Sub-frontal niches of plankton communities driven by transport and trophic interactions at ocean fronts

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Major revisions for manuscript EGUSPHERE-2023-471, submitted to Biogeosciences (15 Mar 2023)

1. List of significant changes to the manuscript :

- reference to the supplementary text added in section 2.2
- modification of section 2.5, renamed “Temporal evolution of the fronts”, to clarify the use of satellite data during and after the cruises
- modification of the discussion to address the use of the frontal age and of statistical models
- modification of the conclusion, to develop the potential of the Lagrangian approach
- The various issues with the figures were fixed and the legibility of the axes labels was improved as much as possible.
- Bibliographical references were added as suggested, and all minor editorial issues were fixed

2. Point by point response to reviewers

2.1. Referee 1

The manuscript of Mangolte et al. constitutes an interesting analysis on plankton communities dynamics in response to a frontal region in the California Current. As explain by the authors, although fronts are well known to be ecological hotspots with high plankton diversity due to the injection of nutrients into the euphotic layer, the mechanisms between nutrient supply and higher trophic levels is still poorly understood. Furthermore, the impacts of the fronts on plankton distribution and on the behavior of the plankton communities have been scarcely studied in situ. Since several years, researchers have fully realized the significance of this problem, but limited by the observation means (especially biological parameters), the current understanding is very limited.

Based on these backgrounds, I think this work is a very good attempt.

In this study, *in situ* datasets were achieved during several cruises lead in the California Current between 2008 and 2017 with a similar sampling methodology consisting to perform CTD stations spaced at high resolution along transects across frontal structures. These fronts have been identified thanks to satellite observations and the use of a MVP. Plankton samples were analyzed post cruises with 3 methods : flow cytometry, HPLC and ZooScan. This methodology is clear. The identification of frontal structures is well supported by supplementary information in Appendix.

The authors used these large datasets to study the response of plankton communities (in term of biomass and taxonomy) to frontal dynamics. Generally, the results are fairly well presented and are interpreted appropriately in the discussion.

We thank the reviewer for their kind remarks and their constructive criticism, which will help improve the manuscript.

In the conclusion, the authors are well aware of the limitations of their method and in particular they highlighted the importance of leading Lagrangian cruises with instruments able to sample at high

temporal and spatial resolution the physical and biological variables. This part could be improved. Indeed, it lacks a bit of connection with the context and the scientific questions developed in the introduction.

We have rephrased the first paragraphs of the conclusion as follows, to better connect the perspectives (specifically the use of a Lagrangian perspective) to the general questions raised in the introduction.

"In this study, we describe the taxonomic structure and fine scale spatial organization of plankton communities across ten fronts in the California Current Ecosystem upwelling region. The hypothesis of frontal nutrient injections explains the predominance of diatoms at fronts, but needs to be supplemented by other processes (i.e., biotic interactions and transport) to explain the differential responses of the other plankton groups and the cross-frontal patchiness. The high horizontal and taxonomic resolution of our dataset allowed us to gain a more complete view of fronts as complex structures driven by the coupling of physical and biological processes. The understanding of the role of fronts on marine ecosystems by empirical means can be further improved in two ways. Firstly, frontal communities should be sampled at appropriate horizontal, vertical, taxonomic and temporal resolution. While many instruments can achieve excellent performance at one scale, the challenge lies in simultaneously increasing all the dimensions of resolution, which can be achieved by strategically combining multiple shipboard and autonomous instruments. Secondly, the quantification of the role of the key processes at fronts requires the adoption of a Lagrangian perspective to follow the evolution of the community as it is advected by the currents, which should include in-situ biological rates (growth and grazing) along the drifter trajectory combined with high resolution altimetry measurements to characterize the regional circulation.

The elucidation of the structure of frontal ecosystems and of the processes driving them should then allow the development of parametrizations that will permit fronts to be included in global climate models and fishery management models in order to ultimately evaluate their contributions to the cycling of matter and energy in the ocean."

The appendix section is very supplied with figures. Although these results are interesting, the authors should consider if all of them are really relevant. Indeed, in my opinion the total number of additional figures is excessive.

We acknowledge that all the supplementary figures might not be of interest to every reader, but prefer to keep a published record of as much information as possible.

Finally, for me the grammar is ok, but I am not a native English speaker, that is why I let the English editing service check.

I recommend the manuscript for minor revisions prior to publication in Biogeosciences.

Specific comments

We thank the reviewer for taking the time to give such detailed feedback, it is greatly appreciated !

1. Introduction

After a concise presentation of the context of this study (i.e., fronts and their potential impact on plankton), the authors have well exposed their hypothesis based on the work of Lévy et al., 2018 as well as their scientific questions. Then, the authors provided a short description of the region studied and introduced the CCE-LTER program and cruises during which the data were acquired.

However, the end of the Introduction (Ln 52-63) is a little confusing, with a lot of information. The information is relevant, although the more technical details should be indicated in the methodology. I think this last paragraph should be simplified. Based on the objectives that the authors have previously defined, they can just briefly explain how they would answer them.

We agree with the reviewer that the last paragraph of the introduction is very dense and contains information that is repeated and developed in the method and results sections, but we believe it is necessary to give an overview of the dataset because these technical details constrain and justify our approach.

Ln 12 : I understand that it is an introductory sentence for open your Introduction, but can you provide some references. We propose to add the following references : Hoskins BJ (1982), The mathematical theory of frontogenesis, Annu.Rev. Fluid Mech., 14, 31–151, doi: 10.1146/annurev.fl.14.010182.001023; Pollard R, Regier L (1992) Vorticity and vertical circulation at an ocean front. J Phys Oceanogr 22:609–625.; Belkin, I. M. and Helber, R. W.: Physical oceanography of fronts: An editorial, Deep. Res. Part II Top. Stud. Oceanogr., 119, 1–2, 2015.

Ln 43 : Do not write in italics “California Current Ecosystem”. corrected

Ln 48 : Define the acronym SSH as Sea Surface Height. done

Ln 52 : Here there is a change of topic, please, start a new paragraph. done

Ln 52-53 : “The empirical measurements [...]” : This sentence should be in the methodology section.

Ln 54 : Move “(with a spacing of 1 to 5 km between stations)” in the methodology section (Ln 68).

Ln 55-61 : “We identified [...], We first investigate [...], We find [...], We examine [...]” : I think here the authors provided too much detail which should be in the Results section.

Ln 61-63 : “We find that [...]” : This sentence should be in the Results section.

Ln 52-63 : The comments on the last paragraph are addressed above.

2. Methods

My main remark concerns the section 2.2. Indeed, in this section the authors explained how the fronts have been identified (supported by supplementary information in Appendix). I understand why the authors have organized their manuscript like this. However, they should add a sentence at the beginning of this part to clearly indicate that all the characteristics of these frontal structures are

described in the Appendix. (I think it is difficult for the reader to well understand this part without read before the Appendix).

We thank the reviewer for noticing this oversight. We have added the following sentence at the end of the first paragraph of section 2.2 :

"[...] This led to a total of ten segments, each containing one front (Fig. 2). In this section, we describe the common procedure we applied to identify these ten fronts; their individual characteristics and their temporal evolution (up to a few months before and after each transect, reconstructed with satellite data as described in section 2.5) are presented in detail in the supplementary text."

Furthermore, this section 2.2 is closely related to the section 2.5 named 'regional context' concerning the satellite products used in addition to the MVP data to identify these fronts. That is why, I suggest to move this section 'regional context' just after the section 2.2.

We have clarified the different uses of satellite data in sections 2.2 (positioning of the transects at sea, during the cruises) and in section 2.5 (analysis of the temporal evolution of the fronts in the months before and after the cruises) and renamed the latter "Temporal evolution of the fronts".

Ln 65 : Remove "California Current Ecosystem Long Term Ecological Research". You have previously defined the acronym CCE-LTER in the Introduction (Ln 43). done

Ln 67-68 : "[...] stations regularly spaced at high resolution" : Provide here the resolution. done

Ln 119 : Add a reference to the section 'regional context*' after 'SSH'. *section 2.5 in the manuscript or 2.3 in the revised manuscript (if you follow my previous suggestion). As explained above, the satellite data of section 2.5 are not relevant to section 2.2.

Ln 130-134 : "The distribution of density [...]" : This sentence should be in the Results section. We believe that including this element in the method section helps to understand the rationale behind the procedure we chose to use to define the fronts.

Ln 135 : Do not start a new paragraph. corrected

Ln 175 : Remove "Sea Surface Temperature" and "Sea Surface Height". You have previously defined these acronyms. removed

Ln 182 : Add references after FSLE. We have added the following references : d'Ovidio, Francesco, et al. "Mixing structures in the Mediterranean Sea from finite‐size Lyapunov exponents." Geophysical Research Letters 31.17 (2004).; Fifani, Gina, et al. "Drifting speed of Lagrangian fronts and oil spill dispersal at the ocean surface." *Remote Sensing* 13.22 (2021): 4499.

3. Results

Ln 190 : Replace “then” with “secondly”. done

Ln 195-196 : “In particular front C3 [...]” : I understand that you referred here to Fig. 5. But please indicate that for help the reader. It is also necessary for all this section (Ln 198-205). done
Ln 207-221 : Here also please indicate at which figures you referred for help the reader.done

Ln 231-233 : Please keep the same name (calanoids or copepods) in the text as in Fig. 6. (See also my comments about Fig. 6 in the Technical corrections). Thank you for this remark, we will make the correction.

Ln 236 : “wide physical fronts (such as E1 and F3)” and “narrow fronts (such as A and C2)”. Can you provide an order of magnitude to highlight why fronts E1 and F3 are wider than fronts A and C2 ? done

4. Discussion

This discussion contains rich information and the organization in scientific questions is very appreciable.

Ln 279 : “This dataset” refers to our dataset or the dataset used in the works that you cited previously ? Please clarify this sentence. We changed the sentence to “The dataset used in the present study provides snapshots of the planktonic ecosystem during each overnight transect but cannot capture their time evolution over several days.”

Ln 292 : Concerning the use of the SPASSO software during cruises, you can also add the following references : Rousselet et al. (2018) (https://doi.org/10.5194/bg-15-2411-2018) and Barrillon et al. (2023) (https://doi.org/10.5194/bg-20-141-2023). Thank you, we have included these references.

Ln 293 : Add references We have added the following references : Barth J. A., Pierce, S. D., & Smith, R. L. (2000). A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System [Article]. Deep-Sea Research Part Ii-Topical Studies in Oceanography, 47(5-6), 783-810. https://doi.org/10.1016/s0967-0645(99)00127-7; Kosro P. M., & Huyer, A. (1986). CTD and velocity surveys of seaward jets off northern California, July 1981 and 1982, JULY 1981 AND 1982 [Article]. Journal of Geophysical Research: Oceans, 91(C6), 7680-7690. https://doi.org/10.1029/JC091iC06p07680; Zaba K. D., Franks, P. J. S., & Ohman, M. D. (2021). The California Undercurrent as a Source of Upwelled Waters in a Coastal Filament [Article]. Journal of Geophysical Research: Oceans, 126(2), 13, Article e2020JC016602. https://doi.org/10.1029/2020jc016602

Ln 317 : Add references We have added the following references : Aleksandra M. Lewandowska, Maren Striebel, Ulrike Feudel, Helmut Hillebrand, Ulrich Sommer, The importance of phytoplankton trait variability in spring bloom formation, *ICES Journal of Marine Science*, Volume 72, Issue 6, July/August 2015, Pages 1908–1915, https://doi.org/10.1093/icesjms/fsv059; Eiane, Ketil, and Mark D. Ohman. "Stage-specific mortality of Calanus finmarchicus, Pseudocalanus elongatus and Oithona similis on Fladen Ground, North Sea, during a spring bloom." *Marine Ecology Progress Series* 268

(2004): 183-193.; Bouquet, Jean-Marie, et al. "Increased fitness of a key appendicularian zooplankton species under warmer, acidified seawater conditions." *PLoS One* 13.1 (2018): e0190625.; Kotori, Moriyuki. "Life cycle and growth rate of the chaetognath Parasagitta elegans in the northern North Pacific Ocean." *Plankton Biology and Ecology* 46.2 (1999): 153-158.

5. Conclusion

This part is a little short and can be improved (see my general comments). We addressed this in the general comments above.

Technical corrections

We thank the reviewer for the careful attention with which they read our manuscript. All the suggested corrections below have been made in the revised manuscript.

Ln 28 : remove one “between”

Ln 44 : Write “Table 1” not “Tab. 1” (the word "Table" is never abbreviated and should be capitalized when followed by a number, following the Biogeosciences guidelines).

Ln 67 : Add parenthesis after “(Fig. 1”

Ln 78, 80, 84, 86 : Add a space between “100” and “m”.

Ln 92 : Add a space between “100” and “%”.

Ln 93 : Add a space before “The”.

Ln 129 : Add a space between “50” and “m”.

Ln 263 : Add a space between “100” and “m”.

Ln 268 : Write “Fig. 6” not “fig. 6”. See also Ln 271 and legend of figure 7. (Check I all the manuscript).

Ln 275 : Add a space between “10” and “m”.

Ln 277 : Add a space between “20” and “m”.

Ln 281 : Write in capitals “First”

In all the manuscript for Appendix figures do not write “sup. Fig Ax” or “Sup. Fig. Ax” just “Fig. Ax”.

In all the manuscript, units should be written exponentially (e.g. m s^{-1} not m/s) following the Biogeosciences guidelines. (See Ln 93, 105, 294 in the text and check also the units in the figures).

Please, consider changing the written of the coordinates in your maps, with a degree sign and a space when naming the direction (e.g. 36 ° N, 120 ° W), following the Biogeosciences guidelines.

Check the units on the legend of your figures. There are a lot of plots were units are missed.

There are some figures (for instance Fig. 3, 4, 5, A5, A11, A12, A13) where the typography is very small. I understand that sometime you have constraints for making figures, but where it is possible please increase the size of typography for help the reader. We have improved the figures as much as possible to make them more legible. Regarding fig 04, given the space constraints, there is a tradeoff between the size of the plots themselves and the legibility of the labels, and we chose to maximize the plot size since visualizing the patterns across the fronts is more relevant to understanding our results than knowing the exact values.

Figure 1 (all issues below have been addressed)

Add “Latitude” and “Longitude” on the axis.

On the SST panel, the red crosses are not very visible on this colormap. Please, consider changing the color of the crosses.

On the Chl-a panel, the contrast of Chl-a is not very visible. Maybe, you can modify the color scale.

Correct the legend as : “Transect names (A, C2, C3, E1, E2, F1, F2, F3) ”

Figure 3

Legend : Define acronyms PRO as *Prochlorococcus* and SYN as *Synechococcus*. done

Figure 6

Although *calanoids* is an order of copepods, please keep the same name in the figure and in the legend. done

Figure 8

Nice figure ! Thank you !

Figures A1, A2, A3, A4

Add “Latitude” and “Longitude” on the axis. done

Indicate in the legend that the black dots correspond to the CTD stations. In my opinion there are not all necessary and you can just keep the ones that indicate the transects with the frontal stations.done

As for Fig. 1, the red crosses are not very visible on this colormap. improved

Add units of FSLE. Is it day $^{-1}$? yes, now clarified

Figure A6

Correct the legend as : “Prochlorococcus on the top row, Synechococcus on the bottom row [...]”. HPLC (left column) and Flow Cytometry (right column). done

Figures A11, A12, A13

Please consider if all these figures are really relevant (see my general comments). My suggestion is to choose only a few fronts that can be considered representative of all observed. please see comment above

Furthermore on these figures, there are a lot of panels and the typography is minuscule. I suggest to present a limited number of variables. We have enlarged the figures to improve legibility

2.2. Referee 2

Mangolte et al. perform a meta-analysis of the nearly 10 years of data collected in the CCE-LTER cross-front studies to try to identify the physical and biological processes driving plankton community distribution. This is a worthy effort, and the authors do a good job wrestling with data that is undoubtedly patchy, complex, and representing snapshot views on time-evolving fronts.

1. One of the major challenges of extracting process-based information out of snapshots of time-evolving physical-biological features is that you often do not sample enough stages of the feature to get a sense of how the biological processes lead into one another. I found this paper overall good but the analysis is a bit descriptive as far as marine ecology/biology papers are concerned, e.g., there are no statistical analyses to distinguish between the various drivers of the plankton community dynamics (more below). Nonetheless – descriptive papers are okay – but if you're going to go the descriptive route there does seem to be a missed opportunity here to rearrange and/or present the data in terms of the frontal age. In the manuscript, all the data are presented in chronological order in terms of the years in which the cruises were conducted. What if you reordered the data with C3, F1, F2 at the beginning and "older" fronts later in the plots? There certainly seems to be some taxa (e.g., some gelatinous carnivores) where the negative FEF tend to be present in the younger fronts. I wonder if more patterns will emerge if you take the frontal age as a key organizing factor. (Also, I acknowledge that in the Southern CCE there are some persistent fronts where the older vs. younger definition does not apply, but certainly there seem to be a gradient with some of these frontal systems).

We thank the reviewer for their fair comments, and we have extended the Discussion to better justify our approach in the revision. Unambiguous assignment of frontal age is very problematic and uncertain. Our attempt to characterize the age of the fronts is now addressed in section 4.2 :

" The most intuitive explanation for the high abundance of these groups is increased growth in response to the supply of nutrients. In order to test this relationship, we attempted to characterize the age of the fronts, which we assumed to be a proxy of the duration of the supply of nutrients by the ageostrophic circulation. Most of the fronts included in this analysis are relatively stable, and the physical structures underlining them (SST or SSH gradients and FSLE ridges) are generally visible on satellite images at least a few weeks before each transect was conducted, depending on the cloud cover (supp. videos). Such timescales, in principle, are long enough to support the local growth of phytoplankton (Lewandowska et al., 2015) and most meso-zooplankton (Kotori, 1999; Bouquet et al., 2018; Eiane and Ohman, 2004). However the cloud cover, the complexity of the structures and their spatial movement make it difficult to precisely date the appearance of the gradients identified in the transects. It should also be noted that injections of nutrients at fronts should only produce an increase of the growth rates if the phytoplankton population is nutrient-deprived, which is not the case for every front (Fig. A10). Interestingly, however, the "younger" fronts (F1-F2, which can only be identified on satellite images for a few days before the transects) show less zooplankton enhancement than the other fronts. The zooplankton taxon with the fastest reproduction rate, the appendicularians, is also the one most strikingly enhanced at fronts (Fig. 5). But despite these observations, a robust causal link is difficult to establish because of the many large uncertainties associated with both the estimation of "frontal age" and with biological growth rates, particularly the reproduction rates of zooplankton, which are highly variable at taxonomical resolutions finer than the present dataset. Finally, we cannot rule out the possibility that peaks of both biomass and secondary production are attributable to advection along the front of a more productive water parcel. Community structure does not depend only on the local frontal dynamics, but is also strongly influenced by the regional context,

which in our study region is dominated bythe coastal upwelling. Consequently, the description of these local dynamics alone is not sufficient to explain the community structure. Instead, the elucidation of the relative importance of these two processes (frontal injections of nutrients and advection) requires taking into account the history of the water parcels by adopting a Lagrangian perspective (Gangrade and Franks, 2023)."

2. Regarding statistical analyses, this is what I would expect out of a classical meta-analysis. There are 24 functional groups, a measure of their aggregation (via the FEF), and a variety of potential physical and biogeochemical quantities measured – what if the authors were to create a statistical model (either classical multivariate, like a generalized linear mixed model, or machine learning based, like a random forest model or something similar) with the species-specific FEF as response variable and the relative gradients of T, S, density, nitrate, phosphate, silicate, and their prey and predator FEF as explanatory variables? Or, instead of the FEF one could also focus on the size of the plankton biomass peaks and distance to center as the response variable. This may help elucidate a dominant mechanism that can then be summarized in a nice schematic like Fig. 8. As such, Fig. 8 shows a generic set of processes whereby two plankton community meet at a front and the sampling cuts across the communities and the front. This is fine – but just from inspection there are some interesting patterns that do not seem to be captured in the schematic, e.g., Fig 7 suggests on average, the biomass peaks occur on the cold side of the front, and that there is a declining effect by trophic level. The potential with this dataset is quite high, and it often takes some carefully crafted statistical models to cut through some of the fine-scale variability to arrive at a set of overarching mechanisms.

We understand the reviewer's request for a statistical analysis, but standard meta-analysis methods are not appropriate here. We have highly nonlinear relationships and, importantly, they vary depending on the unquantifiable history of circulation, previous nutrient inputs, and residence times of organisms at different frontal features. In the absence of this background information on the previous history of water masses prior to our sampling, we cannot build a statistical model that uses any of these variables in a useful explanatory manner. We now provide guidance to future investigators to indicate the additional variables of interest that would be necessary to conduct such statistical modeling in the future. The difficulties involved in the use of a statistical model are addressed at the end of the discussion, in section 4.3 :

"Despite the richness of this dataset, there is not enough information on the potential drivers to quantify the contribution of each process. For instance, the elucidation of biotic interactions requires knowledge of nutrient fluxes and growth and grazing rates, not just the nutrient stocks and abundances. In addition, given the intensity of the mesoscale circulation, knowledge of the conditions upstream of the fronts is needed. Even with the information that is available, there are significant uncertainties, particularly for the age and location of the frontal supply of nutrients (detailed above). Furthermore, interactions among different drivers need to be taken into account."

My minor comments are mostly focused on the figures:

- I particularly found the overlapping y-axes quite difficult to read, especially when they started to overlap with adjacent panels. E.g., Figure 4, C2-C3 columns, I had no way to read the yaxis labels on the phytoplankton and zooplankton panels. Also the plot title labels in Figures A11-13 are overlapping with each other and the axes labels, which make things hard to read. If these plots are made in python (sort of looks to be the case?) then try using plt.tight_layout() to fix this. Otherwise, increase the vertical and/or horizontal spacing

between panels. We have improved the figures as much as possible to make them more legible. Regarding fig 04, given the space constraints, there is a tradeoff between the size of the plots themselves and the legibility of the labels, and we chose to maximize the plot size since visualizing the patterns across the fronts is more relevant to understanding our results than knowing the exact values.

- Figure 2. Need to add some indication in the figure legend as to what the small black dots refer to. done
- Figure 5. “arraw” should be “array”? or “panel”? corrected