# Authors's reply to Anonymous Referee #1 comments on on egusphere-2022-1008 Tzortzis et al.

Dear referee,

Thank you very much for your constructive comments and suggestions, as well as your corrections of the grammar and spelling in order to improve the quality of the manuscript. According to the Biogeosciences guidelines, hereinafter we address the main points you raised. We are confident that following your remarks and suggestions, as well as the ones from the other anonymous referee, we can improve our manuscript for publication in Biogeosciences. Your comments are in black, our replies in blue.

## General Comments

In the manuscript "The contrasted phytoplankton dynamics across a frontal system in the southwestern Mediterranean Sea", Tzortzis et al. compare the phytoplankton communities at two different water masses separated by a frontal region. The work is original. The sampling design to analyze the two water masses separated by a front, and the phytoplanktonic community that characterizes them, is very interesting. Especially having a tool like the CytoBuoy.

We thank you for these positive comments about our work.

However, the manuscript needs improvement in many aspects before it can be considered for publication. In general, it is a disorganized text. The story does not flow, the paragraphs do not focus on clear topics, there are very long and confusing sentences, there are methodological descriptions in the results and results in the discussion... All sections should be carefully reviewed and improved. Especially the introduction and discussion.

We apologize for not being clear enough. We will rework each section in order to make our scientific message flow, taking into account your useful suggestions and those of the second referee.

The study area is barely described or named, why is it so relevant to focus on that particular front (besides the scope of the satellite)?

We will improve the description of the study area, including more information on the general dynamics of the Algerian sub-basin and on the specific situation encountered during our 2018 cruise. The importance of the frontal area studied in the present article is due to the fact that most of the in-situ studies related to the physical-biological coupling at finescale have focused on extreme situations occurring in boundary currents, where intense fronts and dramatic contrasts in water properties are found but are not representative of the global ocean. Indeed, vast oceanic regions are dominated by weak fronts continuously created,

moved and dissipated, which separate different water masses with similar properties. Very few studies exist in these regions due to the difficulty of performing in situ experiments over these short-lived and small features. In our previous work Tzortzis et al. (2021) we showed that the fine-scale front observed during our 2018 cruise in an oligotrophic and moderately energetic region (the SW Mediterranean) also drove phytoplankton diversity patterns. In the present study we aim at explaining how, by combining the available hydrological and cytometric data recorded at high spatio-temporal frequency.

Moreover, in the first paragraph of the introduction, the authors mention the context of climate change. How will climate change affect the presence and intensity of the fronts? And in turn, how a possible change in the intensity and frequency of the fronts will affect the associated phytoplankton communities? As a reader, I feel like I am being shown an interesting image, but in black and white instead of full color.

The impact of climate change on the ocean is a topic of current research, but many uncertainties remain (Collins et al., 2010 ; Cheng et al., 2022 ; Yao et al., 2022, etc). The predictions concerning the consequences of global warming on ocean circulation are already observable in the Southern Ocean, where the Subantarctic Front is particularly affected (Jia-Rui Shi et al., 2021).
Future climate-driven changes to ocean circulation patterns have the potential to alter dispersal pathways, potentially affecting the ability of species to track and adapt to climate change (Wilson et al., 2016). This impact may be very important in the Mediterranean Sea (MerMex Group, 2011).
The fact that the links between finescale and biological processes are still unknown (see below for more explanation and references) implies that the impact of climate change on them is speculative.
The objective of this study is to contribute to improving our knowledge of the finescale physical-biological coupling, by focusing on the distribution of the phytoplankton and its possible explanation (cell cycle). Our study does not aim to understand the consequence of climate change-induced changes in fronts. Since our study is not related to climate change, we decided to remove the reference to climate change in the Introduction in the reworked manuscript.

## Specific Comments

### Introduction

The authors describe in ~15 lines the relevance of phytoplankton and ocean fronts. In my opinion, more information is needed. Knowing the abundance and diversity of phytoplankton is important, but its role in the carbon cycle should also be highlighted, which changes depending on whether the community is dominated by small or large species. Moreover, an oceanic front is not defined, the authors describe briefly the

physical-biological interaction. I also miss an intro to the study region.

We will improve this part following your suggestions. Here we provide a draft of this section that we will be included in the reworked version of the manuscript:

"Phytoplankton forms the basis of the marine food web and plays a crucial role in biogeochemical processes, including the efficiency of the biological carbon pump, i.e., fixing CO2 and exporting it into the ocean depth (Field et al., 1998 ; De La Rocha and Passow, 2007). This process is critical for global ocean sequestration of carbon and therefore for the modulation of atmospheric $CO_2$. Furthermore, the biological carbon pump is also modulated by the size structure of the phytoplankton community. Indeed small or large phytoplankton species are associated with different efficiencies for particle export, remineralization, and transfer to deep ocean (Boyd and Newton, 1999 ; Guidi et al., 2009 ; Hilligsøe et al., 2011 ; Mouw et al., 2016, etc). Finally, phytoplankton is responsible for half of the primary production of the planet (Field et al., 1998), while its biomass is only < 1 % of the global biomass (Winder et al., 2010). Thanks to the photosynthesis, phytoplankton fuels the ocean in free $O_2$.
That is why it is primordial to understand the factors that rule phytoplankton abundance and diversity, particularly in the context of climate change (Hays et al., 2005 ; Behrenfeld et al., 2006 ; Winder and Sommer, 2012 ; Bates et al., 2018, etc). Indeed, a consequence of the climate change on the phytoplankton is to modulate its ability to export $CO_2$ into the deep ocean (Laws et al., 2000). Furthermore, the studies of Lomas et al. (2009), Menkes et al. (2016) and Barrillon et al. (2023) have shown that impulse events such as storms can generate mixing and stirring of the surface layer and trigger transitional peaks in primary production, mainly explained, for the first two references, by nitracline shoaling and grazer dilution. The occurrence of such intense events will tend to increase in the context of global change, impacting even further the functioning of the biological carbon pump."

Furthermore, below we provide a brief description of the study area:

"The region south of the Balearic Islands is characterized by the presence of both fresh surface waters coming from the Atlantic (AW) and more saline waters from the Mediterranean region (Millot, 1999; Millot et al., 2006).
AW enters the Mediterranean Sea through the Strait of Gibraltar and then forms a counterclockwise circulation along the continental slope of the western Mediterranean basin, caused by the combination of the Coriolis effect and the topographical forcing (Millot, 1999; Millot and Taupier-Letage, 2005; Millot et al., 2006). In the southwest part of the basin, this circulation is dominated by the Algerian Current (AC), which can form meanders and mesoscale eddies due to baroclinic and barotropic instabilities (e.g., Millot, 1999). These eddies spread over the basin and join the study area south of the Balearic Islands, carrying with them the newly arrived AW, known as younger AW. In this region, the younger AW encounters the older AW sometimes also called resident AW or local AW (Balbín et al., 2012). The older AW is AW modified by cooling and evaporation during its progression along the northern part of the western Mediterranean basin. The presence of these two types

of water makes this area particularly suitable for the formation of frontal structures (Balbín et al., 2014)."

After that brief introduction, the difficulty of an in situ study is described, and without continuing the story fluently, they begin to talk about an oceanographic campaign/project. I think the information is relevant, although the more technical details should be indicated in the methodology.

We will move the technical details of the campaign in the methodology, and improve the transition between the difficulty of an in situ study and our particular campaign.

Finally, the last paragraph is confusing. There is a lot of information, but not all makes sense, and it is kind of disorganized. The last paragraph of the introduction should clearly define the objectives of the study and how the authors would answer them.

We will clarify this part in the reworked manuscript following these suggestions:
"The objectives of this study are to assess whether the observed contrasted abundances across the front are due to different growth and loss rates. Using high-frequency flow cytometry measurements across the front dividing two water masses, we were able to separately analyze each phytoplankton functional group and reconstruct their biovolume dynamics over a diel cycle in each water mass."

Ln 16: Phytoplankton are essential for marine ecosystems, but not really for the functioning of the oceans... Oceans can function without life.
Ln 16-17: Revise the sentence. The $CO_2$ assimilated by phytoplankton can be exported to deep waters when they die or are partially eaten, being decomposed at depth; that's the biological pump. But not when they are eaten by higher trophic layers.

Our sentence was unclear and we plan to modify it as follow:

"Phytoplankton plays a crucial role in the oceans by regulating climate and forming the base of the food chain (Sterner et al., 1994). Its capacity to perform photosynthesis influences the global carbon cycle, by fixing $CO_2$ and exporting it into the ocean depth through the biological pump. Phytoplankton production also supports higher trophic levels, impacting ecosystem functioning."

Ln 20-22: Add references.

We plan to add here the following references: (Clayton et al., 2014 ; Mahadevan 2016 ; Lévy et al., 2018).

Ln 22-23: Revise the sentence. It seems that the idea the authors are trying to convey is that the temporal scale of growth/evolution of the phytoplankton community is due

to a fine-scale coupling. It seems that the fronts are the ideal environment for phytoplankton when it is not necessarily true.

We plan to better explain our point of view by adding a sentence as follows:
“Indeed, the phytoplankton dynamics temporal scale is of the same order of magnitude as the one of finescale processes such as eddies, filaments or fronts, suggesting the possibility of a close coupling between phytoplankton growth and finescale forcing. This does not necessarily imply that phytoplankton can grow only in presence of fronts, but fronts create favorable conditions for phytoplankton and life in general (Clayton et al., 2014 ; Mahadevan 2016 ; Lévy et al., 2018).”

Ln 27: Here there is a change of topic, please, start a new paragraph.

We will rework the manuscript to take into account your suggestions.

Ln 24-27: Revise sentence. First, the sentence is too long.
In my opinion, the use of "could" makes the facts described less solid. It is established that fine-scale frontal structures induce vertical velocity. Is there any study where no vertical velocity is associated with these structures?

We will modify it in the manuscript, following your grammar suggestion.

Different physical processes associated with finescale structures are able to generate vertical velocities, such as deformations of the flow and spatial inhomogeneities (Giordani et al., 2006), eddy perturbation (Martin & Richards, 2001 ; Pilo et al., 2018), linear Ekman pumping (McGillicuddy et al., 1998 ; Gaube et al., 2015), or eddy-wind interactions (McGillicuddy et al., 2007). That is why to our knowledge the majority of studies about vertical velocities have focused on finescale structures (fronts or eddies) because these are suitable places for the formation of vertical motions (Rudnick, 1996 ; Pascual et al., 2015 ; Rousselet et al., 2019 ; Barceló-Llull et al., 2021).

Vertical velocities do not modulate light availability. Vertical velocities move the phytoplankton cells along the water column and depending on the “resulting” depth they will have more or less light.

We plan to add refs and to modify the sentence as follow:
“Previous studies have well established that vertical motions impact biogeochemistry (Mahadevan & Tandon, 2006 ; Mahadevan, 2016 ; McGillicuddy, 2016). Upward vertical velocities drive deep nutrients into the euphotic layer and also move the phytoplankton cells along the water column resulting in changing light conditions.”

Ln 33-35: I do not understand this sentence. Are you saying that little is known about the phytoplankton diel cycle? Not only there are laboratory experiments, but also models, in particular individual-based models, that study this fact. For example, several

studies by Geider et al.

We just want to highlight the importance of performing in situ measurements at high frequency to sample the phytoplankton cycle in natural conditions. Although a lot of knowledge has been obtained from laboratory experiments or models, only a few studies have performed in situ measurements at high frequency and resolution. This is a reason to lead cruises using Lagrangian sampling strategy and automated flow cytometer.
Thank you for your reference, we will include it in the sentence as follows:
"Although progress in the understanding of phytoplankton cell cycle has been obtained from incubation, sample manipulation (Worden and Binder, 2003) and models (Geider et al., 1997 ; MacIntyre et al., 2000), performing in situ measurements at high frequency and resolution is a necessity to better understand these biological processes and their responses to the environment. An efficient solution is to lead Lagrangian cruises using automated flow cytometers sampling at high frequency in order to resolve the phytoplankton diurnal cycle in situ, which is challenging using more conventional methods such as cultures or counting by optical microscopy (Thyssen et al., 2008 ; Fontana et al., 2018)."

Ln 44-48: Please, rephrase these sentences with a clearer and simpler message.

We plan to modify the sentence as follow:
"In our previous work, we identified the two water masses as both Atlantic Water (AW), but at different stages of mixing due to their different routes in the Western Mediterranean Sea. The AW located south of the front, characterized by absolute salinity ($S_A$) between 37 g $kg^{-1}$ and 37.5 g $kg^{-1}$, corresponds to AW more recently entered into the Mediterranean Sea by the Gibraltar strait, thus being named "younger AW". The AW found north of the front is characterized by a higher $S_A$ (37.5 g $kg^{-1}$ to 38 g $kg^{-1}$) and corresponds to the surface water having circulated in the cyclonic gyre of the western Mediterranean for some years and then is referred to as "older AW". This water is also referred to as "local AW" (Barceló-Llull et al., 2019) or "resident AW" (Balbín et al., 2012)."

Ln 46-48: Could the authors provide some details about the nutrient concentration of both water masses?

Unfortunately, it was not possible for both technical and funding reasons to perform nutrient measurements during the 2018 cruise, that is why we cannot provide nutrient concentrations of both water masses. Nevertheless we acknowledge the importance of this information and these measurements are planned for our future cruise planned this spring (mid-April to mid-May 2023).

Ln 49-50: This sentence looks like part of the results section. I understand that you are referring to Tzortzis et al. (2021), but it is not clear.

We will modify the sentence as follows:

"Coupled with these hydrological measurements, measurements of phytoplankton abundance by flow cytometry were also described in our previous study. Tzortzis et al. (2021) showed that contrasted phytoplankton abundances were observed in these two water masses, with the smallest phytoplankton such as *Synechococcus* dominating south of the front in the younger AW, while microplankton is more abundant north of the front in the older AW."

Ln 51: This study, or Tzortzis et al. (2021)? I imagine is Tzortzis et al. (2021), then this first sentence and probably the open questions should be in the previous paragraph.

We apologize for the lack of clarity. We will not change the paragraph but we will modify the sentence as follows:
"As a consequence, our previous study constitutes an important improvement in the understanding of the role of frontal structures at finescale on phytoplankton distribution in a moderately energetic ocean. Nevertheless, open questions remain concerning the mechanisms generating this observed distribution: Is it exclusively driven by the dynamics of the ocean currents ? What is the role of biological processes ?

In the present study, we attempt to explain the particular patterns of phytoplankton abundances observed by automated flow cytometry during the PROTEVSMED-SWOT cruise [...]."

## Materials and methods

Ln 70-73: I don't think this information is relevant.

We will move the sentence about SWOT in the perspective section.

Ln 73-76: These facts should be in the introduction.

As suggested, we will move this part in the new version of the introduction (see above)

Ln 77: Please, consider indicating that the measures have a high spatial and temporal resolution.
Ln 77: I am not sure if you can use in situ sensors when they are on board. It is kind of repetitive.
Ln 77-70: Here you are describing in situ measurements, that are described in the next subsection.
Ln 80-82: Repetitive information (introduction).
Ln 76 and 83: Please, describe the sampling strategy details in a single paragraph.
Ln 84 and 85: Please, mention the source of the remote sensing datasets.

Following your suggestions we will modify Figure 1 (see page 21 of this document) and we will modify this part as follows:

"The PROTEVSMED-SWOT cruise followed an adaptive Lagrangian strategy to measure at **high spatial and temporal resolution** several physical and biological variables with both in situ sensors and analysis of the sea surface water intake. The vessel route was designed ad-hoc on the basis of daily remote sensing dataset provided by the Software Package for an Adaptive Satellite-based Sampling for Oceanographic cruises (SPASSO, https://spasso.mio.osupytheas.fr, last access: February 6, 2023). SPASSO used altimetry-derived currents **from AVISO** ("Archiving, Validation and Interpretation of Satellite Oceanographic", https://www.aviso.altimetry.fr, last access: January 18, 2023 ) and ocean color observations. Chlorophyll a concentrations ([chl*a*], level 3, 1 km resolution) were provided by **CMEMS**, "Copernicus Marine Environment Monitoring Service", https://marine.copernicus.eu, last access: January 18, 2023. In addition, ocean color composite maps were provided by **CLS with the support of the CNES**). They were constructed using a simple weighted average over the previous 5 d of data gathered by the Suomi/NPP/VIIRS sensor. SPASSO generated maps of dynamical and biogeochemical structures in both near real time (NRT) and delayed time (DT).
Maps of [chl*a*] allowed us to identify two water masses, characterized by distinct [chl*a*] values and separated by a zonal front at around 38° 30' N. This front was also detected using the in situ horizontal velocities, temperature and salinity, as described in our previous study. These two water masses were sampled along a designated route of the ship, represented in black in Fig. 1. Special attention was paid to adapting the temporal sampling in order to measure the phytoplankton diel cycle in each water mass. This was achieved by continuously sampling across both water masses along transects. While the ship did not remain in each water mass for 24h, day-to-day variability remained low and measurements from several days were combined into one diel cycle (Fig. 1). The shape depicted by the ship's track led us to call these area north–south (NS) hippodrome (bold black line in Fig. 1) performed between 11 May at 02:00 and 13 May at 08:30 UTC."

Ln 91-94: What are the temporal and spatial resolution of the temperature and salinity measurements?

Temperature and salinity were measured thanks to a thermosalinograph (TSG). The TSG was equipped with two sensors: a CTD Sea-Bird Electronics SBE 45 sensor installed in the wet lab, connected to the surface water and which continuously pumped seawater at 3 m depth ; and an SBE 38 temperature sensor installed at the entry of the water intake. The TSG measurements are achieved **each 30 min,** which corresponds to a ~ **2 km spatial resolution** at typical ship speeds.

Ln 94-115: One paragraph. Moreover, revise the information provided, there is some repetitiveness regarding the optical signals.
Ln 104: 1.5 $cm^3$ is the water volume analyzed? Please, consider expressing the volume in mL, in my experience, it is a more common unit used in this kind of study.
Ln 112: Again, please consider using cell per mL
Ln 115-116: Totally out of place.

We used a subunit of the international system (SI) as requested by Biogeosciences, but below we will convert it into mL as in the reworked manuscript, following your suggestions.

We have reworked this section (Ln 91-116):

"During the cruise, the irradiance (wavelengths between 400 and 1000 nm) was measured by a CMP6 pyranometer (Kipp and Zonen; https://www.campbellsci.fr/cmp6, last access: January 19, 2023). The sea surface temperature and salinity were measured continuously with a **frequency of 30 min along the ship route** by a thermosalinograph (TSG), which is an underway sensor able to pump seawater at 3 m. The data were converted into conservative temperature ($\Theta$) and absolute salinity ($S_A$) using the TEOS-10 standards of McDougall et al. (2012). To automatically sample and analyze the phytoplankton cells, an automated CytoSense flow cytometer (CytoBuoy b.v.) was installed on board and connected to the seawater circuit of the TSG. A sheath fluid made of 0.1 µm filtered seawater stretched the sample in order to separate, align, center and drive the individual particles (i.e. cells) through a laser beam (488 nm wavelength). Several optical signals were recorded when each particle crossed the laser beam: the forward angle light scatter (FWS) and 90° side-ward angle scatter (SWS), related to the size and the structure (granularity) of the particles. Two distinct fluorescence emissions induced by the light excitation were also recorded, a red fluorescence (FLR) induced by chlorophyll a content and an orange fluorescence (FLO) induced by the phycoerythrin pigment content. The CytoUSB software (Cytobuoy b.v.) was used to configure and control the flow cytometer and set two distinct protocols, **running sequentially every 30 min**. A total of 1164 samples were analyzed during the cruise. The first protocol (FLR6) was dedicated to the analysis of the smaller phytoplankton, using a red fluorescence (FLR) trigger threshold fixed at 6 mV, and a volume analyzed set up at **1.5 mL**. The second protocol (FLR25) targeted nanophytoplankton and microphytoplankton with a FLR trigger level fixed at 25 mV and an analyzed volume of **4 mL**. The FLR trigger was used to discriminate the red fluorescing phytoplanktonic cells from other particles (such heterotrophic prokaryotes, nanoflagellates, ciliates, etc.). Recorded data were analyzed with the CytoClus software (Cytobuoy b.v.) which retrieves information from the 4 pulse shapes curves (FWS, SWS, FLO, FLR) obtained for every single cell. These curves were then projected into distinct two-dimensional planes (cytograms) by computing the curves' integral. Using a combination of various cytograms (e.g., FWS vs. FLR, FLO vs. FLR) allows us to determine optimal cell clusters (i.e, cells sharing similar optical properties). These clusters have been demonstrated in the literature to represent phytoplankton functional groups (PFGs) (Dubelaar and Jonker, 2000; Reynolds, 2006; Thyssen et al., 2008; Edwards et al., 2015). Finally, the PFGs abundance (**cells per milliliter**) and mean light scatter and fluorescence intensities were extracted from each sample."

Ln 118-124: Please, make it clear that this size-structured population model was applied to every phytoplankton population/group identified previously using the CytoBuoy.

We applied the size-structured population model of Sosik et al. (2003) to every phytoplankton group identified by the CytoSense flow cytometer. However, we only analyzed the results obtained for *Synechococcus* and the two nanophytoplankton groups because the size distributions of the picophytoplankton groups were very noisy. Furthermore, microphytoplankton and Cryptophytes were not abundant enough to allow a reliable determination of their abundances and cell cycle.

Ln 126: To use the model, the light scatter signal (FWS) recorded for each cell by the flow cytometer must be converted to size (diameter) using a power law relationship (Sosik et al., 2003), and then to biovolume (v).
I imagine that to convert size into volume you are considering that all the species are spherical. Then, please consider indicating this fact and that you are converting the FWS signal to Equivalent Spherical Diameter.Please, indicate the units of both measurements. Also for the rest of the variables (t, E, g, μ*,...).
Ln 128: I am not sure if N is the number of cells in all the size classes or at each size class.
Ln 133: How many size classes were determined and how? Does it follow a log distribution?
Ln 135: I am not sure what exactly is "this probability". Is it the probability of cells growing in a time interval? Is it a probability or a proportion?
Ln 141: Instead of however, besides seems more appropriate.
Ln 141-142: Repetitive information.
Ln 147: I consider kind of inappropriate the use of a "decrease in cell size", it is a division. A phytoplanktonic cell decreases in size if the growth conditions are not optimal, and that is not an indication that there is a doubling event.
Ln 150-151: This sentence is confusing. Why do you talk about N(0) when is not used in the equations 5. (Two equations = two labels, please. Similarly, with equations 8)
Ln 153: A(t) is a tridiagonal transition matrix that contains.
Ln 159: Could you elaborate on what you mean by optimal parameters, please?
Ln 160: Standard deviations of the errors?
Ln 166: There is no information about this equation.
Ln 167-169: I do not understand this explanation.
Moreover, the definition of "bar l" (I do not know how to write the loss symbol here) confuses me. If it is the daily average population loss rate, how dt is 1 hour? On the other hand, what do you mean exactly by loss? The number of cells moving from one size class to another, or death?
What is the description of T1day NT0?

I have no experience using this kind of model, but any reader should be able to understand the methodology followed in the study without having to read previous studies. So please, review this section carefully and try to make it as clear as possible.

In order to follow all your comments above, we will completely rework section 2.3 of the manuscript, concerning the size-structured population model. We hope that this new version here below will clarify this approach.

**The size-structured population model**

We used the size-structured population model described by Sosik et al. (2003) and adapted by Dugenne et al. (2014) and Marrec et al. (2018), to estimate phytoplankton in situ growth rates.

The model uses as input the phytoplankton cell volume (biovolume) derived from cell light scatter intensities (FWS). Biovolumes were estimated using coefficients previously obtained by measuring a set of silica beads with the flow cytometer following the same settings used for phytoplankton analysis. The coefficients $\beta_0$ and $\beta_1$ used to convert FWS (arbitrary units, a.u.) to biovolume $v$ ($\mu m^3$) were derived from a log-log regression between FSW and silica bead volumes. These methods come from the studies of Koch et al. (1996) and Foladori et al. (2008).

$v = exp(\beta_0) \times FWS^{\beta 1}$ with in our case $\beta_1 = 0.9228$ and $\beta_0 = -5.8702$

In the size-structured population model, cells are classified into several size classes according to their dimensions at time $t$. $\Delta v$ is chosen in order to have enough number of classes $m$ to cover the entire observed biovolume $v$, from $v_1$ to $v_m$ (cf Figure A). Classes are logarithmically spaced as follows:

for i in 1,2,…,m $v_i = v_1 \, 2^{(i-1)\Delta v}$ with $\Delta v$ constant

For *Synechococcus*, $\Delta v = \frac{1}{6}$ and $m = 40$, so that the model size classes encompassed our full measured size distributions.

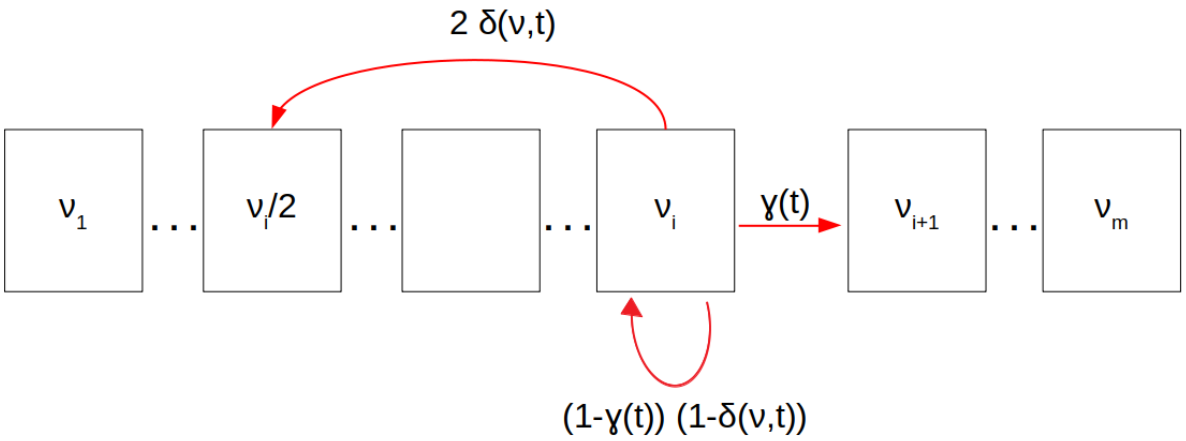


Figure A: Cell cycle stages in the size-structured population model. Cells may grow to the next size class ($\gamma$) or be at equilibrium ($1-\gamma(t)$) ($1-\delta(\nu,t)$). Above a particular size, cells are large enough to divide in two daughter cells with probability ($\delta$). Figure adapted from Sosik et al. (2003).

At any time $t$, the number of cells in size classes $\vec{N}$ (and $\vec{w}$ its corresponding normalized distribution), was projected to $t + dt$ via matrix multiplication:

$$\vec{N}(t + dt) = A(t)\,\vec{N}(t) \qquad \text{and} \qquad \vec{w}(t + dt) = \frac{A(t)\,\vec{N}(t)}{\sum A(t)\,\vec{N}(t)}$$

We chose $dt$ = 10 min (i.e., $\frac{10}{60}$ h) as Sosik et al. (2003) and Dugenne et al. (2014), because for this time step, cells are unlikely to grow more than one size class.

$A(t)$ is a tridiagonal transition matrix that contains (cf Figure B):

1) $\gamma$: the probability of cellular growth
2) $\delta$: the probability of cells entering mitosis
3) the cells stasis, i.e., the probability for cells to maintain their state (i.e size) in equilibrium during the temporal projection.

$$\begin{array}{c} \\ v_1(t+dt) \\ \vdots \\ v_j(t+dt) \\ \vdots \\ v_m(t+dt) \end{array} \begin{array}{c} \begin{array}{cccccc} v_1(t) & \dots & v_j(t) & \dots & v_m(t) \end{array} \\ \begin{pmatrix} 1-\gamma(t) & \dots & 2.\delta(v_j,t) & \dots & 0 \\ & & & & \\ 0 & \ddots & (1-\gamma(t)).(1-\delta(v_j,t)) & \ddots & 0 \\ & & & & \\ 0 & \ddots & 0 & \ddots & 1-\delta(v_m,t) \end{pmatrix} \end{array}$$

Figure B: Matrix transition A(t). (Figure extracted from Dugenne, 2017 (thesis)).

The temporal projection

$N_{|v=v1}\ (t+dt) = (1 - \gamma(t)).N_{v=v1}(t) + 2\delta(v_j,\ t).N_{v=vj}(t)$

$N_{|v=vm}\ (t+dt) = (1 - \delta(t)).N_{v=vm}(t) + \gamma(t).N_{v=vm-1}(t)$

Probability of cellular growth

The probability of cells growing to the next size class ($\gamma$) depends only on the light intensity (irradiance) necessary for photosynthesis, expressed as:

$$\gamma(t) = \gamma_{max}\ [\ 1 - exp(-\frac{E(t)}{E^*})]$$

$\gamma_{max}$: maximum proportion of cells growing (dimensionless quantity)
E: irradiance (µE $m^{-2}$ $s^{-1}$)
E*: irradiance normalizing constant (µE $m^{-2}$ $s^{-1}$)

Probability of cells entering mitosis

According to Dugenne et al. (2014), $\delta$ expresses a proportion (between 0 and 1) modeled by the combination of two Normal distributions ($\mathcal{N}$). One is linked to the cell size, the other is linked to the time of cell division. Both imply an optimum, reached at $\overline{v}$ and $\overline{t}$ respectively, for cell division above which the cell size and the timing of division is suboptimal.

$$\delta(t,\ v) = \delta_{max}\ \mathcal{N}(\overline{v},\sigma_v^2)\ \mathcal{N}(\overline{t},\sigma_t^2)$$

$\delta_{max}$: maximum proportion of cells entering mitosis (dimensionless quantity)
$\overline{v}$: mean of the size Normal distribution (µ$m^3$)
$\sigma_v$: standard deviation of the size Normal distribution (µ$m^3$)

$\bar{t}$: mean of the time Normal distribution (h)

$\sigma_t$: standard deviation of the time Normal distribution (h)

Cells stasis

A third functional proportion is included in the transition matrix $A(t)$, to represent cell stasis. Since this function illustrates a non-transition, it is modeled by the proportion of cells that neither divided nor grew between $t$ and $t + dt$.

$$[1 - \gamma(t)]\,[1 - \delta(t, v)]$$

Optimal parameters

The set of parameters, $\theta$ is estimated by maximum likelihood function, assuming errors between observed $\vec{w}$ and predicted $\widehat{w}$ normalized size distributions. Their standard deviations are estimated by a Markov Chain Monte Carlo approach (Geyer, 1992 ; Neal, 1993) that sample $\theta$ from their prior density distribution, obtained after running 200 optimizations on bootstrapped residuals to approximate the parameter posterior distribution using the normal likelihood. (The likelihood function represents the probability of random variable realizations conditional on particular values of the statistical parameters).

$$\theta = [\gamma_{max}, E^*, \delta_{max}, \bar{v}, \sigma_v, \bar{t}, \sigma_t] = argmin(\sum(\theta))$$

$$\sum(\theta) = \sum_{t}^{t+dt} \sum_{i=1}^{m} (w(t) - \widehat{w}(t,\theta))^2$$

$$\widehat{w}(t,\theta) = A(t\text{-}dt, \theta)\, \vec{w}(t\text{-}dt) \quad \text{and} \quad \widehat{N}(t,\theta) = A(t\text{-}dt, \theta)\, \vec{N}(t\text{-}dt)$$

Table: Model parameters being optimized.

| Parameters | Definition | Interval | Units |
|---|---|---|---|
| $\gamma_{max}$ | Maximum proportions of cells in growing phase | [0, 1] | ∅ |
| $E^*$ | Irradiance normalizing constant | [0,∞[ | µE $m^{-2}$ $s^{-1}$ |

| | | | |
|---|---|---|---|
| $\delta_{max}$ | Maximum proportion of cells entering mitosis | [0,1] | ∅ |
| $\overline{v}$ | Mean of the size Normal distribution | $[v_{min}\ ,\ v_{max}]$ | µm$^3$ |
| $\sigma_v$ | Standard deviation of the size Normal distribution | [10$^{-06}$,∞[ | µm$^3$ |
| $\overline{t}$ | Mean of the time Normal distribution | $[1,\ 24\frac{1}{dt}+1]$ | hours |
| $\sigma_t$ | Standard deviation of the time Normal distribution | [10$^{-06}$,∞[ | hours |

Growth rate and loss rate

Once optimal parameters are identified, the growth rate is calculated using the time projection of the initial size distribution $\hat{N}$. 200 iterations were run to estimate the standard deviation of group-specific growth rates.

$$\mu_{size} = \frac{1}{t+dt} ln\left(\frac{\sum_{i=1}^{m} \widehat{N}_i(t+dt)}{\sum_{i=1}^{m} \hat{N}_i(t)}\right)$$

$\hat{N}$: observed size distribution at $t = 0$ (cells cm$^{-3}$)
$i$: i$^{th}$ size class
$\widehat{N}$: predicted size distribution (cells cm$^{-3}$)
$m$: number of size classes
$dt$: time step (h)
$t + dt$: temporal integration of the distribution projection (h), $t + dt = 24$ h
$\mu_{size}$: growth rates (day$^{-1}$)

The model estimates a population intrinsic growth rate $\mu_{size}$ , and a specific loss rate, over a 24 h period.

The daily average population loss rate $\bar{l}$ is obtained by the difference between the intrinsic growth rates $\mu_{size}$ and the hourly logarithmic of observed size distribution $\vec{N}$.

$$\bar{l} = \int_{}^{dt} \mu_{size}(dt) \; - \; \frac{1}{dt} \, ln(\frac{\vec{N}(t+dt)}{\vec{N}(t)})$$

As a consequence, the net growth rate is expressed as $r(t) = \mu_{size}(t) - l(t)$.

**Results**

Ln 176-188: This information should be included in the methodology section. Also, at the end of this explanation, it will be interesting to indicate how to convert the scatter signal to size and volume.The details about how every species was differentiated, in my opinion, are not necessary, therefore I propose the authors move it to the supplementary, together with Figure 2.

Following your suggestions, we will modify the text by moving: the description of how to identify the phytoplankton groups in the methodology section, and the remaining information and the figure to the supplementary material.

Ln 210-211: The information about the figures does not fit here. It will be more appropriate to move to the beginning of the next paragraph.

We will move it in the reworked version of the manuscript.

On the other hand, please explain the background information. Does it make reference to the proportion (percentage) of cells of each biovolume? If it is a percentage, why it does not vary between 0 and 1?

We will change the terms, instead of proportion we will use frequency; indeed, the background colors represent the number of particles of a specific biovolume. For a given time, the sum of the frequency is equal to the total number of particles.

Ln 211-216: How was reconstructed the 24-hour irradiance curve should be explained in the methodology.

We will move this part in the methodology.

Ln 221, 222, 231, and 232: Please, include the standard deviation value together with the mean value.

We will add that in the text and maintain it in the table, too.

Ln 217-233: Please, explain in this section why there is no information about the other 6 groups identified.

We will move the explanation from the Discussion in this section:
"We have also modeled the diurnal cycle for the picophytoplankton groups, i.e., Pico1, Pico2, Pico3, PicoHFLR. However, we obtained very noisy size distributions and couldn't obtain a valid measurement of the growth rates, hence these distributions are not considered further in this study. As microphytoplankton and Cryptophytes were not abundant enough to allow a reliable determination of their abundances and cell cycles, they were not taken into consideration in this study."

**Discussion**

Ln 236: Please, add some references.

Although it has been clearly demonstrated that phytoplankton plays a fundamental role in the ocean ecosystem functioning **(Watson et al., 1991 ; Field et al., 1998 ; Allen et al., 2005)**, numerous questions remain about their population dynamics in relation to finescale structures.

Ln 245-246: What do you mean by transiting in all the cell cycle stages? That they are growing and dividing?
Ln 254: What do you mean by extensive distribution?

We apologize for the lack of clarity, our intent here is to compare the *Synechococcus* distributions in the two different water masses. We will modify the text as follows:
"In the older AW the cells have all along the day a large size-class distribution centered approximately at 0.3 $\mu m^3$ while in the younger AW (Fig. 4a, 4c) the distribution is narrower and centered approximately at 0.2 $\mu m^3$ (Fig. 4b, 4d)."

Ln 265: Is it really the only reference for this fact?

There are others references, we will modify the sentence as follows:
"Picophytoplankton is often characterized by the presence of several taxa with potentially different effects on the population dynamics, whereas nanophytoplankton is mostly dominated by diatoms in the Mediterranean Sea **(Siokou-Frangou et al., 2010 ; Marty et al., 2002 ; Navarro et al., 2014 ; El Hourany et al., 2019)**."

Ln 269-274: Basically the same was said in the introduction.
Ln 275: Please, revise this sentence.

We will remove these sentences.

Ln 284: The fact that light and irradiance are essential for phytoplankton growth was known before 2001.

Here we referred to the fact that vertical velocities impact biogeochemistry, driving nutrients in the euphotic layers and the phytoplankton cells along the water column where these organisms will receive more or less light as a function of the depth (see our previous answer).

We agree that our sentence was not clear, so we will rework these sentences as follows:
"The early experimental works of Huisman, 1999 ; Jenkin et al., 1937 and Marshall et al., 1928 have well established that the light and nutrients are essential for phytoplankton growth. The availability of these two variables for the phytoplankton is driven by physical dynamics such as vertical velocities (Lévy et al., 2001 ; Pidcock et al., 2016 ; Mahadevan, 2016)."

Ln 285: Then is expected a higher nutrient concentration in the old AW? For that reason, there is a higher contribution of larger cells?

Yes, indeed we expect a higher nutrient concentration in the older AW since this water probably experiences more upwelling and longer temporal vicinity of the coast along its route (Bethoux, 1989 ; Schroeder et al., 2010 ; see introduction). Moreover, it is known that a higher concentration of nutrients is favorable to larger cells. Indeed, their better surface:size ratio due to their small size confers them a better capacity to inhabit areas with very low nutrient concentration compared to larger phytoplankton (Kiørboe, 1993 ; Marañón, 2015).

**Conclusions and perspectives**

Ln 305-309: This is not a conclusion.

We used to begin the conclusion section with a short summary of the thematics. We will completely rework the Conclusion taking into account your comments and those of the other referee:

"Phytoplankton structure and dynamics are a complex result of many interacting biological and physical phenomena. Finescale structures, and in particular fronts, generate vertical velocities which displace phytoplankton cells and nutrients in the water column, thus influencing phytoplankton communities. These mechanisms are only partially understood because the spatial scale of these structures and their ephemeral nature make them particularly difficult to study in situ; as a consequence only a few studies have been performed in finescale frontal regions. The estimates of specific growth rates for the various phytoplankton groups is one of the keys to better understand how environmental conditions affect phytoplankton dynamics. In this study, we followed the dynamics of several phytoplankton groups in two distinct water masses both in terms of hydrology and phytoplankton abundances, in order to explain their particular distribution.

The originality of our work resides in the fact that we used a size-structured population model applied in two water masses identified using a Lagrangian sampling strategy. To our knowledge that has never been done before. This strategy allowed us to reconstruct the diurnal cycle for several phytoplankton groups and to identify contrasted dynamics in the two water masses. For *Synechococcus* and nanophytoplankton, we found the higher cell size in the older AW located to the north of the front, associated with the lower abundances. A possible explanation is that the older AW is more enriched in nutrients than the younger AW, thus favoring the largest cells. This remains a hypothesis because of a lack of nutrient data. Furthermore, in the oligotrophic region such as the Mediterranean Sea, a narrow trophic variation of the nutrient concentration is sufficient to generate higher abundance of phytoplankton. Another novelty of our study is that we applied this model on several phytoplankton groups identified by flow cytometry, whereas previous studies only applied it to *Synechococcus* and *Prochlorococcus*. We obtained good results for *Synechococcus* and nanophytoplankton. However, our results were noisy for picophytoplankton groups probably because these latter contain several taxa with differing dynamics.

Our work paves the way for many research perspectives. Direct integration of growth rates in biogeochemical models (Cullen et al., 1993) should be taken into account for a better assessment of the biogeochemical contribution of phytoplankton in oligotrophic ecosystems and to better forecast its evolution in the context of global change. Furthermore, we plan future experiments again in the South Western Mediterranean in spring 2023, after the launch of the SWOT satellite which will provide high resolution altimetry-derived current. Involving high-resolution nutrient measurements (and also high-precision ones, considering the oligotrophy of the Mediterranean Sea), coupled with metabarcoding (to address the biodiversity of phytoplankton), zooplankton and virus sampling, we will improve the understanding of zooplankton grazing and viral lysis on the different phytoplankton groups. Furthermore, we aim to explore how biogeochemical and ecological role of the finescales in regions of weak circulation are different from the ones more documented in highly energetic regions like boundary currents. In the Mediterranean sea, the low nutrient content is indeed the perfect condition when addressing this question, because even weak horizontal or vertical nutrient redistributions associated with the finescale circulation are likely to result in a biological response (Talmy et al., 2014 ; Hashihama et al., 2021)."

**Technical corrections**

Ln 6: Delete the space between "numerous" and ";".
Ln 21: Add a comma after (days-weeks).
Ln 41: Delete parenthesis after altimetry.
Ln 87: Once the front "is" localized.
Ln 103: 1164 samples "were" analyzed.
Ln 122: Maybe light availability is more adequate?
Ln 129: Please, consider changing investigated by counted.
Ln 134 and141: ... between the time interval t...
Ln 135-136: ... necessary to carry out photosynthesis?
Ln 157: Is there a typo? The probability of division is not denoted by γ?

Ln 163-164: You already defined those symbols; it is kind of redundant to do it again.
Ln 185: [chla]?
Ln 207: Please, consider using disregarding instead of eliminating.
Ln 227: Observed biovolume (observed and in situ are kind of repetitive), and predicted biovolume (check also Ln 219).
Ln 219-220: all species populations in both water masses?
Ln 222: No comma before the parenthesis.
Ln 221, 223, 224, 229, 230, 240: l or "bar l"?
Ln 239-240: The structure of the phytoplankton community.
Delete the point after the manuscript title and after the abstract.
Please, use 1 or 2 decimal numbers for all the variables measurements, to keep the format along the manuscript (e.g., Ln 46, 48, 221).
Please, use the same format for the dates along the manuscript (e.g., Ln 70 and 93).
Please, revise the use of the word indeed, it is repeated quite often throughout the text.

Thank you, we will correct that in the reworked manuscript.

**Figure 1.**
Panel a is very small, impossible to appreciate the information. Moreover, the colormap scale is minuscule and does not indicate the variable (and units) that represents.
In panel b, it would be interesting to indicate where the sampling events took place.
In panel c, in my opinion, the clock diagrams are not necessary.
Legend: The purple box encloses a (b) zoom of the sampling region with overlaid chlorophyll-a concentration (units). _____. The red line represents _____, the dark blue box _____, and the light blue box _____.
I am not an English native, but I think that the lines and boxes are superimposed to the chl map. The other way around will not allow you to see lines and boxes.

We have modified Figure 1 (see below). In panel a, we have increased the size of the map and colormap. We have also changed the color of the route of the ship for more visibility, and we added the units. In panel b, we have also increased the map. The sampling events took place all along the transects, that is why for us it is not necessary to indicate that in addition. Concerning panel c, we kindly disagree, because we think that the clock diagrams help the reader to understand the reconstruction of a day of 24 h period thanks to the 4 transects in each water mass.

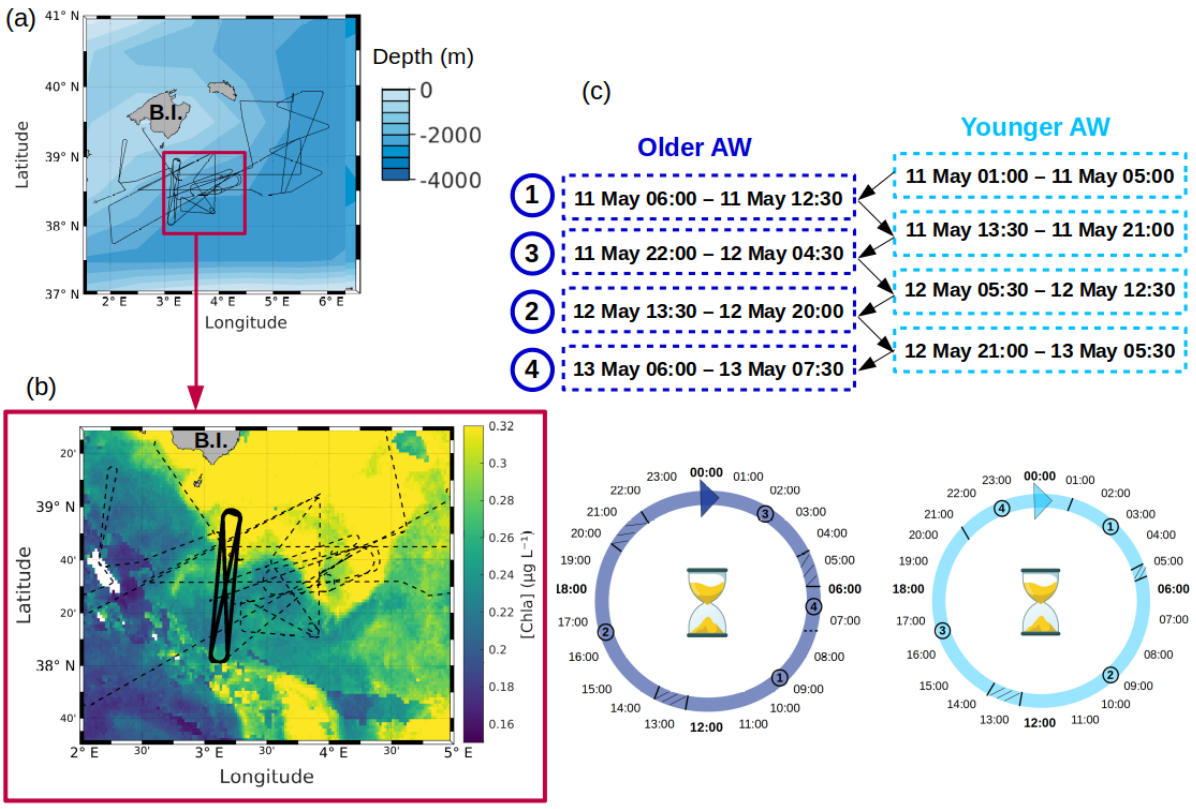


Figure 1: (a) Route of the RV Beautemps-Beaupré during the PROTEVSMED-SWOT cruise. The purple box encloses a (b) zoom of the sampling region with overlaid chlorophyll-a concentration (µg $L^{-1}$) of 11 May 2018. In panel (b) black dotted line represents the route of the ship and the bold black line represents the route of the Lagrangian sampling across the older AW (delimited by the box in dark blue) and the younger AW (delimited by the box in light blue). (c) Dates of the transects across the older AW and the younger AW, used to reconstruct a day of 24 h period in each water mass.

**Figure 2.**
As previously indicated, I do not consider this figure of relevance to the main text.

We will move this figure in supplementary information.

**Figure 2.**
Legend: Background colors indicate the two water masses…

We think that you speak about figure 3 ? In this case, indeed the background colors indicate the two water masses.

**Figures 4-6.**
Explain what represents the red line and the background color.
Correct all the color bars (by figure) to vary all in the same range.
We will modify the caption, the colorbars and the colormaps as follows:

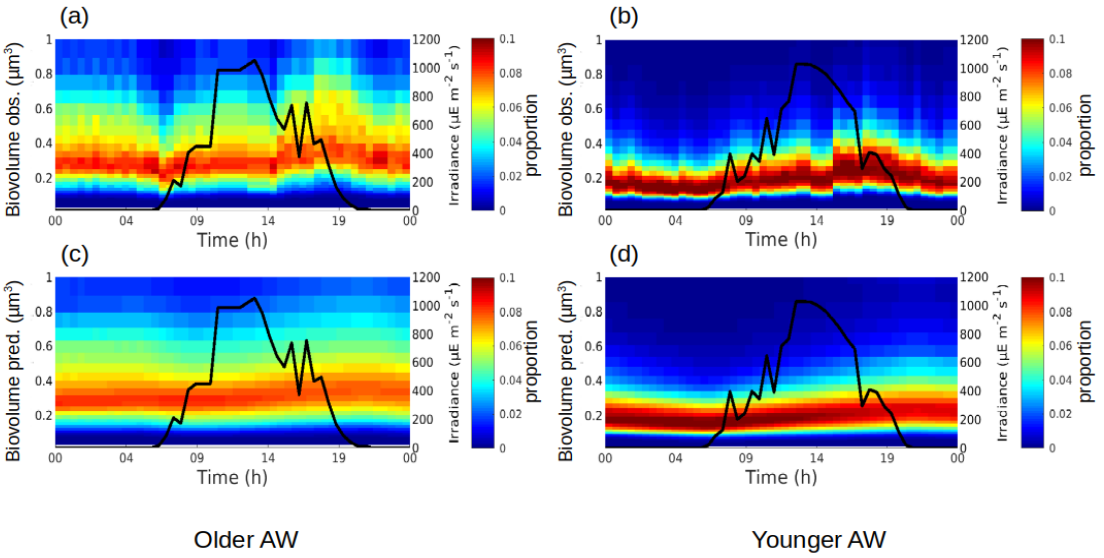


Figure 4: The background color represents the *Synechococcus* cell size distribution (i.e., biovolume in µm$^3$) observed (a, b) and predicted by the model (c, d) in the older AW (a, c) and in the younger AW (b, d) during 24 h. The line represents the irradiance (µE m$^{-2}$ s$^{-1}$).

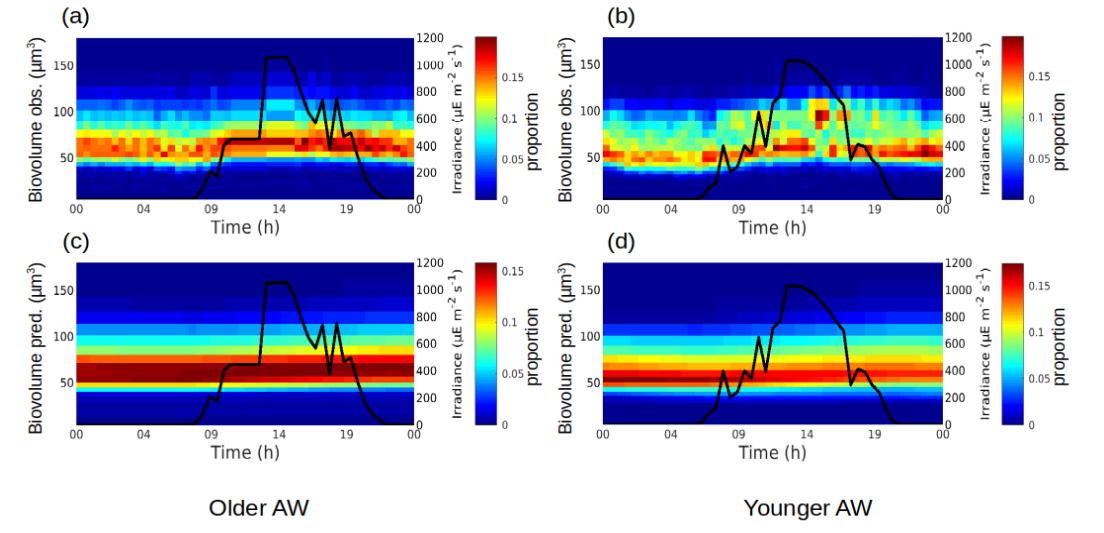


Figure 5: The background color represents the RNano cell size distribution (i.e., biovolume in µm$^3$) observed (a, b) and predicted by the model (c, d) in the older AW (a, c) and in the younger AW (b, d) during 24 h. The line represents the irradiance (µE m$^{-2}$ s$^{-1}$).

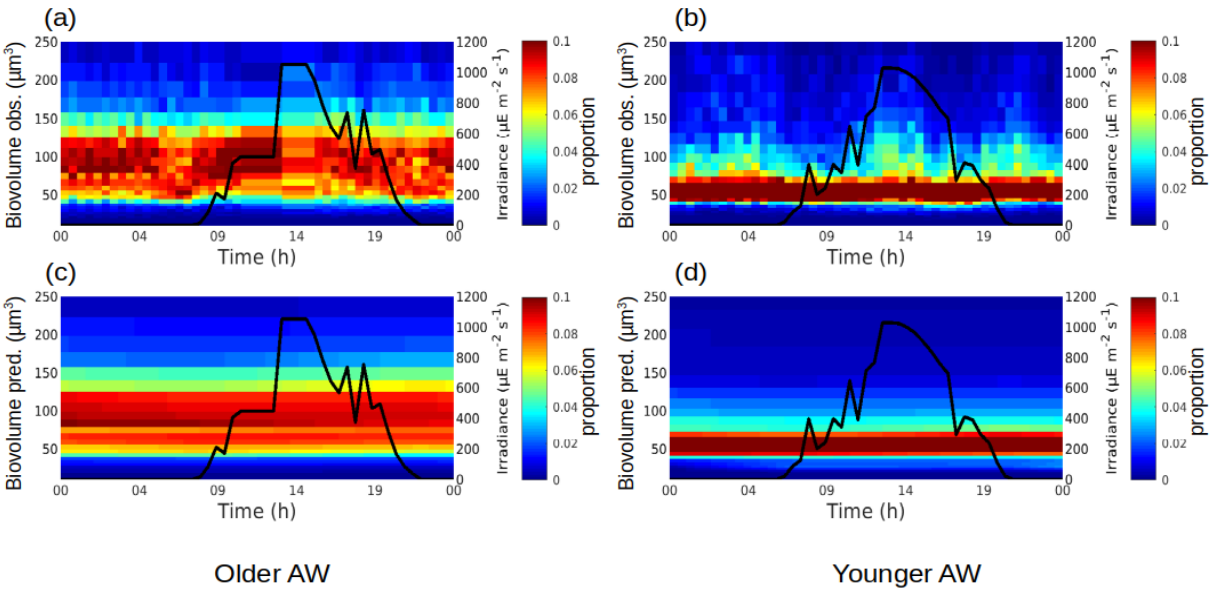


Figure 6: The background color represents the SNano cell size distribution (i.e., biovolume in $\mu m^3$) observed (a, b) and predicted by the model (c, d) in the older AW (a, c) and in the younger AW (b, d) during 24 h. The line represents the irradiance ($\mu E\ m^{-2}\ s^{-1}$).

**Figure 7.**
A very small figure, with some details difficult to appreciate. Even the legend is difficult to read.

We hope this new arrangement makes the figure clearer.

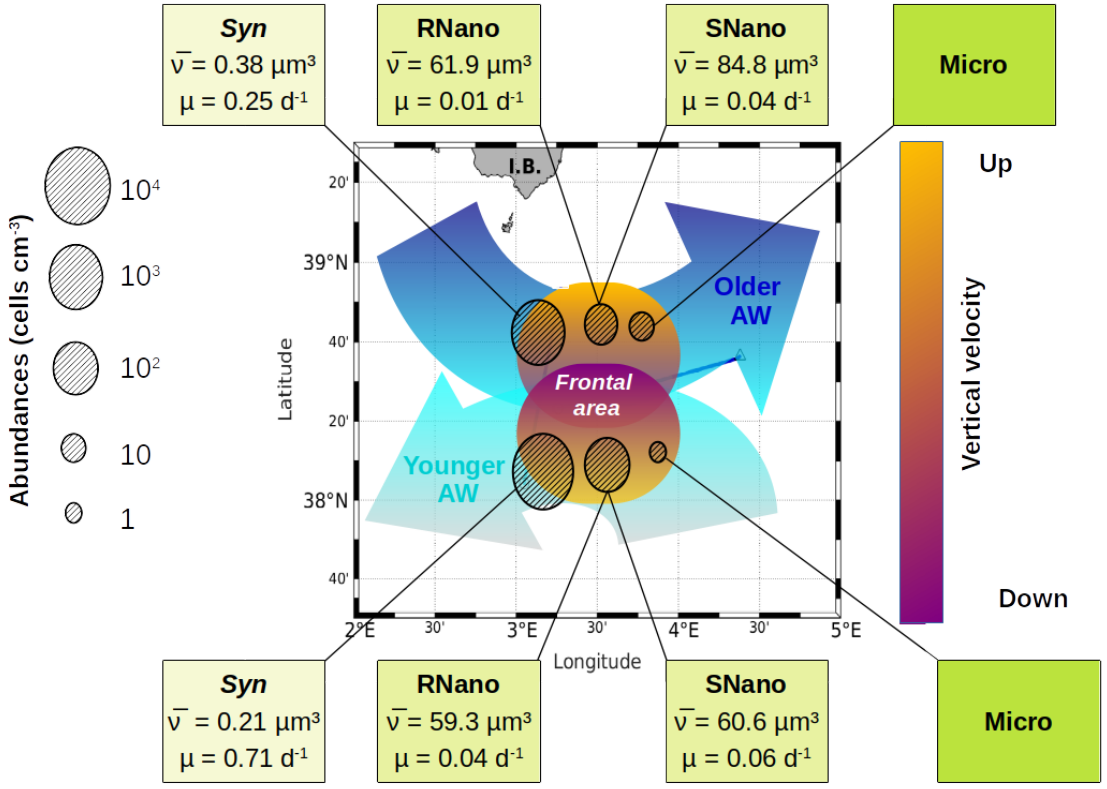


Figure 7: The contrasted distribution of phytoplankton in the frontal area. The circles represent the abundances of the several phytoplankton groups in the two water masses separated by the front. The boxes indicate the biovolume ($v$) and the growth rates (µ) for each phytoplankton group, as estimated from the model. Figure adapted from Tzortzis et al. (2021).

**Table 2.**

Indicate also that there is information about the standard deviation.

As mentioned in the methodology, statistics are included in the model. The growth rates were estimated using the maximum likelihood function and 200 iterations were run to estimate the standard deviation of group-specific growth rates using a Markov Chain Monte Carlo (Geyer, 1992 ; Neal, 1993).

Define every variable on its own.

This will be done.

µ ratio should not be adimensional? The equation and its meaning are already defined in the text.

As described in the new version of the methods (see above) µ is a temporal rate.

Define the acronym PFG.

We mentioned in the manuscript (Ln 111) that PFG(s) means “phytoplankton functional groups”.

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