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Plankton community response to fronts : winners and losers

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Abstract

Fronts are particularly productive regions of the ocean, and biodiversity hotspots for many marine species. Here we use an ocean-ecosystem model to investigate the effect of fronts on plankton ecology. We focus on energetic fronts in Western Boundary Current systems that efficiently inject nutrients into the euphotic layer and which are physical boundaries between productive and oligotrophic provinces. We found that the fronts form an environment distinct from both provinces, favorable to some plankton groups (diatoms, dinoflagellates and large carnivorous zooplankton) and less favorable to others (pico-phytoplankton, coccolithophores, small grazers), and with an overall larger diversity. In agreement with previous understanding, we find that bottom-up abiotic processes (nutrient enrichment) explain the prevalence of groups with fast growing rates (the “winners”). Importantly, our results also show that biotic interactions within the ecosystem may play a larger role than previously thought. We show that the winners can have a negative impact on other plankton species (the “losers”) through two indirect competitive processes: community shading (modification of the light environment by the plankton community leading to light-limitation of some plankton groups) and shared predation (where an increase in one functional group leads to increased grazing by a shared predator on another functional group).

Keywords : phytoplankton, biodiversity, fronts, marine ecology, modelling

Introduction

Plankton is the generic name given to aquatic free-floating organisms that include a huge variety of lifeforms with different functions, morphologies and trophic strategies. The composition of plankton communities varies spatially and temporally at

many different scales, and influences the higher levels of the marine food web as well as marine biogeochemical cycles. The diversity of an ecosystem is intricately linked to its functioning, with consequences on its productivity and stability (Tilman et al., 2014). Many factors have been shown to affect the diversity of planktonic ecosystems, from abiotic parameters (temperature, nutrients and light) to biotic interactions (competition e.g. Barton et al., 2010, predation e.g. Prowe et al., 2012; Vallina et al., 2014 and dispersion i.e. transport and mixing by oceanic currents, e.g. Ward et al., 2021). The ocean is very heterogeneous and many attempts have been made at classifying it into wide biogeographical provinces (Longhurst, 2007; Beaugrand et al., 2019). However, the physical properties of water masses can vary significantly over distances as small as a few kilometers (submesoscale) to a few dozens of kilometers (mesoscale) (McWilliams, 2016). Understanding how these variations translate into changes in ecological properties is one of the major challenges of ocean sciences. Fronts are regions of rapid transition with specific dynamics and properties, usually associated with a geostrophic horizontal along-front current and a vertical cross-frontal ageostrophic circulation responsible for exchanges between the surface and subsurface, whose intensity and vertical extent depends on the density gradient (McWilliams, 2016; Lévy et al., 2018). This ageostrophic vertical circulation can lead to the upwelling of nutrients (Allen et al., 2005) and subduction of organic matter (Stukel et al., 2017; Omand and Mahadevan, 2015).

Thus frontal dynamics can potentially affect marine ecosystems through many processes which can be classified into active (stimulation of the growth of primary producers by the supply of nutrients), passive (dispersion and mixing by the currents) and reactive (interactions within the ecosystem, such as competition and predation) (Lévy et al., 2018). The interactions between such a variety of processes are expected to drive a complex set of responses in the plankton community. Our general objective is to improve the understanding of how energetic oceanic fronts structure plankton communities and impact biodiversity. More specifically, we built on the previous work by Lévy et al. (2014a), who explored the role of oceanic dispersal in setting patterns of phytoplankton diversity, and focus on the respective roles of bottom up (active) versus top down (reactive) processes. We ask the following questions :

- How is the plankton community modified by the specific vertical dynamics of frontal zones ? Do all plankton benefit from the supply of nutrients, or are there "winners" and "losers" ? Which physiological traits, such as size and functional group, determine their success ?
- Is the response of the community driven by bottom-up processes (modification of the growth rate), top-down processes (predation) or a combination of both ? What are the roles of direct and indirect trophic interactions in the food web ?
- To what extent do the localized community structure modifications induced by frontal dynamics depend on the large scale context (latitude, season) ?
- Do fronts have a measurable effect on diversity ?

Observations over fronts are still very sparse, given the difficulty in sampling the appropriate scales, nevertheless dedicated field studies provide growing evidence of the structuring effect of fronts on the planktonic community. Several observations have suggested that the supply of nutrients by the vertical circulation can sustain a higher biomass of phytoplankton - mainly fast-growing diatoms - over a front compared to the surrounding, more oligotrophic waters (Tréguer et al., 2018; Taylor et al., 2012; Hernández-Carrasco et al., 2020), in one case extending the diatom bloom by several weeks (Allen et al., 2005). Other observations have shown that fronts can favor the coexistence of different taxa of phytoplankton (*Ostreococcus* eco-

types in the Kuroshio Extension front Clayton et al., 2017 or on the contrary separate them on either side (*Prochlorococcus* and *Synechococcus* in a front in the California Current Ecosystem Taylor et al., 2012). The enhancement of other groups of phytoplankton at fronts, such as the diazotroph *Trichodesmium* in coherent frontal filaments in the South Pacific (Benavides et al., 2021), has also been reported. The increased abundance and production of some zooplankton groups, especially copepods, has also been recorded in a few studies (Ohman et al., 2012; Luo et al., 2014). In addition, fronts have been shown to be foraging grounds for higher predators (Lara-Lopez et al., 2012; Bost et al., 2009; Bon et al., 2015), but it is difficult to evaluate how much the top-down pressure impacts the plankton. While it is known that frontal jets can transport plankton over long distances (for instance, the coastal *Ostreococcus* ecotypes found in the open-ocean Kuroshio Extension (Clayton et al., 2017), the biological consequences on the local frontal communities (increased competition, additional food source for predators, etc.) are not well-understood. Modelling results show that the high biomass values encountered at fronts can result from in-situ production, transport from a more productive region, or both (Clayton et al., 2013).

In order to address these questions, we examine the case of quasi-persistent fronts in Western Boundary Current (WBC) systems such as the Gulf Stream and North Atlantic Current (NAC) in the Atlantic Ocean or the Kuroshio in the Pacific Ocean. Such structures have lateral scales of order 10-50 km and constitute boundaries between very contrasted ecological provinces on either side. These fronts are relatively stable because the topographical and atmospheric forcings that generate them are steady; in addition they are associated with large vertical velocities that reach well into the nutricline and provide an efficient nutrient supply pathway to the euphotic layer (Lévy et al., 2018).

Methods

In order to evaluate the impacts of frontal dynamics on plankton community structure and diversity, we used an ecosystem model describing multiple functional groups and sizes of plankton embedded in a physical model of two energetic mid-latitude wind-forced fronts. The frontal zone that contains the two fronts is located between a productive, seasonally blooming system in the North, and a more oligotrophic system in the South (figure 1). Thus the fronts act as geographical boundaries between two contrasted biogeochemical provinces while having their own dynamics (strong horizontal currents and input of nutrients from below the nutricline). This model configuration is similar to Lévy et al. (2015), with the same physical model but with an updated version of the ecosystem model (DARWIN, figure 3) that allows a size-structured description of the planktonic groups (Dutkiewicz et al., 2021).

The physical model accounts for variations in environmental conditions from the scale of oceanic gyres (1000 km) down to the scale of mesoscale eddies (10-100 km) and transient submesoscale features (1-10 km), and for seasonality. In this paper, we will focus on the physical scale of surface intensified zonal jets which have a cross-frontal width of 20-50 km and a longitudinal extension of 1000 km, and are persistent throughout the year.

Physical model

The model configuration is a simplified representation of a Western Boundary Current (WBC) system, separating two wind and buoyancy forced oceanic gyres. The model domain features a box of horizontal dimensions 2,000 km x 3,000 km, rotated by 45° on the β -plane, with closed boundaries and a flat bottom at 4,000 m (figure 1). The model was forced with a repeating, idealized (sinusoidal) seasonal cycle of wind and buoyancy fluxes. Density follows a bilinear equation of state and

mostly mirrors temperature, as salinity variations in the model are small. The ocean circulation and thermodynamics were assessed by solving the primitive equations with the ocean circulation model Nucleus for European Modelling of the Ocean (NEMO; Madec (2008)) on a $1/54^\circ$ horizontal resolution (approximately 2 km) and 30 vertical level grid which resolves the euphotic layer with 12 vertical levels in the top 200 m (see Lévy et al., 2010, for details). This resolution allowed us to simulate a sharp and energetic WBC system (highlighted in figure 1c).

The forcing generates a cold subpolar gyre in the north of the domain and a warm subtropical gyre in the south (figure 1a), separated by a WBC that flows eastward into the open ocean from the western corner (figure 1c, red meandering jet). The subpolar gyre is characterized by very intense winter mixing (figure 2a), leading to a raised nutricline (figure 1b). In contrast the nutrient flux in the subtropical gyre is very low, leading to an oligotrophic environment with a depressed nutricline. The model also generates a secondary zonal eastward jet located approximately 5° north of the main WBC jet (figure 1c, dark blue jet). Both jets are associated with strong sea-surface temperature (SST) gradients (figure 1a) and are baroclinically unstable: they meander and shed eddies, while remaining in approximately the same location (within the light blue and light red boxes in figure 1c). Importantly, they are associated with strong vertical velocities which drive the upwelling of nitrate into the euphotic zone (figure 2c), resulting in a higher nitrate transport at the two fronts compared to their immediate background (figure 2a-b) and a locally raised nitrocline (figure 1b). The main jet is more energetic than the secondary jet, with eddy kinetic energy levels approximately 5 times stronger (figure 1 in Lévy et al. (2014a)). Because of their geographical locations, in the following sections the main jet will be referred to as the subtropical jet and the secondary jet as the subpolar jet.

Despite the simplified model geometry and forcing, the absence of realistic topography and the closed boundaries, our idealized simulations capture the features of WBC systems which are important for this study, i.e. an energetic frontal system separating two contrasted bio-regions. Secondary jets such as the one simulated here have been observed in the ocean (Maximenko et al., 2008) and are ubiquitous properties of turbulent flows that emerge when the horizontal grid resolution is fine enough. When compared to the North Atlantic system, the subtropical jet can be thought of as the Gulf Stream, and the subpolar jet as the North Atlantic Current. This physical model was previously used to investigate the impact of (sub)-mesoscale dynamics on various processes such as biogeochemical fluxes or phytoplankton diversity (Lévy et al., 2012a, 2014a, 2015; Resplandy et al., 2012).

Ecosystem model

The ecosystem model captures plankton diversity along the two dimensions of function and size (figure 3). There are a total of 30 phytoplankton types. The biogeochemical function dimension resolves 4 phytoplankton functional groups, each containing a range of size classes: picophytoplankton (4 sizes ranging from ESD 0.6 to 2 μm), coccolithophores (5 sizes ranging from ESD 3 to 15 μm), diatoms (11 sizes ranging from ESD 3 to 150 μm) and dinoflagellates (10 sizes ranging from ESD 6 to 228 μm). This makes 16 size classes in total which are spaced uniformly in log space from 0.6 to 228 μm equivalent spherical diameter (ESD). This ecosystem model is identical to Dutkiewicz et al. (2021) except that nitrogen fixing diazotrophs are not included. Model parametrizations important to this study are described below, but for more details on the full model, equations and parameter values, the reader is referred to Dutkiewicz et al. (2015, 2020, 2021). This model is able to capture observed global distributions of size classes and functional groups, as shown by the previous studies of

Dutkiewicz et al. (2020, 2021); Sonnewald et al. (2020).

Phytoplankton growth rates depend on nutrients, light and temperature with a multiplicative form for growth limitation factors. The model resolves the cycling of four limiting nutrients, phosphorus, nitrogen, silica and iron. However, in our simplified simulations, phosphorus, silica and iron are always present in sufficient quantities and therefore phytoplankton growth is only limited by nitrogen availability.

Functional groups differ by the resources they use (coccolithophores use calcium carbonate to build their shells, while diatoms use silicic acid), trophic modes (picophytoplankton, coccolithophores and diatoms are autotrophic groups while dinoflagellates are mixotrophic), nutrient uptake parameters (maximum growth rate and nutrient saturation), elemental composition (stoichiometry), palatability (cells who have a protective shell are less vulnerable to grazers) and light affinity. Smaller phytoplankton (“gleaners” such as the pico-phytoplankton and coccolithophores) have a high affinity for nutrients and a low maximum growth rate, while larger phytoplankton (“opportunists” such as diatoms and dinoflagellates) have a low affinity for nutrients and a high maximum growth rate. As a result, gleaners have a higher growth rate in oligotrophic conditions while opportunists have a higher growth rate when nutrient concentrations are closer to saturation. Within each group, most parameters follow allometric scaling relationships with size. Specifically, growth rates increase with size for picophytoplankton and decrease with size for the other groups (coccolithophores, diatoms, and dinoflagellates). In this model version, the temperature limitation of phytoplankton growth is the same for all phytoplankton types, therefore phytoplankton niches are mostly determined by light and nutrient availability. The penetration of light in the water column depends on incoming radiation (determined by season and latitude) and the concentration of particulate matter, including living cells. As a result, the development of phytoplankton at the surface can shade cells located deeper and limit their growth. Community shading -the modification of the light environment of phytoplankton by another phytoplankton group- is distinct from the self-shading of a single group by its own pigments. This mechanism, which allows indirect interactions between different phytoplankton species, can have significant biogeochemical consequences (Shigesada and Okubo, 1981; Kubryakova and Kubryakov, 2020).

The model also includes 16 zooplankton types which graze on plankton (phyto- or zoo-) 5 to 20 times smaller than themselves, but preferentially 10 times smaller. A Holling III parameterization (Holling, 1959) is used for grazing, which implies that grazing reaches a saturated rate at high prey abundances, and that prey have a small refuge at low prey abundance. Zooplankton types fall into 2 categories : the 6 smaller types (6.6 to 47 μm) are herbivores whose prey include pico-phytoplankton, coccolithophores and diatoms. The remaining 10 types (70 to 2425 μm) consume large phytoplankton but also consume smaller zooplankton and dinoflagellates and represent both large grazers and carnivorous species; we will refer to them as carnivores for simplicity. In addition, dinoflagellates are mixotrophic and their growth parametrization is identical to that of exclusively autotrophic or heterotrophic plankton, but with lower maximum growth and grazing rates.

An important feature of this model is that each size class contains phytoplankton types from different functional groups. Since prey are targeted by their size, each predator grazes on multiple prey types belonging to different phytoplankton (and also zooplankton) groups. This feature of the model allows for a mechanism known as “apparent competition” or “shared predation” : when two phytoplankton types share a common predator, they can have an indirect negative impact on one another, with the higher abundance of one leading to a lower abundance of the other (Holt and Bonsall, 2017). If one prey type increases in biomass, this will lead to an increased biomass in the common predator which will then exert stronger grazing on all other prey types.

Simulation set-up

Ocean velocities, temperature and vertical mixing coefficients were generated by running the physical model with a horizontal grid resolution of $1/54^\circ$, within the NEMO model framework. Five consecutive years of bi-diurnal (48 h averages) physical fields were then averaged over a $1/9^\circ$ (10 km) grid and used to drive the DARWIN ecosystem model in off-line mode within the Massachusetts Institute of Technology general circulation model (MITgcm) framework (Marshall et al. (1997)). Averaging from $1/54^\circ$ to $1/9^\circ$ preserved the intensity of horizontal and vertical transport at the jets while significantly reducing the computational cost of the simulations (Lévy et al., 2012b). In our base simulation, tracers (plankton and nutrients) were embedded in the 3D flow and also subjected to vertical diffusive mixing. The model was integrated forward for twenty years, by repeating the five years of bi-diurnal forcings provided by the physical model four times. We initialized the ecosystem model run with identical biomass distributions for all plankton types constant over the model domain, and using nutrient fields obtained from Lévy et al. (2012a). Model output fields (plankton biomass, growth rates, etc.) were saved every 2 days. Our analysis is based on the last five years of the 20 year model run, giving five different realizations of seasonally evolving frontal structures which slightly differ from one another due to the chaotic nature of the flow (Lévy et al., 2014b). A mean seasonal climatology was constructed from these five years and is used as the basis of the following results.

Evaluation of the impact of fronts

In order to compare the phytoplankton community structure inside and outside the time-evolving fronts, the precise location of the fronts was assessed at each time step. Fronts were identified on the basis of a temperature gradient criterion. To compute the temperature gradient, we used the temperature fields at 100 m depth smoothed spatially with a running average over 5 grid points in order to eliminate some of the patchiness of the temperature gradient. 100 m depth gradients were preferred to surface gradients because the amplitude of surface gradients strongly vary seasonally. In our analysis, we contrast properties at the fronts (dark red and dark blue in figure 1c) with their immediate surroundings (light red and light blue in figure 1c), within the WBC region. Within each of the two fixed areas around each front (light red and light blue regions), and at each time step, grid points where the temperature gradient was above $0.025^\circ\text{C}/\text{km}$ were considered "fronts" and grid points where the temperature gradient was below this value were considered "background". We will thus contrast the subtropical front (dark red) with the subtropical background (light red), and the subpolar front (dark blue) with the subpolar background (light blue). With this method, comparing communities over fronts and over background allowed us to quantify local modifications generated by frontal conditions. We will also contrast this properties with those in the neighboring large-scale biogeochemical provinces, i.e. in the subtropical gyre (orange triangle) and in the subpolar gyre (turquoise triangle).

Quantification of diversity

We use the Shannon index to measure total phytoplankton diversity. Since the number of types is initially fixed and there is no species extinction in our model, the Shannon Index in this case measures the evenness of the plankton community. We normalize it by its maximum constant value (reached when all 30 phytoplankton types are present in equal proportion) in order to get a quantity that varies between 0 and 1 ($Diversity = \frac{-\sum_{i=1}^N P_i \log(P_i)}{\log(N)}$ with P_i the relative abundance of each type, and N the number of types ($N=30$ for total diversity)). We also use the Shannon index to measure group diversity (with $N=4$ and P_i is the relative abundance of each group). Similarly, within each group, we measure intra-group diversity by com-

puting the Shannon index of the types included in this group. These additional measures are useful to determine whether changes in total diversity are driven by changes in the proportions of each group or are driven by changes in the proportions of the size classes within a group (and for the latter which of the 4 groups drives the change in total diversity).

To sum up, in order to address the questions raised in the introduction, we use a model with an intermediate level of complexity: the simplified geometry allows the high resolution necessary to resolve mesoscale fronts while maintaining the degree of realism needed to evaluate the role of the large scale context (latitude and season). The ecosystem model is complex enough to investigate which characteristics (size and functional group) determine the response of plankton to frontal dynamics, with a relatively modest number of phytoplankton types.

Results

We examine changes in the composition and functioning of the planktonic ecosystem induced by fronts in a WBC system. We start by presenting the main characteristics of the basin-scale context in which this WBC system is located. Then we present the two permanent frontal features in the WBC region and compare them with their immediate surroundings in order to provide a measure of the local effect of the fronts. We then focus on two contrasted situations : an oligotrophic regime, represented by the subtropical front during summer (June-July-August), and a bloom regime, represented by the subpolar front during spring (February-March-April). By comparing these two regimes, we are able to explore how the local effect of fronts might vary with the environmental context. We find that both fronts are associated with increased net primary production (NPP) and increased diversity (figure 4), in agreement with previous studies at fronts (Lévy et al., 2015), but that different types of plankton can have different responses, with some "winners" and some "losers" (figure S4). Our aim is to identify more precisely who are these "winners" and "losers" and understand why they behave in such a way. We first investigate the effect of abiotic factors such as the *active* injection of nutrients by the vertical transport associated with frontal dynamics. We then examine biotic factors (competition and predation) which arise as *reactive* processes over fronts.

Large scale community structure

The model's subtropical gyre is characterized by weak NPP seasonality (fig 4a) and by a phytoplankton community dominated by pico-phytoplankton, which account for about 50% of the total phytoplankton biomass (figure S1); coccolithophores being the second most abundant group accounting for 30% of the biomass, followed by dinoflagellates (13%) and diatoms (7%). Pico-phytoplankton are distributed evenly in the euphotic layer but the three other groups have a maximum of abundance at the DCM (Deep Chlorophyll Maximum at 120m, figure S2). Within each phytoplankton group, smaller types are more abundant than larger ones (figure S3). This size structuring results from the allometric scaling relationship between the maximum growth rate and cell size. Zooplankton are also structured according to size (figure S3). Herbivores, and to a certain extent carnivores, have weak seasonality and are evenly distributed in the euphotic layer, mirroring the distribution of the most abundant pico-phytoplankton group which drive the food chain (figure S1, S2).

The subpolar gyre is more productive than the subtropical gyre, and shows a strong seasonality with a bloom early in the spring (fig 4a). During the bloom, diatoms show a pronounced size structuring, with larger size classes contributing less than smaller ones, however the size classes within the other groups are more evenly distributed (figure S3). During the rest of the year, more oligotrophic conditions prevail and the community structure is more similar to that of the subtropical gyre, with

a strong size structuring for all groups and subsurface maxima of phytoplankton biomass (not shown). The distribution of zooplankton is closely related to the distribution of their prey, with a temporal succession of trophic levels: the diatom bloom is followed by a bloom of herbivores, itself followed by a carnivore bloom throughout summer.

The community structure of phytoplankton influences the zooplankton community composition, mainly through bottom-up processes: zooplankton of intermediate sizes (32 -154 μ m), which consume diatoms, are the most abundant during the bloom, while smaller herbivores (who consume pico-phytoplankton) have a higher abundance in oligotrophic conditions (figure S3). However, the low biomass of the smallest herbivores (especially during the bloom, figure S3b) is caused by the grazing pressure by their own predators (carnivorous zooplankton) rather than the lack of prey (pico-phytoplankton) and constitutes an example of top-down control via shared predation : diatoms have an indirect negative effect on small herbivores because they share a predator with them (carnivores zooplankton).

The WBC region displays characteristics which are intermediate between the subpolar and subtropical gyres, with a bloom of smaller amplitude than in the subpolar gyre, which also starts earlier (figure 4a). The community composition in the WBC region is also intermediate, with a strong dominance of pico-phytoplankton and coccolithophores, except during the bloom (figure 5).

The vertical distribution in the WBC region (fig S5) is similar to the gyres S2, with abundance maxima in the subsurface in oligotrophic conditions and at the surface in the bloom regime. The size structure within the groups (figure 6, 7) is also similar to the gyres (figureS3), with smaller sizes generally more abundant than larger ones.

Diversity

During most of the year, total diversity decreases from North to South: it is larger in the subpolar gyre than in the subtropical gyre due to a more even distribution of the different plankton types, and intermediate in the WBC region (figure 4b); within the WBC however NPP and diversity are higher at the fronts than in their immediate background. During the spring bloom, the large scale gradient of diversity disappears. In the subpolar front, diatoms (and dinoflagellates) briefly catch up over the other groups during the bloom months (figure 5a), leading to a very even community and a seasonal maximum in diversity (figure 4b). In contrast in the subpolar region, the bloom is associated with a temporary dominance of diatoms (figure S1a), leading to a drop in diversity. This is illustrated by the bell-shaped productivity/diversity distribution (figure 4c): during the bloom period, diversity increases with productivity in the subtropical gyre and WBC, but decreases with productivity in the subpolar gyre.

Throughout the year NPP and diversity are significantly more elevated at fronts compared to their respective backgrounds (diversity increases by 4% in the subpolar front and 10% in the subtropical front compared with their immediate background, figure 4b). Notably the amplitude of this local variation over cross-frontal horizontal scales of 10-100 km is of the same order of magnitude as the large-scale variation over meridional scales 1000s of km corresponding to the contrast between the subtropical and subpolar gyres. For instance the variation of diversity at the subtropical front is 0.07, which is more than 60% of the 0.11 difference between the gyres (figure 4b). The elevation of NPP is a known feature of frontal regions (Mahadevan, 2016; Liu and Levine, 2016), captured by our model. It results from the larger supply of nutrients at fronts, driven by the frontal dynamics (figure 2). The different phytoplankton types, however, respond in different ways to this extra nutrient supply; these differences are explored in the next sections.

"Winners and Losers" of frontal dynamics

We now focus on the differences in the abundances of different plankton groups between fronts and their respective backgrounds (figure 5).

Diatoms have a consistently higher abundance in both the subtropical and subpolar fronts throughout the year. Similarly, dinoflagellates almost always have a higher abundance within both types of fronts, except during the peak of the bloom in the subpolar front. On the other hand, the effect of the fronts on pico-phytoplankton and coccolithophores differs between the subpolar and subtropical fronts and varies during the year. In the subtropical front, pico-phytoplankton are less abundant in the front during the bloom and show no significant deviation from background conditions during the rest of the year; in the subpolar front they are slightly less abundant at the front than in the background during the entire year. In the subtropical front, the abundance of coccolithophores is higher than in the background before/after the bloom and lower during the bloom. In the subpolar front, the abundance of coccolithophores is much lower than in the background during the bloom, while before/after the bloom there is no significant difference between front and background. The differences in plankton abundances between fronts and their backgrounds also vary with depth (figure 9, S5). The general pattern is that frontal biomass tends to be higher than the background close to the surface and lower at depth, suggesting that different processes are involved at different depths. The depth at which this inversion occurs is variable. For instance, for pico-phytoplankton the inversion occurs at around 80m in the oligotrophic regime and 50m in the bloom regime. When the inversion occurs at the surface (such as for coccolithophores in the bloom regime), the biomass in the front is lower than in the background in the entire water column. In other cases (such as for diatoms in the oligotrophic regime), the opposite happens, and the biomass is always higher at the front. Within each group, the differences in abundance between the front and the background also vary with size (figure 6a-b, 7a-b) : larger sizes benefit more from the larger nutrient supply at fronts than smaller ones despite being generally less abundant.

The increase of phytoplankton diversity at the fronts can be explained by the combination of two effects: the increase of group diversity (more evenness in the representation of each group, figure 5), and the increase of intra-group diversity (more evenness among the size classes within each group, figure 6, 7). In the WBC region, pico-phytoplankton and coccolithophores tend to be more abundant than diatoms and dinoflagellates, so the comparatively larger frontal enhancement of the latter leads to a more even community at the front. Similarly, since the smaller sizes also tend to be more abundant than the larger, the fronts create a more even community by enhancing large phytoplankton.

The variation of zooplankton biomass at fronts (figure 8) has similar features to the variation of phytoplankton described above, indicating that the changes in phytoplankton are transferred up the trophic chain : the four smallest herbivores, which graze exclusively on picophytoplankton, are also "losers" with a lower biomass at fronts; the carnivores, which graze essentially on winners, are also winners; the situation is more contrasted for the largest herbivores, which graze both on winners and losers depending on the front and season.

In order to understand the differences in the abundances of different phytoplankton groups, in the next two sections we focus on the two main terms which controls them : photosynthetic growth rates and grazing pressure.

Bottom-up (growth rate)

The differences in growth rate among phytoplankton types in the WBC region is largely explained by their nutrient affinity and maximum growth rate, both of which are dependent on their size and functional group, with higher growth rates for gleaners in oligotrophic conditions (figure 6c) and higher growth rate for opportunists when nutrient concentrations are closer to saturation (figure 7c), and, within each group, increasing growth rates with size for pico-phytoplankton and decreasing with size for the other groups (coccolithophores, diatoms, and dinoflagellates).

We might expect that the larger supply of nutrients at fronts (figure 2) would lead to larger phytoplankton growth rates in comparison with background conditions. Although this is generally the case, our results show that this effect is not systematic for all phytoplankton types : while the growth rates of diatoms are consistently larger over fronts, the response of the other groups varies ; in general their growth rates are larger over fronts in the oligotrophic regime and are lower in the bloom regime (figure 6c-7c). This less intuitive response is due to the fact that the increase in nutrient supply is not the only factor impacting phytoplankton growth rates over fronts : another important factor is light. The increase in biomass in some phytoplankton groups over fronts modifies the optical environment, resulting in more light absorption at the surface and thus less light penetrating deeper in the water column. In our case the groups that produce the shading effect (mostly surface diatoms) are distinct from those who suffer from it (mostly pico-phytoplankton and coccolithophores at subsurface). For such groups, near the surface where light is plentiful, front-enhanced nutrient supplies lead to higher growth rates over the fronts. In contrast, at depth, where light progressively becomes the limiting resource, community shading leads to lower growth rates. Community shading is illustrated by the case of picophytoplankton at the subtropical front in summer, where the contrasted effects of the front on the growth rate with depth are translated in a similar impact in terms of abundances (figure 9). The net effect on the vertically-integrated biomass thus results from the balance between the increase at the surface (effect of nutrients) and the decrease at depth (effect of light). This net effect of community shading is not always negative; while it contributes to the decrease in pico-phytoplankton and coccolithophore biomass during the bloom (figure 7b), it has no impact on the pico-plankton integrated biomass over the subtropical front because the two effects nearly compensate (figure 6b and figure 9).

In contrast, an effect of fronts on growth rates which is more systematic is that within each group, the growth rates of the larger types tend to respond to the nutrient addition relatively more than the smaller types (figure 6d and 7d). This effect, which reflects the allometric relationships used to parameterize the growth rates, is directly responsible for many of the changes in abundances (figure 6b and 7b) and the resulting increase of intra-group diversity (figure 11).

In brief this analysis shows that the modification of nutrient and light availability over frontal zones in response to physical (nitrate supply) and ecological (community shading) processes drives a bottom-up modification of the plankton community structure, with some organisms able to profit from the changes while others are disadvantaged by them. Importantly, we see that the variation of phytoplankton growth rates over fronts is very similar to the variation in abundances, which suggests that these bottom-up processes explain a significant amount of the structuring of the phytoplankton community: the phytoplankton types whose growth rates are the most enhanced by frontal conditions are the ones whose biomass increases the most at fronts.

Top-down (shared predation)

In the previous section we showed that much of the reactive response to the injection of nutrients in fronts is in the form of bottom-up processes affecting growth rates, mainly due to the rapid response of phytoplankton to the injection of nutrients. However, in our model there are also modulations of the community response that occur due to top down effects, on seasonal time scales. We illustrate this with the case of coccolithophores in the subpolar front (figure 10) : during the bloom, their growth rate is lower at the front because of community shading, however the grazing pressure is increased because they share predators with many other plankton types – in particular diatoms, which do increase at the front. As a result, the biomass of coccolithophores is lowered at the front at a rate (about 20%) which is larger than the variation of the growth rate (5% decrease) would suggest, the bottom-up driven impact being amplified by shared predation. The effect of shared predation is even more prominent after the bloom due to the delayed response of zooplankton growth. During this period, the biomass of coccolithophores is not increased at the front despite an increase of their growth rate, because the increase in grazing pressure is even larger.

Discussion

We used an ocean-ecosystem model to investigate the effect of frontal dynamics on plankton communities. We focus on a WBC region, where two permanent fronts are located, and which constitutes a boundary between a productive gyre in the north and an oligotrophic gyre in the south. We found that, despite being located at the boundary between these two contrasted bio-regions, at a smaller scale fronts form an environment distinct from the background, essentially in response to the local injection of nutrients by the frontal dynamics. In our model, the various modeled phytoplankton and zooplankton types respond differently to this frontal nutrient injection, with a positive effect for some ("winners") and a negative effect for others ("losers"). We find that the most important factor in determining the success of a phytoplankton type at a front is its functional group (figure 11, with size further modulating the responses within each group (figure 6 and 7). In our model domain, diatoms, dinoflagellates and large carnivorous zooplankton generally benefited most from the altered conditions at fronts, while pico-phytoplankton, coccolithophores and grazers have a more variable response that depends on the environmental context (subpolar/subtropical front and seasonal cycle). Within each group, the abundance of the larger size classes tend to increase more (or decrease less) than the smaller ones.

Figure 11a-h provides a synthesis of our main results, averaged annually, and shows the biomass of phyto- and zooplankton in the two gyres, and for the WBC regions, in the fronts and their backgrounds, as well as the intra-group diversity, the group diversity and the total diversity. Frontal dynamics lead to local variations of biomass and diversity, which differ for each functional group : diatoms, dinoflagellates and carnivorous zooplankton tend to increase and be more diverse at the front while picoplankton and coccolithophores show almost no frontal effect in the annual mean because they have varying seasonal responses.

The enhancement of diatom and meso-zooplankton abundance at fronts found here is supported by a handful of targeted in-situ studies in various parts of the globe, for instance in the Kuroshio Extension Front (which is a WBC similar to our model, Clayton et al., 2014), the Iceland-Faeroe Front in the North Atlantic (Allen et al., 2005), the Almeria-Oran Front in the Mediterranean Sea (Claustre et al., 1994; Thibault et al., 1994; Hernández-Carrasco et al., 2020) and fronts in the California Current Ecosystem (Taylor et al., 2012; Ohman et al., 2012). In contrast, observations of the other groups of plankton

are sparse and often inconclusive and contradictory (Benavides et al., 2021; Clayton et al., 2017). This concurs with results from this model study which suggests some indirect responses such as community shading and shared predation can lead to more complex responses in the less opportunist species.

It is worth mentioning that many in-situ studies recorded no specific community at the front but only a sharp transition from one side to the other (e.g. Krause et al., 2015). It is difficult to assess whether there really is no frontal-enhancement (which could be the case for small transient fronts with no nutrient-supplying vertical circulation, or even intermittently in more stable fronts), whether the sampling resolution was too low to capture these small structures or whether the taxonomic resolution was not sufficient to distinguish well between different phytoplankton groups that may have a different response.

We find that the response of the modelled plankton community is mostly driven by bottom-up processes: the phytoplankton growth rates tend to increase near the surface due to nutrient enrichment, and to decrease at depth because of community shading. This bottom-up effect has been suggested by many studies, both from models and observations (Allen et al., 2005; Li et al., 2012). Although it is difficult in empirical studies to attribute the high biomass observed at fronts to nutrient injection without additional evidence (Lehahn et al., 2007), dedicated incubation experiments at fronts have demonstrated this nutrient-driven increase in the growth rate (e.g. Allen et al., 2005).

Transport and dispersion can also contribute to the increase of phytoplankton biomass and diversity at fronts, as suggested by previous studies (Barton et al., 2010; Lévy et al., 2014b; Clayton et al., 2013). In order to further test whether the shape of the response in phytoplankton community is primarily driven by the supply of nutrients or by the transport of phytoplankton, we conducted an additional model experiment where advection of plankton was turned off (as was done in Lévy et al. (2014b)). The similarity between the two simulations (figure 11) shows that plankton dispersion plays a second order role in shaping the plankton response over fronts compared with nutrient enrichment over those fronts.

In our model, top-down processes at fronts modulate the bottom-up effect without inflecting the tendencies imposed by the variations in the growth rate. However the complexity of the food web can create unexpected indirect effects such as when the same predator targets multiple prey (some of them winning and some losing), in a mechanism known as "apparent competition" or "shared predation". The top-down effects described here may strongly depend on the model formulation (Prowse et al., 2012): the grazing parameterization and especially the structure of the food web, which represents zooplankton as "omnivorous". While some zooplankton are filter-feeders that select their prey based only on size, other species are more selective. In addition, there could be other forms of top-down control at fronts that are not yet integrated in our model (for instance involving the vertical mobility and Diurnal Vertical Migration or the behavior of top-predators). Despite the uncertainties associated with them, these results suggest that top-down controls could play an important ecological role in frontal zones by providing a mechanism capable of decoupling the growth and biomass.

We find that the local effect of fronts depends on the large scale context (figure 11). Even with the same nutrient enrichment, the ultimate response of the plankton community depends on many factors such as the background nutrient concentration, the amount of light available, or the vertical distribution of biomass (surface or subsurface maximum). This sensitivity to the large-scale context suggests that our results might not be representative of all regions of the ocean, or of fronts with different characteristics (for instance shallower, or not as persistent).

Finally, we find that plankton diversity is higher at fronts because of the biotic and abiotic processes mentioned above (figure 11). Total phytoplankton diversity (figure 10h) is larger at fronts due to both larger group diversity (figure 11g) and larger intra-group diversity, specifically for diatoms, dinoflagellates and coccolithophores (figure 11b-c-d). It is notable that the

increase in diversity is much more pronounced for the subtropical front than the subpolar front, in agreement with the well-established bell-shaped Productivity/Diversity Relationship (e.g. Vallina et al., 2014), which shows that the processes driving the effects of the fronts on a scale of a few kilometers are essentially the same as the processes responsible for the large scale biogeochemical/ecological provinces in the ocean (more nutrients lead to a more diverse phytoplankton community, up to a point). This suggests that if a front were located in a region rich enough in nutrients (on the descending right side of the PDR distribution), the increased productivity could be associated with a lower diversity (i.e. a frontal bloom dominated by diatoms); this hypothesis could be tested by modelling or in-situ studies targeting such regions.

Conclusion

Our results have shown that the planktonic ecosystem response to enhanced nutrient supply at fronts is more complex than the pure bottom-up response because of ecological interactions such as community shading and shared predation. At present, modelling is the only practical method to examine the mechanisms leading to the modifications of plankton communities by fronts. In order to test these hypotheses in the real ocean, our study suggests that we need to expand spatial and taxonomic resolution. In particular, we need adequate horizontal resolution in order not to miss the specific community that occurs on the front itself and not only on either side; we need sufficient vertical coverage in order to observe the variation in the vertical structure inside and outside fronts; and finally, we need more taxonomic resolution than just Chlorophyll and size-fractionated Chlorophyll in order to capture the full community shifts. However, a complete mechanistic understanding would require high-resolution physiological rates within and outside of fronts as well as sufficient functional resolution within the zooplankton. Such observations would help use understand the feedbacks between the physical dynamics of the fronts and the trophic interactions within the plankton community.

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Competing interests

The authors declare no competing interests.

Data Archiving

The ecosystem model code used in this study is available through <http://www.gitlab.com/jahn/gud>. Note that a more up-to-date version of the ecosystem model used here is available at <http://www.github.com/darwinproject/darwin/>. The data and scripts are available upon request.

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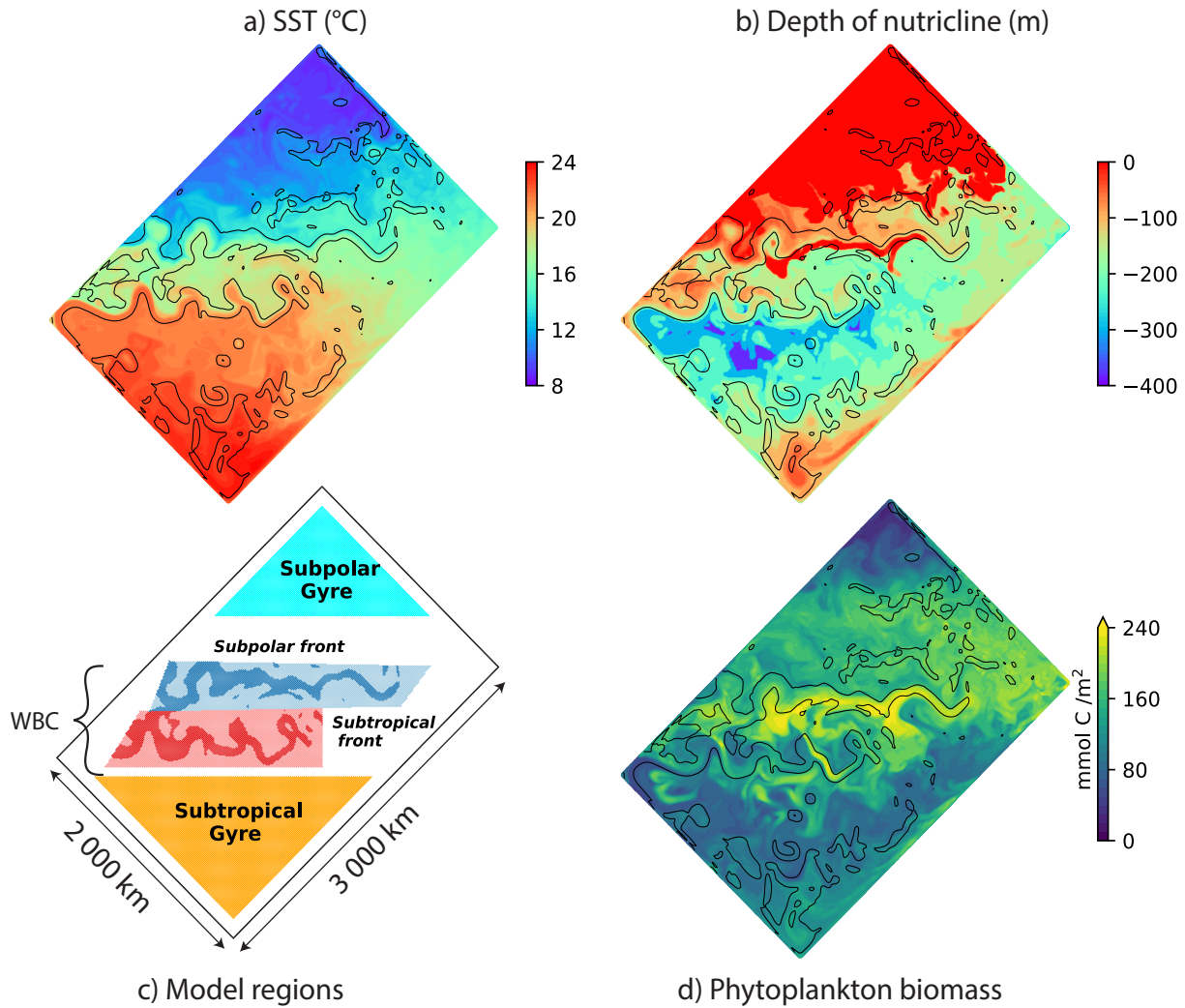


Figure 1: Model configuration. a) SST, b) nutricline depth (defined as the 4 mmolN/m³ isoline), c) division of the model domain into the sub regions used for analysis: subpolar gyre (turquoise triangle), subtropical gyre (orange triangle), and Western Boundary Current region consisting of the subpolar front (dark blue) and subtropical front (dark red) and their respective backgrounds (light blue and light red) d) total phytoplankton biomass (integrated over 0-186m). All fields are shown at day=40 (early february). Note that the positions of the triangles and rectangles delimiting the regions of two gyres and WBC are fixed in time, but the locations of the fronts vary in time as the fronts meander.

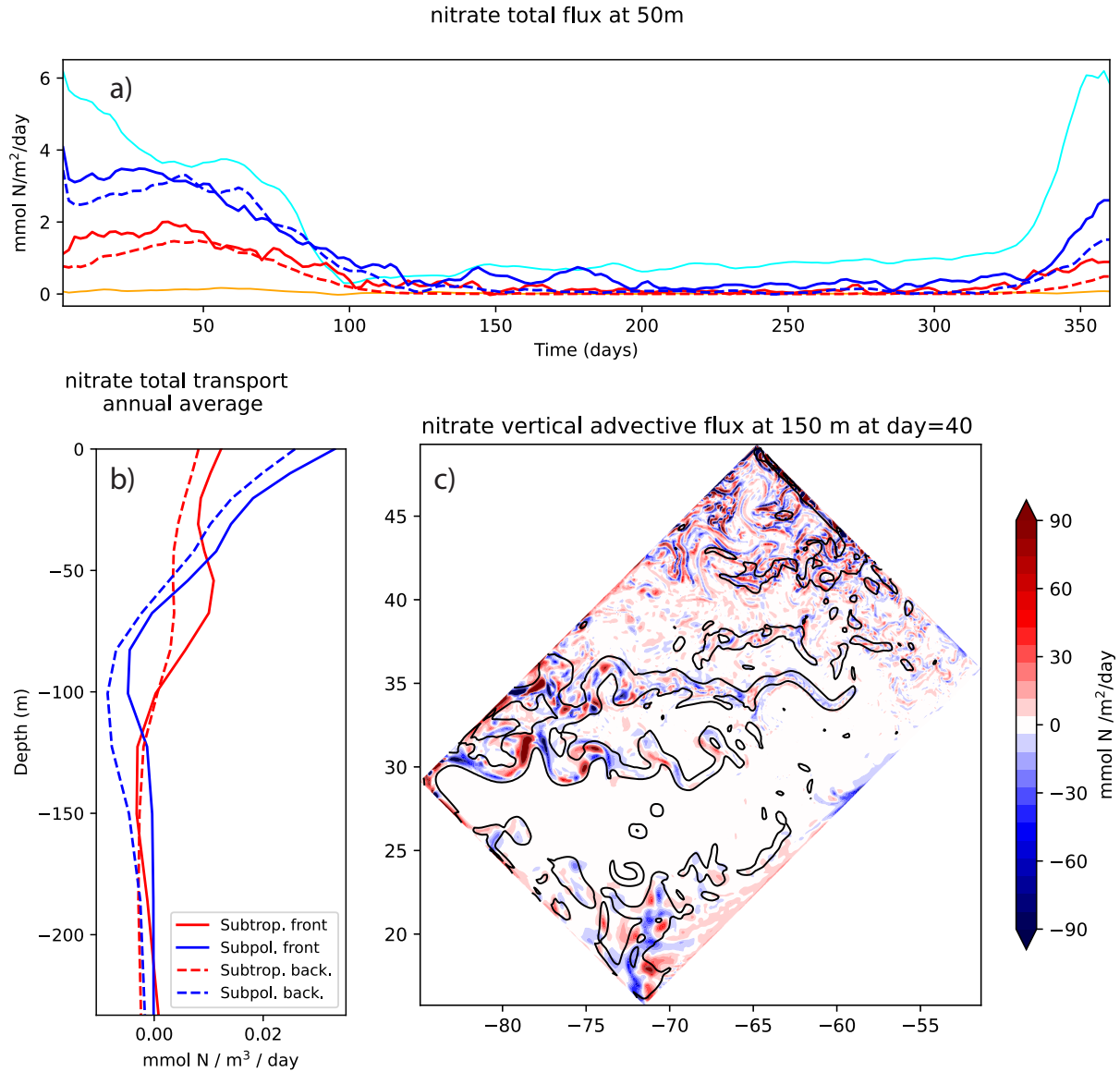


Figure 2: Nitrate supply. a) Seasonal cycle of the nitrate flux at 50 m depth in the gyres and the fronts and their backgrounds. b) Vertical profile of the total nitrate transport, annually averaged. c) Snapshot map on day 40 (early february) of the vertical advective flux at 150m.

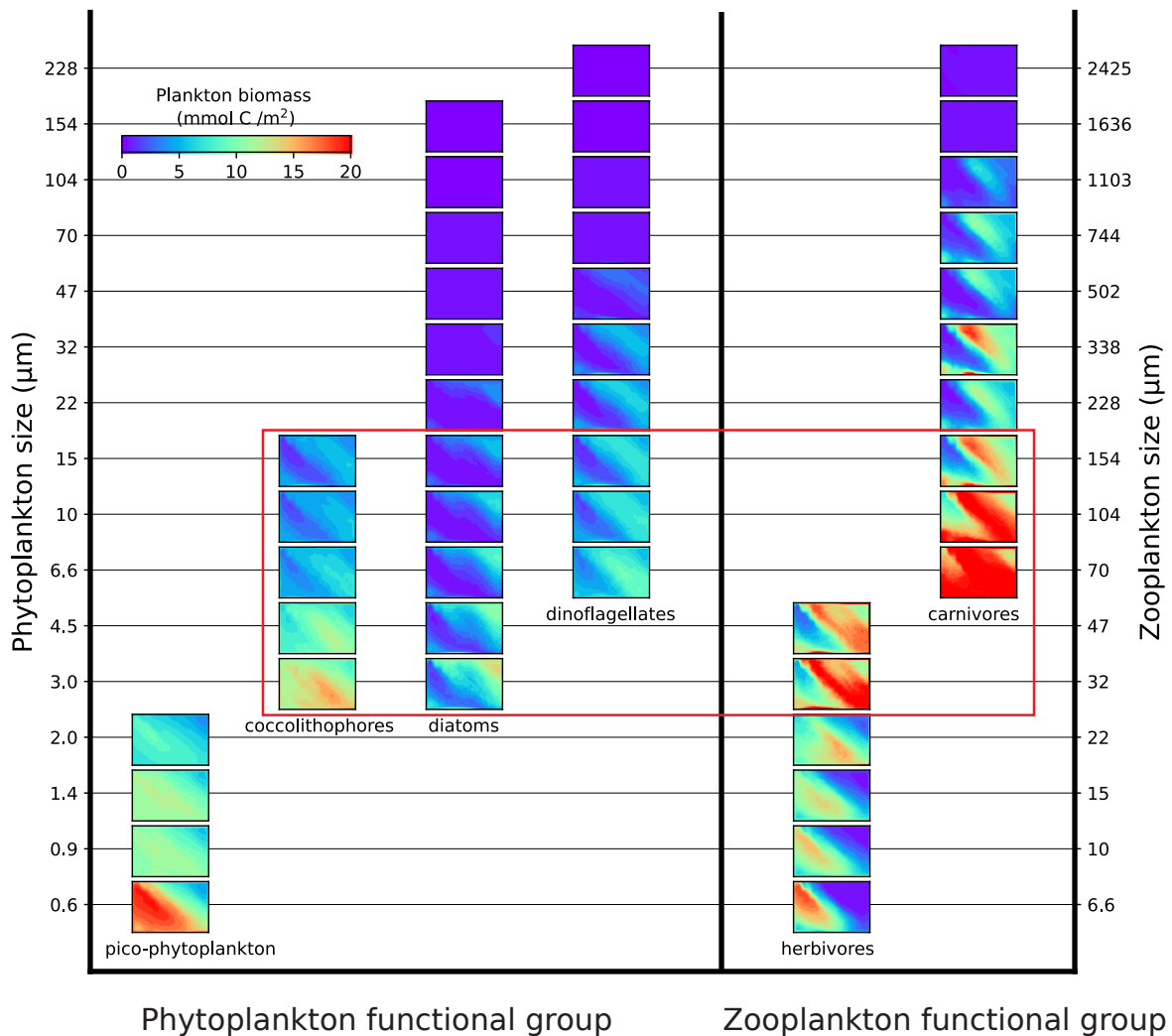


Figure 3: DARWIN ecosystem model with phytoplankton and zooplankton types sorted by size (y-axis, Equivalent Spherical Diameter) and functional group (x-axis). Each panel shows the annual mean biomass of each individual type (integrated from 0-186m) over the model domain, rotated clockwise to save space. Small plankton dominate in the subtropical gyre (bottom left corner of each panel) while larger plankton dominate in the subpolar gyre (upper right corner). The scale of the y-axis differs for phytoplankton and zooplankton such that zooplankton are aligned horizontally with the phytoplankton sizes on which they primarily graze. This representation allows visualization of shared predation (illustrated for cocco., diatoms and dino. by the red rectangle): phytoplankton types of similar size but belonging to different functional groups share the same main predator, which is the zooplankton type on the same horizontal level.

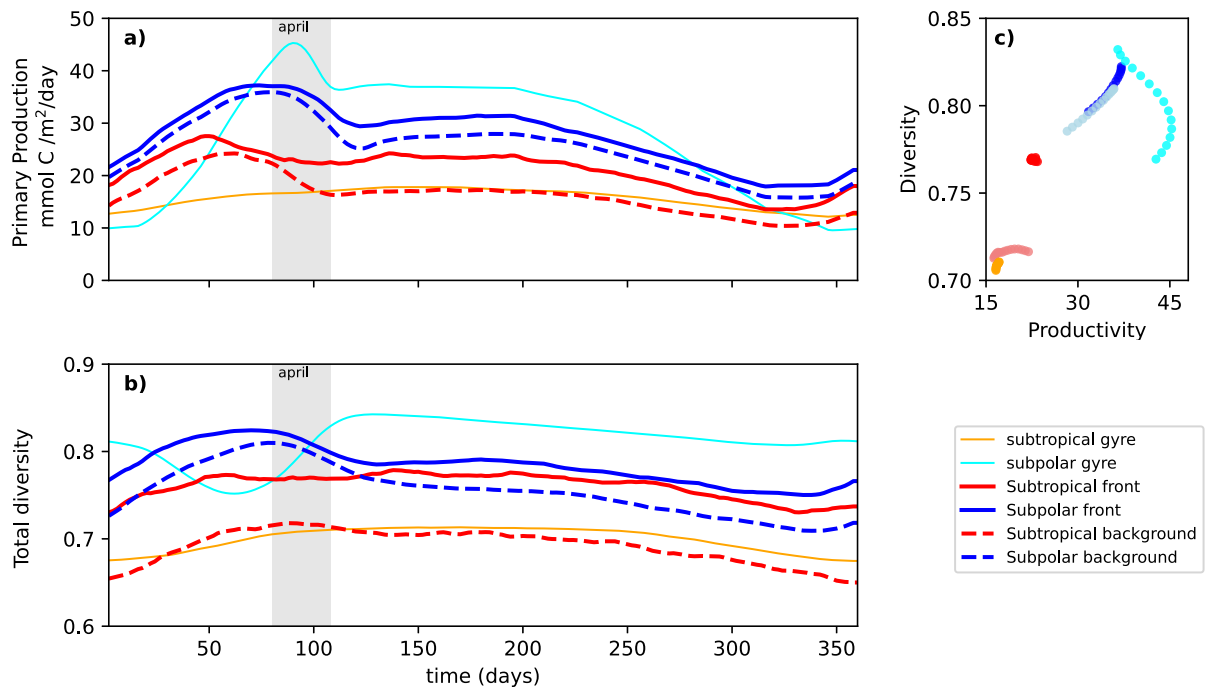


Figure 4: a) Primary production and b) total phytoplankton diversity (Shannon index) annual climatology, averaged within each model region shown in Figure 1c. c) Productivity-Diversity Relationship (i.e. phase diagram of a vs b in April, see shaded rectangle in a and b). Climatologies are computed over five years of simulation. Productivity and diversity show a large scale gradient from south to north. The two fronts are both more productive and more diverse than their respective backgrounds.

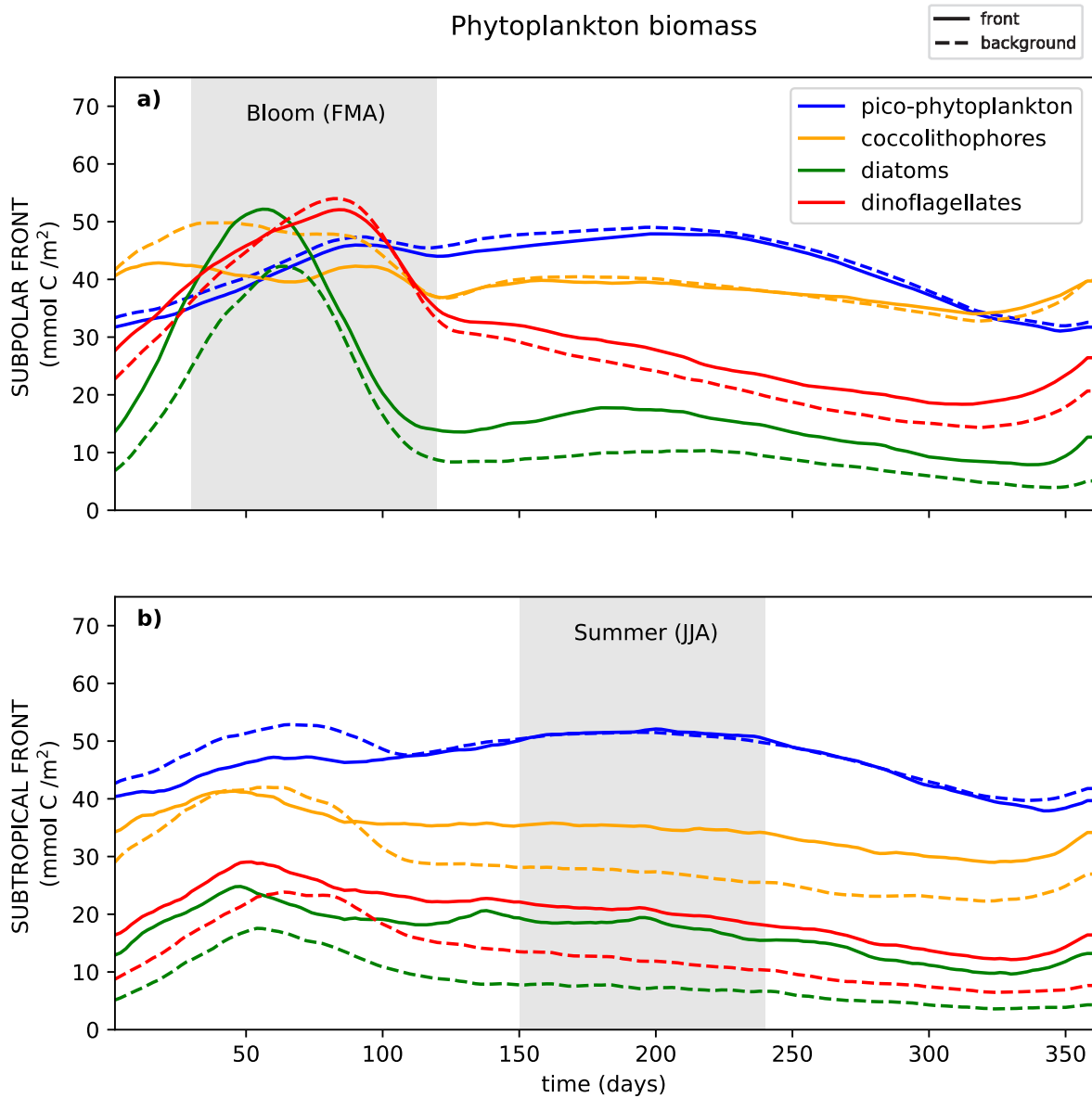


Figure 5: Phytoplankton group biomass annual climatology over the subpolar (a) and subtropical (b) fronts (solid lines) and their respective backgrounds (dashed lines), vertically integrated (0-186m). Climatologies are computed over five years of simulation. The bloom and summer seasons are shaded in grey. Diatoms (green) and dinoflagellates (red) are consistently more abundant over fronts compared to their backgrounds, pico-phytoplankton (blue) are generally less abundant and coccolithophores (orange) can be more or less abundant at fronts depending on the front and the season.

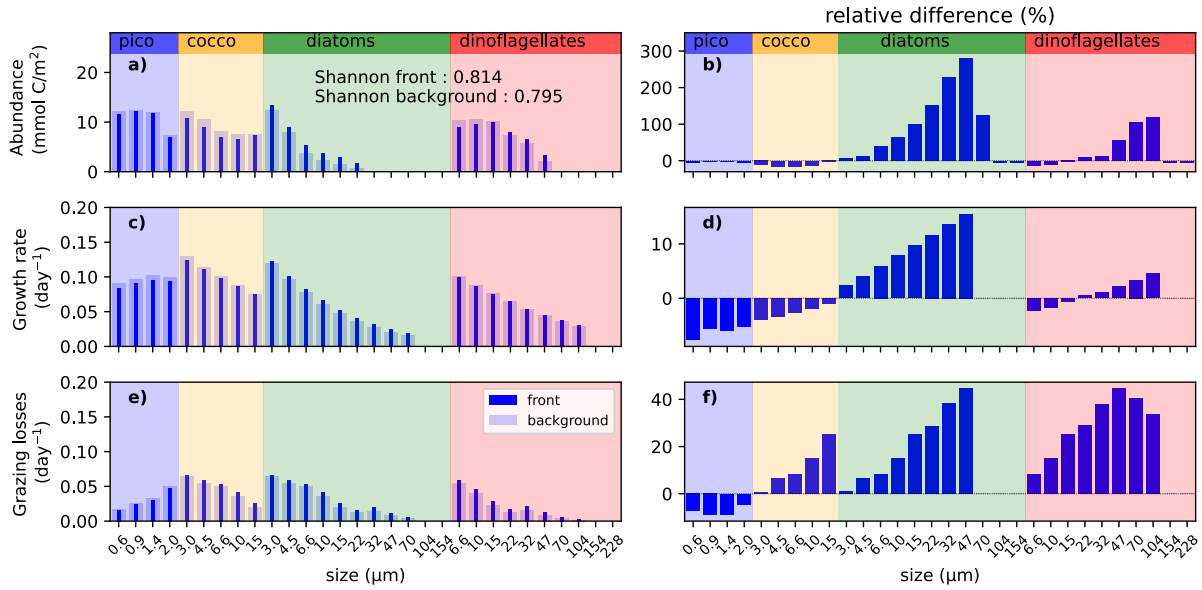


Figure 7: Change in community structure and rates at subpolar front during the bloom. a) Phytoplankton biomass, c) growth rate and e) grazing losses, integrated from 0-186m. Values at the fronts are shown thin bars, and in the backgrounds with thick light bars. Panels on the right (b-d-f) show relative differences between front and background (positive values mean that the variable is higher at the front). Some phytoplankton types and growth rates are enhanced at fronts (winners), others are decreased (losers).

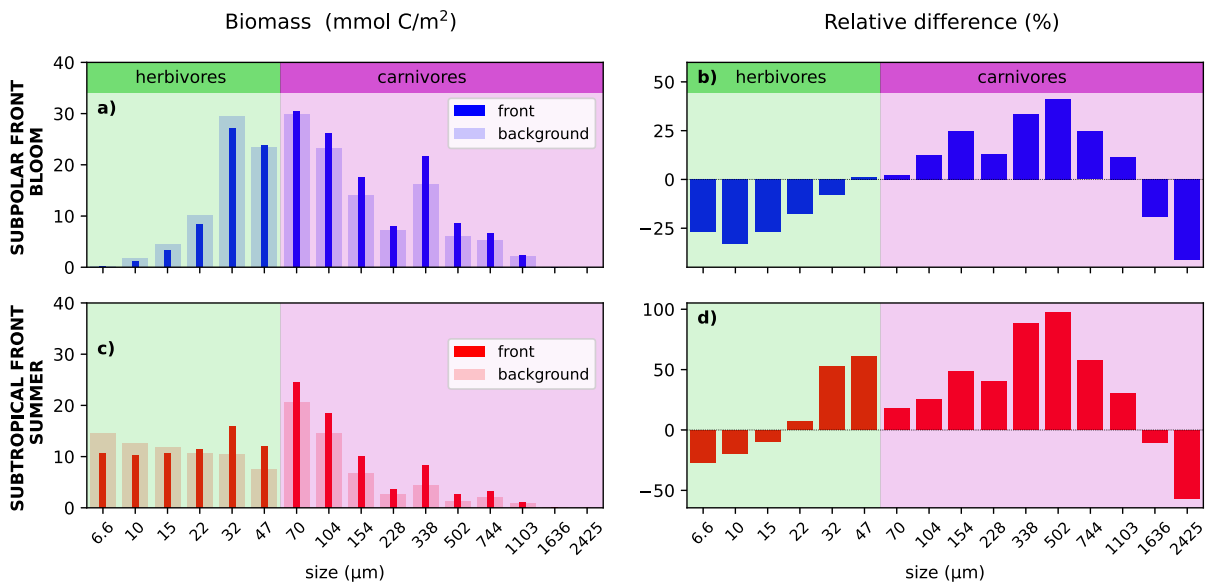


Figure 8: same as Figure 5 and 6 for zooplankton biomass, illustrating the presence of winners (typically small herbivores) and losers (large herbivores and carnivores).

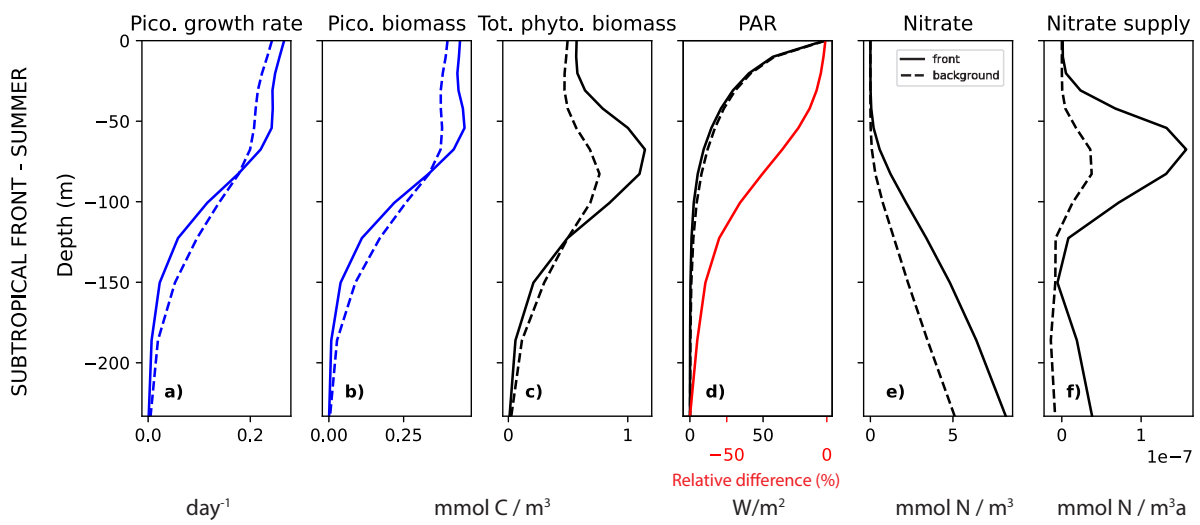


Figure 9: Illustration of community shading. Mean vertical profiles of a) pico-phytoplankton growth rate, b) pico. biomass, c) total phytoplankton biomass, d) Photosynthetically Available Radiation e) nitrate concentration, f) total nitrate supply. In each panel the solid lines are the subtropical front and the dashed lines are the background; the red line in panel d) is the relative difference between the two. Increased nitrate at the front causes increased total biomass, decreased PAR penetration, with a negative feedback on picophytoplankton growth rates at subsurface.

SUBPOLAR FRONT

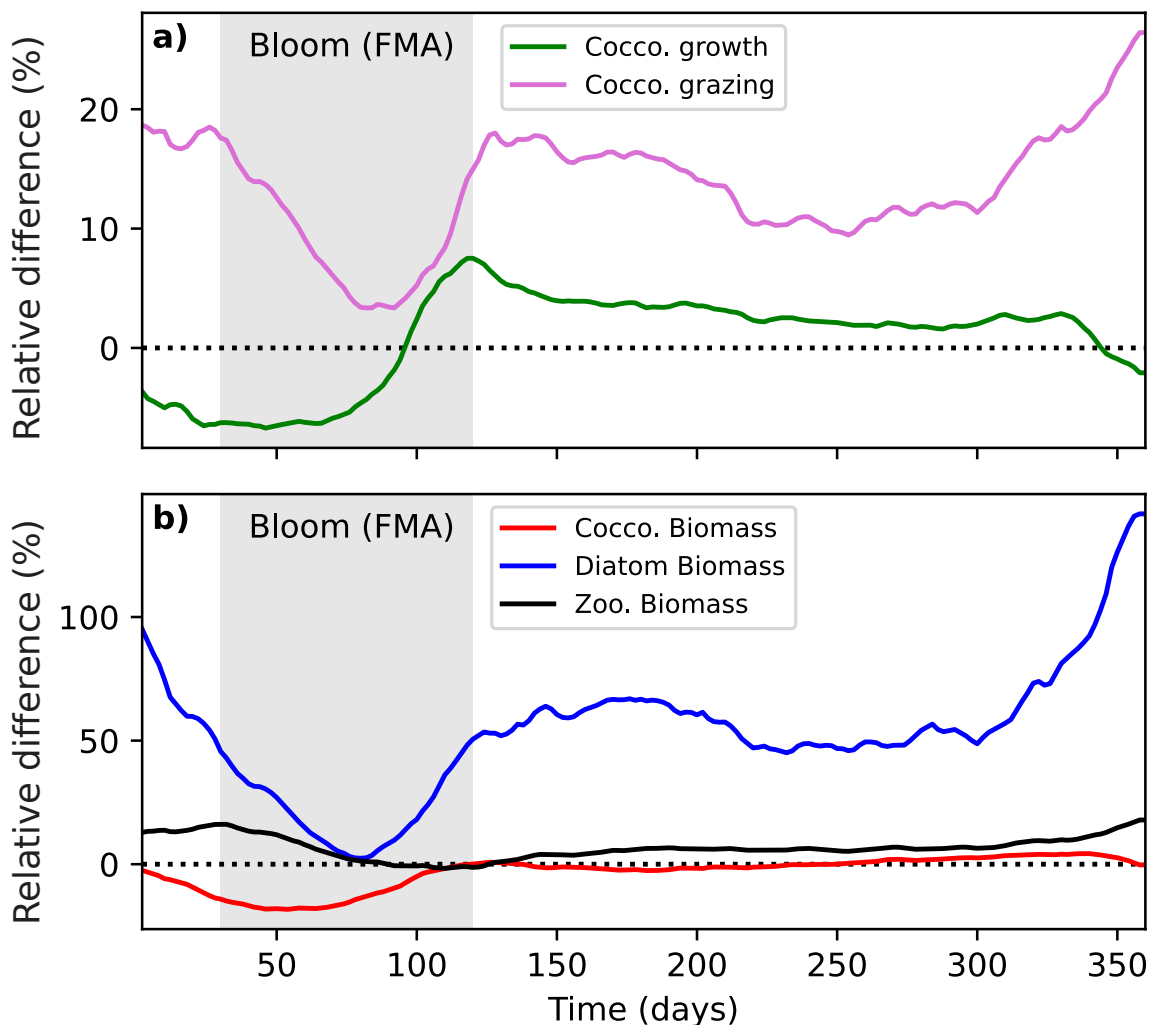


Figure 10: Illustration of shared predation. Annual climatology of the relative difference between the subpolar front and its background for a) the growth rate and grazing losses of the coccolithophores and b) the biomass of cocco., diatoms of the same size classes (3-15 μ m) and their shared predators, the zooplankton sized 32-154 μ m. Positive values mean that the variable is higher at the front. The grazing losses of the cocco. are decoupled from the cocco. biomass and instead follow the diatom biomass through the influence of their shared predator. During the bloom, this leads to a much larger decrease in cocco. biomass (20

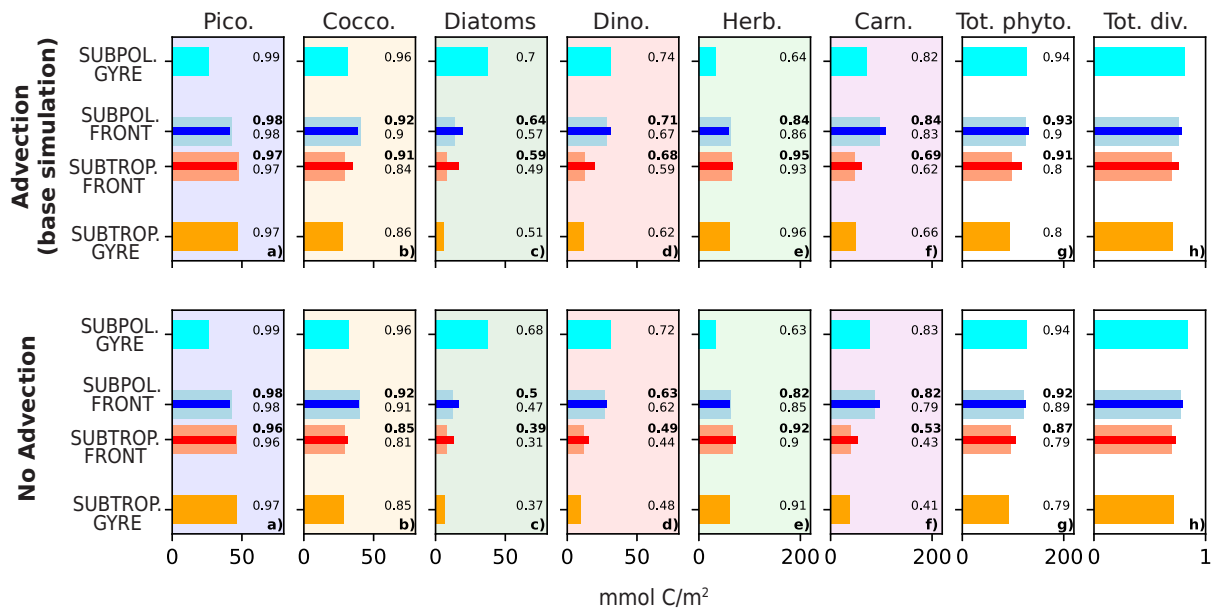
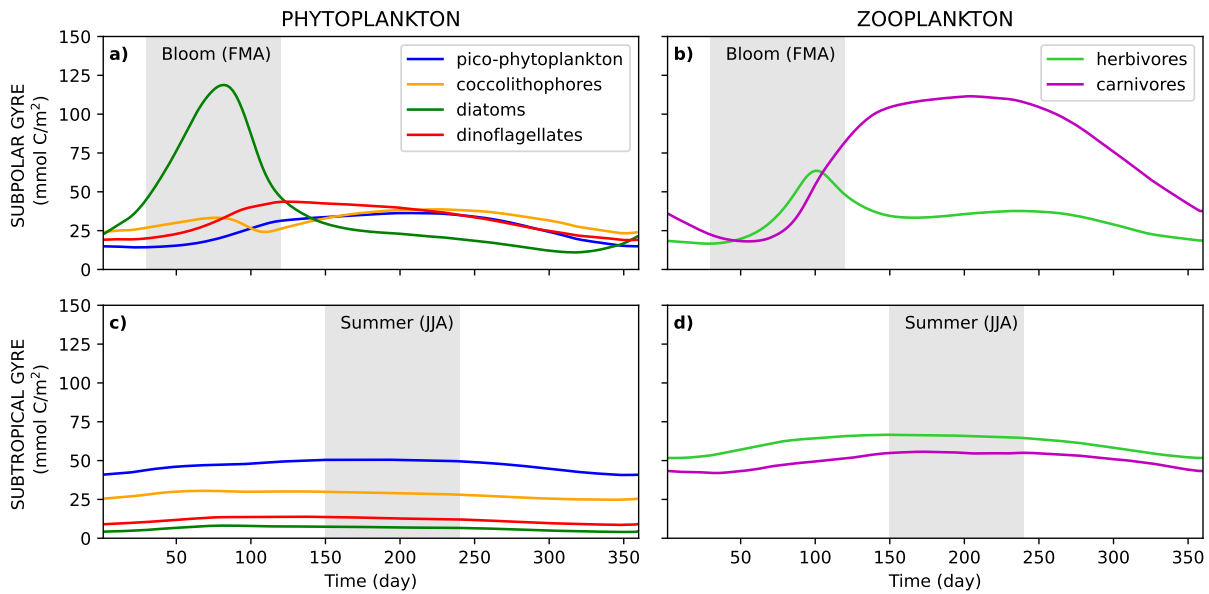
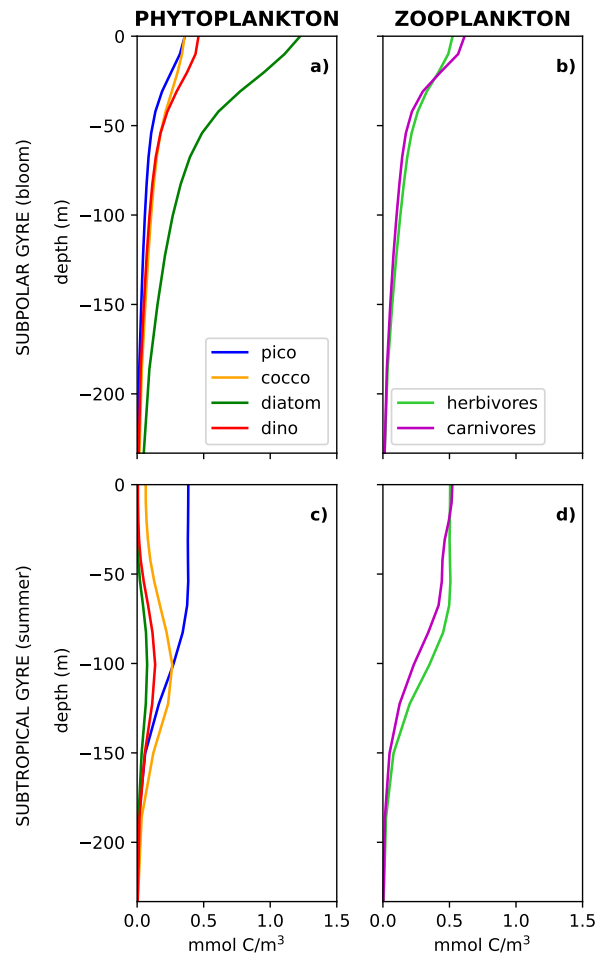


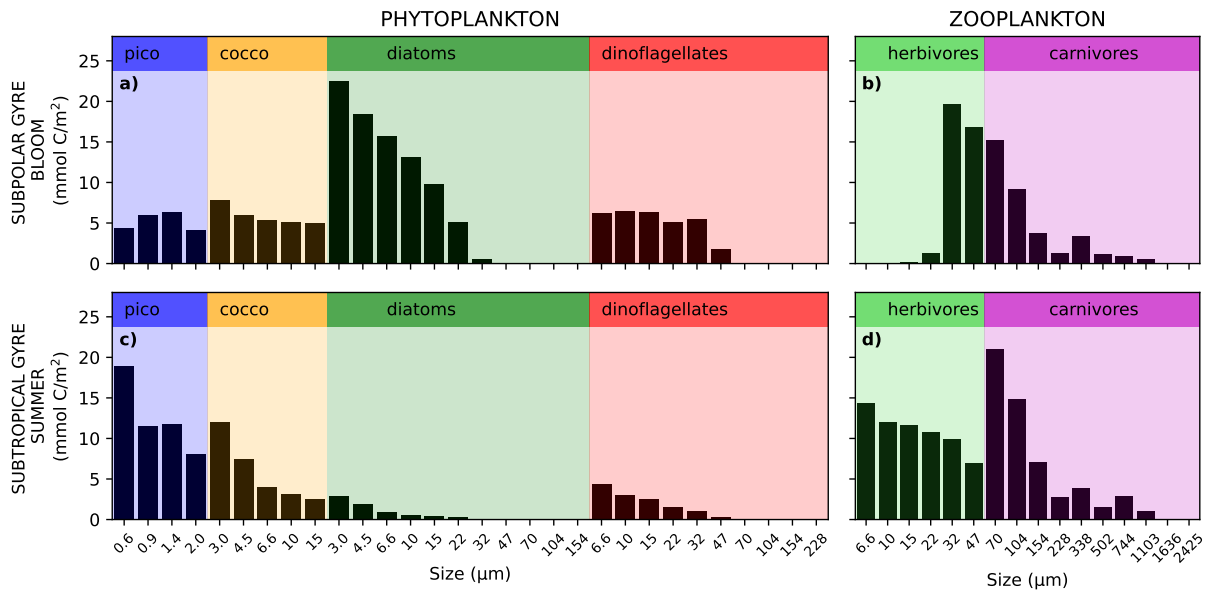
Figure 11: Result synthesis. Annual mean biomass of (a-f) each plankton group, (g) total phytoplankton and (h) total phytoplankton diversity (Shannon index) integrated from 0-186m, averaged over the model regions shown in Figure 1c, with same color code. Values at the fronts are shown with thin bars, and in the backgrounds with thick light bars. Numbers next to each bar show intra-group diversity (a-f) and group diversity (g); bold values are for the fronts. Fronts have a notable local effect while falling within the large scale gradient associated with the two gyres. Diatoms, dinoflagellates and carnivorous zooplankton are winners: they consistently increase at fronts. Pico-phytoplankton, coccolithophores and herbivorous zooplankton have a more complex response and can be winners or losers depending on environmental conditions. Fronts promote a more diverse community through an increase in both group diversity and intra-group diversity. The second row (panels i to p) shows the same diagnostics for a model simulation without plankton dispersion.



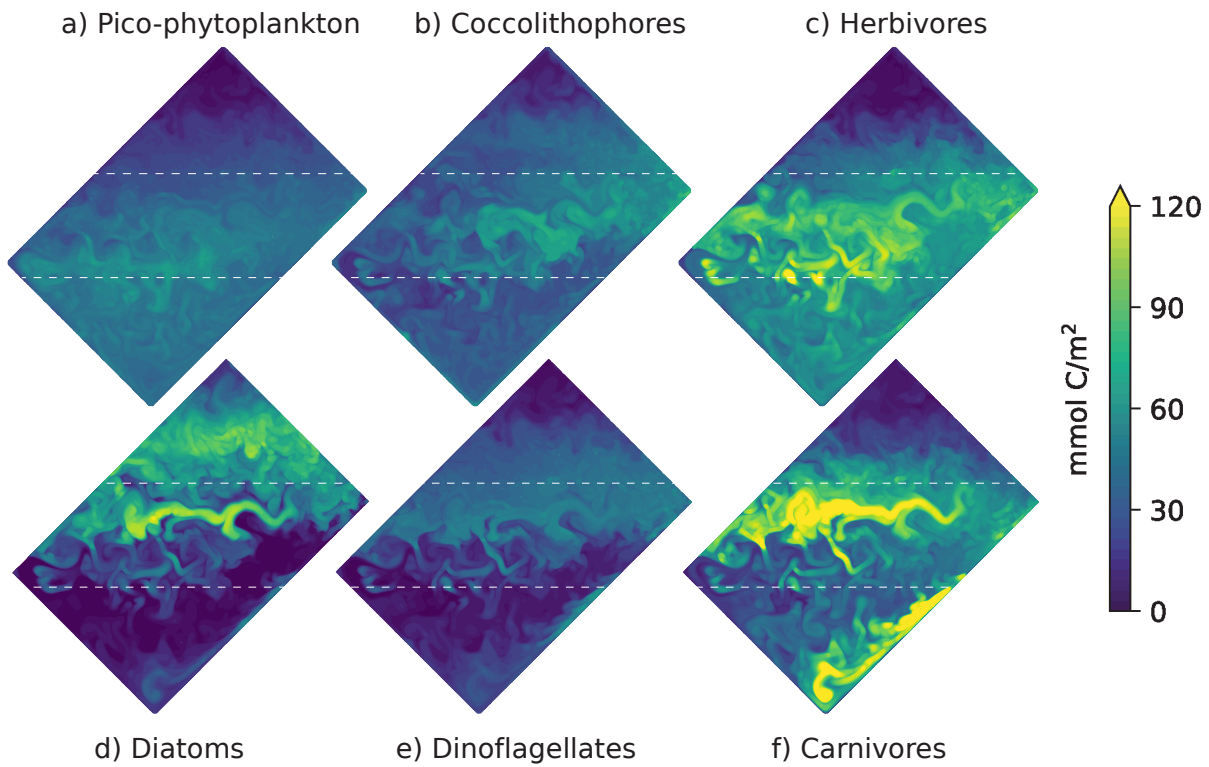
Supplementary Figure S1: Large scale context. Phytoplankton and zooplankton group biomass annual climatology over the subpolar and subtropical gyres, vertically integrated (0-186m). The subpolar gyre is characterised by a strong seasonality with a diatom-dominated bloom and an otherwise very even phytoplankton community; the higher trophic levels develop later in the year (late spring for herbivores and summer for carnivores). The subtropical gyre has no seasonality and is dominated by the smaller phyto- and zooplankton.



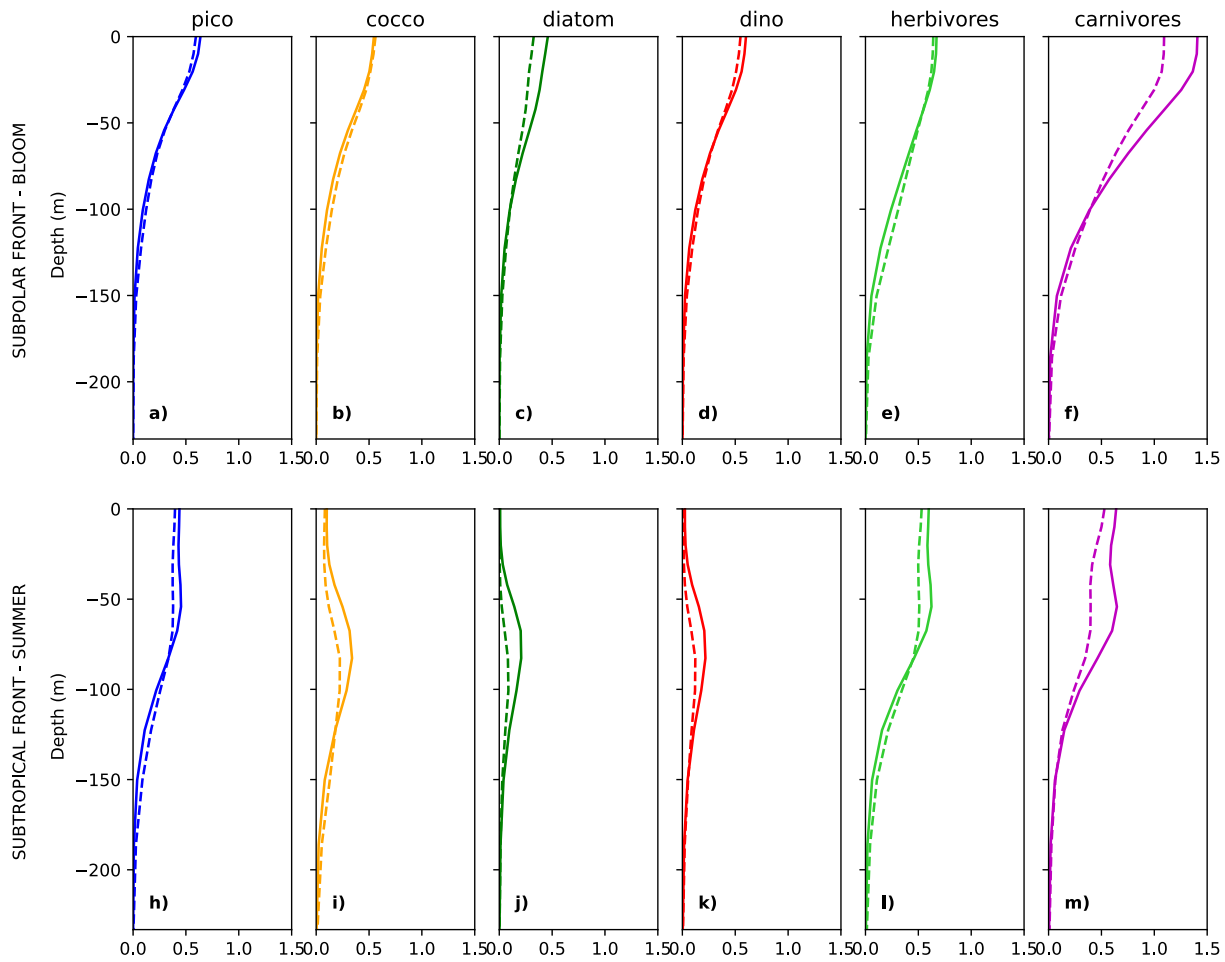
Supplementary Figure S2: Large scale context. Vertical distribution of phytoplankton and zooplankton in the subpolar gyre during the spring bloom (Feb, Mar, Apr) and in the subtropical gyre during summer (Jun, Jul, Aug). Plankton profiles generally show a maximum at the surface decreasing with depth, except in the subtropical gyre in summer where cocco., diatoms and dino. show a subsurface maximum around 100m.



Supplementary Figure S3: Large scale context. Plankton community structure in the subpolar gyre spring bloom (Feb, Mar, Apr) and the subtropical gyre summer (Jun, Jul, Aug). The boundaries of the two gyres correspond to the triangles in Figure 1c. Vertical black bars show the vertically integrated biomass (0-186m) of each type. Types are sorted by functional groups (colored rectangles), and within each group by size (increasing size classes from left to right). Within each group, smaller types are generally more abundant than larger ones.



Supplementary Figure S4: Biomass distribution of the six plankton groups, at day=40 (early february), vertically integrated over 0-186m. Each group shows a different biomass anomaly over the subpolar front compared to values next to the front: positive for diatoms, dinoflagellates, herbivores and carnivores, and negative for pico-phytoplankton and coccolithophores.



Supplementary Figure S5: Mean vertical profiles of each plankton group biomass, at fronts (solid lines) and in their backgrounds (dashed lines), for the subpolar front during the bloom (top panels) and for the subtropical front during summer (bottom panels). The effect of fronts on plankton abundance varies with depth : abundances tend to be increased near the surface and decreased deeper in the water column. The vertically-integrated effect of the front differs depending on the balance between the increase close to the surface and the decrease at depth.