationship between phytoplankton abundance and water height, alongside the emergence of a new 24-hour periodicity. ~~This change could be attributed to a different life cycle of dominant picoorganisms compared to nano- and microphytoplankton,~~

~~as picoeukaryotes (PicoRED) and cyanobacteria (PicoORG) predominated during this period~~ This change could be attributed to differences in the life cycles of the dominant picoorganisms, which became more prevalent than the nano- and micro-phytoplankton that dominated during the spring bloom. Indeed, during this period, the community was largely composed of picoeukaryotes (PicoRED) and cyanobacteria (PicoORG) which are known for their rapid growth rates, short generation times, and ability to quickly respond to changes in environmental conditions (Agawin et al., 2000; Worden et al., 2004). Previous studies have shown a strong link between SST and cyanobacterial growth in waters with an annual mean SST below 14 °C (Li, 1998). The EEC, with an annual mean SST of 12.69 °C (based on MAREL Carnot data), aligns with these findings. We observed higher picoorganism abundance at night (when SST is lower) and lower abundance during the day (when SST is higher; Fig. 14) as it has already been observed in *Synechococcus* dynamics (Xiu-ren and Vaulot, 1996; Sosik et al., 2003). Grazing effects could also explain in part these patterns, as noted by Xiu-ren and Vaulot (1996). Moreover, this daily cycle was also observed in the PicoORG and PicoRED FWS per cell time series (a proxy for cell size; Fig. 14), consistent with the fact that cells increase in size before division (André et al., 1999). We found a strong negative Pearson correlation between abundance and PicoORG FWS per cell ($r = -0.84$, p value < 0.01), and between abundance and PicoRED FWS per cell ($r = -0.78$, p value < 0.01) during this period, supporting this hypothesis.. This kind of daily dynamics for the FWS per cell was also observed for some groups (as NanoRED3) in 2021 and for the data of 2022 before June 9th, but not on the abundance data.

SST plays a crucial role in driving picoeukaryotes and cyanobacterial dynamics, both periodically (e.g., daily cycles) and non-periodically (e.g., marine heatwaves). This link is consistent with previous studies (Chen et al., 2014; Hunter-Cevera et al., 2020). As EEC coastal waters warm due to global change (+1 °C over the past 10 years, with a projected +3.34±0.88 °C by 2100; Hubert et al., 2024; Tinker et al., 2024), monitoring the long-term high-frequency dynamics of ~~picoorganisms~~ pico-phytoplankton, in addition to other size-classes, is of the must importance. These organisms are critical to pelagic food webs and biogeochemical cycles (Xiu-ren and Vaulot, 1996), and understanding how they will respond to warming and associated extreme events is crucial.

5   Conclusions

This study characterizes the multi-scale dynamics of phytoplankton during the springs of 2021 and 2022 off the Liane estuary, and the Boulogne-sur-Mer coastal area in the Eastern English Channel. We evidenced the seasonal successions between key Phytoplankton Functional Groups (PFGs), particularly between MicroRED groups (mostly diatoms) and NanoRED (mostly haptophytes of the genus *Phaeocystis globosa*). Using the Empirical Mode Decomposition and Lomb-Scargle Periodogram method, we identified various modal fluctuations across different temporal scales in phytoplankton abundance, red fluorescence (proxy of chlorophyll *a*), and the Shannon diversity index, highlighting the complex dynamics of population assemblages.

Our findings reveal that much of the variability in these time series occurs at short time scales, ~~with modes on the order of a few days.~~ particularly on the order of a few hours. This indicates that low-frequency sampling may miss significant dynamics in phytoplankton communities. We also observed that these multi-scale fluctuations do not stabilize over time, particularly
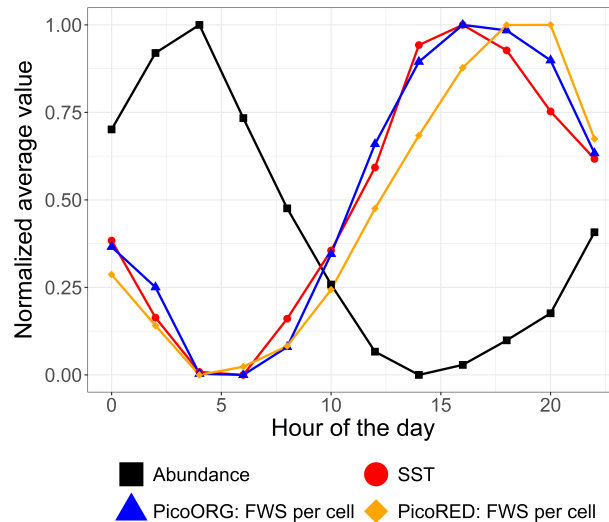
Figure 14. Mean average abundance, SST and cell size proxy (FWS) of the PicoORG (*Synechococcus* spp. like) and PicoRED (picoeukaryotes) groups normalized (between 0 and 1 using the following formula: $\frac{y - y_{\min}}{y_{\max} - y_{\min}}$) for each hour of the day, for the 2022 data after June 9th.

during the seasonal shifts in community ~~composition~~ assemblage, such as the dominance of picoorganisms in summer 2022
445   when sea surface temperature became a major driver of abundance.

The study's limited duration, constrained by the system's design, suggests the need for longer-term monitoring of PFGs, coupled to HF measurements of more abiotic variables as nutrients, light and mixing, to assess whether high-frequency fluctuations become less significant over larger temporal scales (e.g., inter-annual variations) in the context of global change and changing anthropogenic pressures, to better understand the mechanisms of their impact on the whole size-range of main marine primary
450   producers. Additionally, incorporating higher trophic levels, such as zooplankton, could offer insights into top-down control mechanisms, which were not fully addressed here. As previously noted, seasonal variations—which are essential for understanding phytoplankton dynamics—were not fully captured in this study due to its limited temporal coverage. This highlights the need for future research based on longer monitoring periods.

Overall, this study confirms the interest and big potential of combining automated flow cytometry with fixed buoys for
455   high-frequency monitoring of marine ecosystems, though the system's design requires adaptation for long-term use. Given the increasing frequency of extreme events like storms, estuarine loads, and heatwaves in coastal areas, automated monitoring, coupled with robust statistical analyses, is crucial for understanding phytoplankton variability and its impact on marine food webs and biogeochemical cycles. This approach can provide valuable data for models predicting changes in ecosystem structure and function.

 Appendix A: **Glossary**

The definition of the abbreviations used all along this article are provided in Table A1.

Table A1. Glossary.

Abbreviations	Definition
EEC	Eastern English Channel
EMD	Empirical Mode Decomposition
FLO	Orange Fluorescence
FLR	Red Fluorescence
FLY	Yellow Fluorescence
FWS	ForWard Scatter
HF	High Frequency
IMF	Intrinsic Mode Function
LSP	Lomb-Scargle Periodogram
PFG	Phytoplankton Functional Group
ROFI	Region Of Freshwater Influence
SST	Sea Surface Temperature
SWS	SideWard Scatter

Appendix B: Cross-covariance function of 2022 FLR data

The cross-covariance functions between the water height data (REFMAR data; SHOM, 2024) and the FLR data before and after June 9th 2022 are displayed in Fig. B1. An inversion of the link between the two time series was observed, as it was also the case between the water height and the abundance data (Fig 10). This link was yet less important after June 9th, as the area was dominated by picoorganisms.

Appendix C: **Relative time series: stacked area representation**

The relative abundances and FLR values for the two deployments are shown as stacked area plots in Fig. C1. The same patterns described previously are evident: a spring shift in the abundance time series (panel a) from picophytoplankton to nanophytoplankton, and in the FLR time series (panel b) from microphytoplankton to nanophytoplankton. The dominance of pico-organisms—particularly PicoORG—during summer is also observed in the 2022 data. Some extreme events are noticeable as well, such as the relative increase in MicroRED during the strong wind event of May 2021, visible as an expansion of the black area. Quick shifts, corresponding to high-frequency fluctuations, are also observable throughout the time series.
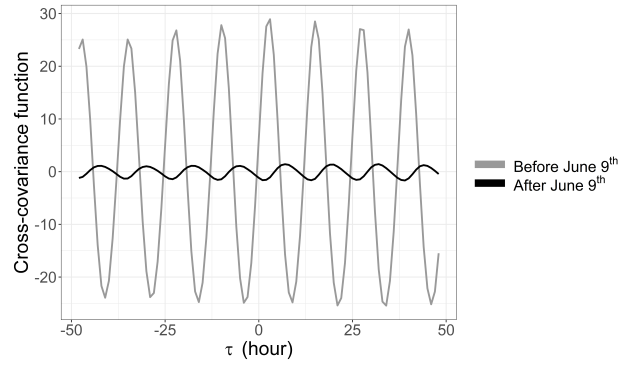
Figure B1. Cross-covariance functions between the water height data (REFMAR data; SHOM, 2024) and the FLR data before and after June 9th 2022.
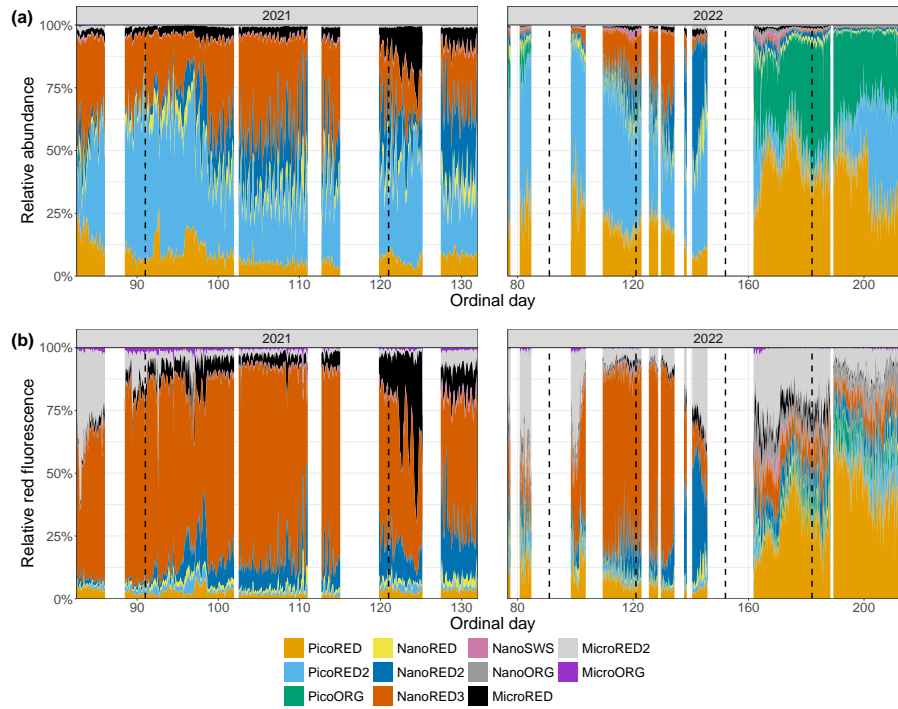
Figure C1. Phytoplankton data recorded for each group with the automated flow cytometer (CytoSub) for each sampled Ordinal day: (a) PFGs relative abundance and (b) PFGs relative red fluorescence (proxy of the chlorophyll *a*). The relative values of each group are computed as the ratio of the group's value to the total sum across all groups. The stacked colored area represent the relative value for each PFG. The black dashed lines indicate the start of each month.

Appendix D: **Wind direction during the extreme events**

475   The wind directions observed during the two strong wind events (see Fig. 7) are shown in Fig. D1. As previously mentioned, the 2021 event was characterized by strong southwesterly winds (ranging from 200° to 260°). In 2022, the event initially featured southwesterly winds (although PFG data were not available for this period), followed by northeasterly winds during the peak in abundance highlighted in Fig. 7. Unfortunately, wind data were not available precisely during this abundance peak.
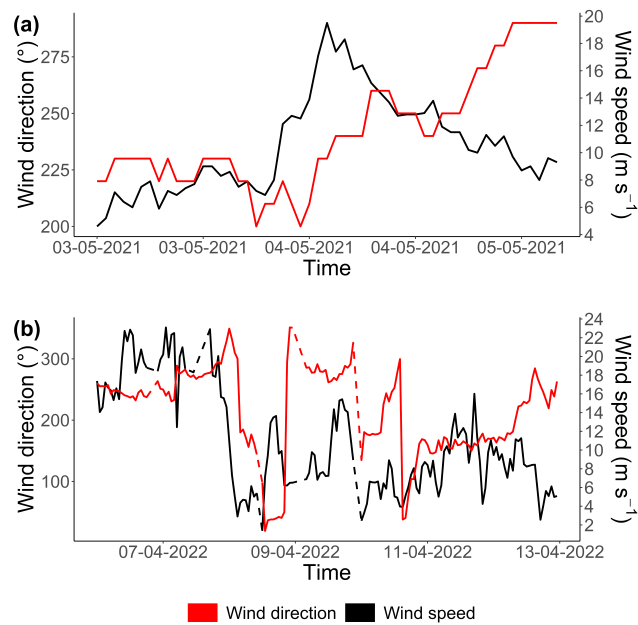
Figure D1. Wind direction (red line, in degrees from true north) and wind speed (black line, in ms⁻¹) recorded during the two strong wind events shown in Fig.7: (a) May 2021 and (b) April 2022. Dashed lines indicate gaps in the time series due to missing data.

Code and data availability. The cytometric data (https://doi.org/10.17882/104948; Robache et al., 2025), the SRN (nutrients) data (https://doi.org/10.17882/50832; Lefebvre et al., 2024), and the MAREL Carnot data (https://doi.org/10.17882/39754; MAREL Carnot, 2024) are accessible from SEANOE portal. The REFMAR data are accessible from SHOM portal (Boulogne-sur-Mer station: http://doi.org/10.17183/REFMAR#111; SHOM, 2024). EMD-LSP analysis have been performed using the 'EMD' (https://doi.org/10.32614/CRAN.package.EMD; Kim and Oh, 2009) and 'lomb' (https://doi.org/10.32614/CRAN.package.lomb; Ruf, 1999) R software packages. All the plots have been made using the 'tidyverse' (https://doi.org/10.32614/CRAN.package.tidyverse) R packages, and more especially the 'ggplot2' (https://doi.org/10.32614/CRAN.package.ggplot2) package (Wickham et al., 2019).

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Competing interests. The authors declare that no competing interests are present.

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