This document contains a point-by-point response to the reviewer 1. The original reviewer comments are in black and our response is written below each main point in blue.

Anonymous Referee #1

I- General comments

The main question addressed by this study is to determine optimal sampling regions in which micronekton biomass observations can provide useful information to better esti- mate the energy transfer efficiency coefficients associated with an ecosystem model. Those coefficients are shown to be tightly linked to specific combinations of four indicators, depending on different environmental conditions (also referred to as regimes in the manuscript). To examine the influence of each indicator, different configurations of environmental regimes are built based on a cluster analysis. The optimal configuration is then investigated using Observing System Simulation Experiments (OSSEs), in which synthetic observations are first randomly selected within the tested regions, then based on two existing observing networks. To assess the quality of the conducted OSSEs, the authors used three metrics: the mean relative error (actual score of the experiment), the residual value of the likelihood (accuracy of the experiment) and the number of iterations of the optimization scheme (convergence speed). The authors found that the optimal combination of the four environmental indicators is associated with productive, warm, moderately stratified waters and weak surface currents, such as those found in tropical regions along the eastern margins (and therefore with the PIRATA moored array). The mechanisms based on the interaction of biological and physical processes that influence the micronekton biomass are also identified.

After some clarification and some necessary major changes (see below), I believe this manuscript is suited to Biogeosciences, as it presents an interesting and novel methodology to identify relevant combinations of environmental forcing variables, prior to performing OSSEs for biogeochemistry. Even though I consider that major revisions to the manuscript are required, note that I do not think that further experiments or diagnostics are necessary.

We thank the reviewer for his encouragements, his careful reading and his constructive comments.

II- Specific comments

1) I slightly struggled with the overall organization of the manuscript. The reader would benefit if the authors follow a more strict structure: e.g, (1) describe the ecological model configuration with more details on the physical forcing, including limitations and caveats about the representations of the biological/physical processes, (2) the Clustering approach and (3) the OSSE system design (i.e., the twin simulation, the data assimilation scheme along with the MLE approach, and the synthetic observations). Then, introduce theoretically the different metrics used to evaluate the observing networks and follow this with the discussion of the results. In Sections 4 and 5, some elements of perspectives seem to be scattered over multiple places, I suggest gathering them together for the sake of clarity.

Following the reviewer suggestions, we made substantial modifications to the manuscript:

(1) We included additional information concerning the physical forcing of the ecological model and its limitations.

Lines 94-98: "FREEGLORYS is a global, non-assimilated simulation that aims at generating a synthetic mean state of the ocean and its variability for oceanic variables (temperature, salinity, sea surface height, currents speed, sea ice coverage). It is produced using the numerical model NEMO with the ORCA025 configuration (eddy-permitting grid with 0.25° horizontal resolution and 75 vertical levels, see Barnier et al., 2006). The model is forced with the ERA-Interim atmospheric reanalysis from the ECMWF".

Lines 105-107: "Overall the simulation reproduces well the dynamics of the ocean but due to the low 1° horizontal resolution, meso-scale features like eddies are not represented. The simulation captures the main temporal variability with a seasonal cycle for micronekton."

(2) We now better introduce the clustering method and justify why it is a valuable approach (See specific comment 2).)

(3) We better introduce the OSSE configuration as required (See specific comment 3).)

We also gathered perspective elements in the discussion: section 4.2 towards eco-regionalization? and 4.3 Limitation and perspectives. It still seems important to us to discuss the perspective of eco-regionalization in a separate subsection since it is a subject that is currently much debated in the different studies of the community. No more perspective elements are present in the conclusions section in the revised version.

Otherwise, the overall organisation of the manuscript changed little and generally follows the structure that the reviewer suggested: (1) description of the model --> section 2.1; (2) clustering approach --> section 2.2; (3) OSSE design --> section 2.3 and the different metric used are introduced theoretically in section 2.4, which is followed by section 3 (Results) and section 4 (Discussion). The vocabulary has however been adapted to match classical OSSE guidelines.

 2) It is important for the casual reader to better introduce the clustering method in subsection 2.2, and explain what is the added value in comparison with more classical sensitivity or correlation analyses. Possible limitations related to clustering could also worth a mention (e.g. possible misleading statistical interpretations, etc).

We agree with the reviewer and modified this section to take into account his comment.

We added a simple definition of the clustering method.

Line131-132: "The k-mean clustering method separates N values in a given number of cluster by minimizing the distance of each value to the mean (called the center) of each cluster."

We also give a justification for our choice.

Line137-140: "The k-mean clustering allows for size-varying class compared to more classical statistical analysis that would consist for example to define the regimes as the quantile of the variables distributions. This latter could lead to under or over estimation of some regimes. The same kind of problem would arise from a classification defined by traditional eco-regions (Longhurst, 1995 and Sutton, 2017), which would not account for the specificity of our forcing fields. This is why performing a clustering on the set of forcing fields used seems a more rigorous approach here."

The main possible limitation of performing clustering concerns the choice of the number of clusters. For example choosing three clusters for a statistical series that present a bi-modal distribution could generate misleading statistical interpretation. But in our case we choose the number of clusters according to the Elbow score (which optimize the number of clusters). And we justify afterwards that the generated clusters match the state-of-the-art regimes (see section 3.1 of the manuscript.)

3) The subsection 2.3 should also better introduce the OSSE procedure, as specific guidelines need to be followed. An overview of those guidelines can be found in the review paper by Hoffman and Atlas (2015), https://doi.org/10.1175/BAMS-D-15-00200.1, while a rigorous framework of strategy and validation techniques is described, for example, by Halliwell et al. (2014), https://doi.org/10.1175/JTECH-D-13-00011.1. Also, note that describing your OSSEs as "twin experiments" is misleading here, as your nature run (TRUTH in the manuscript) has different initial forcing fields than the control run (TWIN in the manuscript). Further information can be found in the two references given above.

Following the reviewer recommendations, we now explain the OSSE configuration with the classical guidelines (examples given in the literature), which are:

1) We justify that the nature run is generated using a state-of-the-art model (section 2.3.1).

2) We justify that the differences between the nature run and the model used for data assimilation have some realism (section 2.3.2)

We added Lines 166-169: "White noise has been preferred to more realistic perturbation to avoid any geographical bias pattern. The implications of this choice are further discussed in section 4.3. Its amplitude, fixed to 10% of error, is however representative of the mean error estimated for ocean circulation models (Lellouche 2012, Ferry 2012)."

3) We show that the assimilation methodology conforms to current practice (section 2.3.3)

We added Lines 173-175: "A MLE is used as assimilation module. Its implementation is based on an adjoint technique (Errico, 1997) to iteratively optimize a cost function that represents the discrepancy between model outputs and observations. This approach conforms to current practices. More details about the implementation of this approach in SEAPODYM can be found

in Senina 2008 and Lehodey 2015."

4) We justify that the simulated observations have a realistic coverage (section 2.3.4)

We added Lines 186-189: "A random sampling of observation within each configuration has been preferred to a more realistic observation network to avoid any geographical bias. But this choice is discussed in section 3.4. The coverage in terms of observation numbers is however quite realistic. We assume a number of 400 observations, which at the resolution of the model (1°x1 month) corresponds for example to the deployment of six moorings during five years."

5) We give the methodology for the evaluation of OSSE (section 2.4)

A figure summarizing the OSSE configuration has also been added, for the reader to follow the different steps (see Figure 1).

We also agree that "twin experiment" was misleading and we do not use it anymore. We adopted the notation NR and CR for the nature and control run respectively.

4) The results mostly show that the performance of each OSSE depends on the geographical locations associated with the synthetic observations rather than the actual design of the in situ networks used to perform the acoustic transects. Could the authors please comment on that matter?

The results show indeed that when using real data sampling locations, the result does not change very much and warm regions still give better performances. This should give confidence in the fact that our conclusions will be robust when the idealized "random sampling" hypothesis will be relaxed. However, this study does not provide a full sensitivity analysis to the network design since both PIRATA and BAS are ship transect database. Preliminary idealized studies (not shown here) show that the design of the network also plays a role and in particular that spatial coherence (moorings) gives better results than temporal coherence (ship transects) and that an optimal number of moorings does exist. But this sensitivity is clearly second order compared to the geographical location of the samplings.

However, we fully agree with the reviewer that this point deserves further comments; we included some in the related section (section 3.4 Testing realistic networks):

Lines 340-346, we added: "This should give confidence in the fact that our results are robust when the "random sampling" hypothesis used in the previous section is relaxed and that more realistic sampling designs are considered. Here in particular, the temporal auto-correlation of the different samplings is very strong since PIRATA and BAS are both underway ship measurements taken from 2-month cruises, repeated annually. The results seem much less dependent to the exact design of the samplings and the seasonality of the measures than to their actual geographical location. Oceanic conditions of the observations (correlated to their geographical location) are the first order of sensitivity."

We also added few lines in the limitation and perspective section about the possibility to further

investigate the sensitivity to the sampling design:

Lines 430-431: "Other perspectives may include a study of the sensitivity to the design of the samplings (the impact of moored instruments in comparison with underway measurements), in the continuity of the work of Lehodey et al., (2015)."

5) To facilitate comparisons between the different OSSEs, the histograms presented separately in Figures 2, 4, 6 and 7 could be gathered together.

It is now done so in the revised version (Figure 3).

6) The first paragraph in the discussion (Section 4) mostly presents conclusions of the previous sections, I would suggest to move it in the last Section (Conclusions).

We moved this section to the conclusions and reformulated the whole to avoid redundancy.

7) In the Conclusions, limitations and caveats associated with the OSSE results need to be further discussed, in addition to the methodological limitations discussed in subsection 4.3.

Following the reviewer suggestion, we added in the conclusion the main limitations associated with the use of OSSE, which was also suggested by reviewer 2:

Lines 452-457: "The main limitation in this study is certainly the absence of realistic modelling of the different sources of errors: the error between the modelled and the true state of the ocean have been modelled with a white noise perturbation that does not allow for spatially inhomogeneous errors. And the observations have been assumed to be directly proportional to biomass. The absence of a realistic observation model converting the acoustic signal into biomass (Jech, 2015) prevents to account for the different types of observation errors. Future studies should include these missing components."

We also recall that our objective was different from traditional OSSE:

Lines 440-443: "Our objective was different from most OSSEs studies designed to correct outputs of operational models, e.g., for weather and physical oceanography forecast systems (Fujii, 2019). Here the objective was to search for the optimal design to estimate the set of invariant fundamental parameters of the model."

8) It might sound minor, but the authors should consider to properly cite the PIRATA and the BAS projects in the acknowledgements section, along with their institutional support. It would help the readers to find the data if they want to use it too in further studies, and it is important for sustaining and justifying long term time series associated with both projects.

We now cite the PIRATA and BAS project in the acknowledgments.

III- Technical corrections

An annotated manuscript (see supplement) is provided along with this document to provide some technical corrections. Note that the annotations on the PDF can be displayed using Google docs.

Please also note the supplement to this comment: https://www.biogeosciences-discuss.net/bg-2019-353/bg-2019-353-RC1- supplement.pdf

We have taken into account most of the technical corrections suggested by the reviewer. A reply to these comments is available as a supplementary material and the corrections can be followed on the tracked changes version of the manuscript.

This document contains a point-by-point response to the reviewer 2. The original reviewer comments are in black and our response is written below each main point in blue.

Anonymous Referee #2

General comments

Unfortunately, it is very difficult to follow parts of the manuscript because of quality of the English language. Normally I would add this to the end of my comments but in this instance, language is the main issue that I have with the manuscript – and a reason why it took me considerably longer to read through it. Many sentences are clumsily or sometimes incorrectly formulated and in certain paragraphs I had to guess the ideas the authors were trying to express. I have included a lot of corrections and questions about language in the specific comments below but I would recommend that the authors go through the manuscript carefully with the help of a native English speaker to make the manuscript more readable and easier to understand.

We thank the reviewer for his careful reading and his useful rephrasing suggestions. We took into account his many comments and hopefully improved the language quality of the manuscript. We also took advices from a native English speaker, who went through the manuscript and corrected the wrong formulations.

What I found missing in the methods section is a good description of the underlying physical model: Neither its vertical nor horizontal resolution is mentioned, it is also not clear how deep the resulting layers z_1, z_2 and z_3 are. In general, it would help to explicitly mention that SEAPODYM-MTL currents, temperature etc are based on an underlying global physical model (at least I assume so, based on l 91). At the moment this is not done and many readers may be confused how the physical transport and stratification are simulated in a model with only 3 layers.

Following the reviewer suggestions, we now give detailed precisions about the underlying physical model in section 2.1.

- We specify the physical model horizontal and vertical resolution: "ORCA025 configuration (eddy-permitting grid with 0.25° horizontal resolution and 75 vertical levels, see Barnier et al., 2006)" (lines 97-98).

- We give an approximate averaged depth for the layers: "These boundaries are defined as follows (an approximate averaged depth is given in brackets): $z_1(x,y,t) = 1.5 \times z_{eu}(x,y,t)$ (50-100 m), $z_2(x,y,t) = 4.5 \times z_{eu}(x,y,t)$ (250-300 m), $z_3(x,y,t) = \min(10.5 \times z_{eu}(x,y,t),1000)$ (350-700 m)" (lines 84-85).

- We also include a description and references for the underlying physical model: " [forcing fields] come from the ocean dynamical simulation FREEGLORYS2V4 produced by Mercator-Ocean. FREEGLORYS2V4 is the global, non-assimilated version of GLORYS2V4 simulation that aims at generating a synthetic mean state of the ocean and its variability for oceanic variables

(temperature, salinity, sea surface height, currents speed, sea-ice coverage). It is produced using the numerical model NEMO with the ORCA025 configuration (eddy-permitting grid with 0.25° horizontal resolution and 75 vertical levels, see Barnier et al., 2006) and forced with the Era-Interim atmospheric reanalysis from the ECMWF." (lines 93-97).

Further details and modifications are also given in the response to specific comments below.

The authors manage to identify certain prevalent ocean conditions (regimes), which are more suitable for parameter estimation in their twin experiment setup. Then they take a leap and state in multiple places throughout the manuscript that these regimes would therefore be better suited for parameter estimation outside the context of twin experiments. I am a bit skeptical about this claim, because the model's ability to simulate the ocean conditions may also be regime-dependent. There may be regimes where the model does not do a good job at simulating the ocean and model parameters do not reflect the actual energy transfer efficiency, while the model may be better suited for other regimes. This strikes me especially true for the relatively simple 3-layer model that is used in the study. Without knowledge of model error it seems difficult to make the claim that certain regions are better suited for parameter estimation than others.

This remark is completely fair. Actually, we do take into account model errors in our experiments but not inhomogeneous model errors.

First, as the reviewer 1 noted, the use of the terminology "twin experiment" was misleading in our case. Indeed, the nature run used to generate the synthetic observations has not the same forcing fields as the control run used to perform the estimation, but a "model error" was introduced (see Fig. 1 in the revised version). We then do not use the expression "twin experiment" anymore.

Second, our control run is forced with the reference forcing fields plus a perturbation that is supposed to account for model error. However, we chose a white noise perturbation that indeed does not take into account any space-dependant or regime-dependant errors. We are conscious of the implications of this choice, which are discussed in section 4.3.

In response to the reviewer comment, we develop this part of section 4.3 emphasizing the limitation of a white noise perturbation by adding:
- Lines 410-411: "The realism of this approach is questionable, as it does not take into account the possible spatial distribution of uncertainty and errors of ocean models. "
- Lines 413-414: "Indeed, we expect forcing fields to be less accurate where the ocean has strong variability."
- Lines 414-415: "However, for the purpose of our study, a spatial homogeneous error was preferable, to avoid introducing any bias."
And we also mention it in the conclusion, in response to reviewer 1 specific comments:
- Lines 452-456: "The main limitation in this study is certainly the absence of realistic modelling of the different sources of errors: the error between the modelled and the true state of the ocean have been modelled with a white noise perturbation that does not allow for spatially inhomogeneous errors. And the observations have been assumed to be directly proportional to biomass. The absence of a realistic observation model converting the acoustic signal into biomass (Jech, 2015) prevents to account for the different types of observation errors. Future studies

should include these missing components. "

Modelling a "real" error is first quite complicated and second if we introduce a regime-dependent error, then we would not be able to highlight the main result of this study, which is the regime dependence to the performance of the estimation.

An attempt in modelling an inhomogeneous error is to take an error proportional to the deviation of a field to its climatology, as we also explain it in section 4.3. This approach has in fact been tested; it was the subject of previous studies:

- Delpech, Audrey (2017). *Sensitivity study of SEAPODYM parameters to physical and biogeochemical forcing fields in the framework of Observing System Simulation Experiment*. Master Thesis from the Ecole Nationale Supérieure de Techniques Avancées (Available upon request).

- Lehodey, Patrick, Titaud, Olivier, Delpech, Audrey and Conchon, Anna (2018) *Optimal design of ecosystem module*. AtlantOS Deliverable, D5.5. AtlantOS, 29 pp. DOI 10.3289/atlantos_d5.5.
  (Available at : https://www.atlantos-h2020.eu/download/deliverables/AtlantOS_D5.5.pdf)

Section 3.2 (linear perturbation) and 4.1.2 of the AtlantOS report cited above show how our results are robust to the introducing of an inhomogeneous error on the forcing fields. In particular, figure 6 of this same report shows that, even if the perturbation is higher in the tropical regions (warm regime), these regions remain the best locations for parameters estimation.

Note that this study was conducted in a slightly different framework since a different physical simulation was used, and the synthetic observations were taken on the tracks of real ship transects. The results can however be interpreted in a similar fashion.

Specific comments

l 5: "migrant and non-migrant micronekton": Does the "migrant" refer to DMV? It would be good to be explicit here.
Yes it does. We now specify "vertically migrant" and we added "DVM" in brackets.

l 15: The "all" is too general.
We removed the "all" and give concrete examples of micronekton predators instead: tunas, swordfishes, turtles, seabirds and marine mammals.

l 16: "Migrations" -> "Migration"
Done.

l 16: It would be good to briefly summarize DMV.
We added (Lines 19-22): "This migration of biomass occur when organisms move up from a deep habitat during to a shallower habitat at night. DVM is generally related to a trade-off between the need for food and predator avoidance (Benoit-Bird, 2009) and seem to be triggered by sunlight (Zaret, 1976)"

l 17: Mesopelagic already implies "inhabiting the twilight zone (200-1000 m)", I would rephrase to "the mesopelagic (inhabiting the twilight zone from 200m to 1000m depth) component of micronekton"

Done.

l 25: Does "develop the datasets" mean to collect observations?

We changed for "collect observations", "develop" was in fact for "methods and models".

l 33: "making this component strongly underestimated" -> "leading to an underestimation bias for this group of micronekton"

This sentence does not exist anymore in the revised version (following referee 1 short comments, we shortened this paragraph).

l 34: "acoustic frequencies associated to traditional net sampling": I am not sure what this means.

The idea was that progresses are expected from the association of many different sampling technics: multi-frequency acoustics, optical measurements and traditional net samplings. We rephrased that sentence as:

"Progresses are expected in the coming years thanks to the combined use of different measurement techniques: multiple acoustic frequencies, traditional net sampling and optical techniques" (Lines 36-38).

l 35: "More accurate biomass estimates should benefit from" -> "The accuracy of biomass estimates is predicted to benefit from"

Done.

l 40: What are "target fish", I would suggest to remove "target" or rephrase.

We removed it.

l 41: Does "the functional groups" refer to the micronekton? If so, please include this information.

Yes, it does refer to micronekton. We added this information.

l 42: "The spatial dynamics of biomass in each group...": Add "In addition to DMV"

Done. We also added: "spatial *horizontal* dynamics" which was missing.

l 43: Which processes are included in "The time of development"?

The times of development include the recruitment time and the mortality. We clarified this sentence (lines 46-47 in the revised version): "The recruitment time and natural mortality of organisms …".

l 57: Make sure to include information here about what is new in this study compared to Lehodey et al. (2015).

What is new compared to Lehodey et al. (2015) is first the goal of the study. While they intended to validate the parameter estimation method, we investigate the sensitivity of the parameter estimation to the environmental conditions by using a clustering approach. We thus perform

OSSE at a global scale and in a more realistic framework by introducing an error on the forcing field.
We now highlight it better in the text.

Lines 58-59: "However, this study was conducted for a single transect in the very idealized framework of twin experiments (the same run is used for observation generation and parameter estimation)"

Lines 62-64: "For this purpose, we use Observing System Simulation Experiments (OSSE) at a global scale. This method allows for simulating synthetic observations in places where an observing system does not exist yet, and to see how useful the synthetic observations are for the estimation. The purpose of the present study …"

l 58: "Therefore, it is useful ...": This sentence is confusing, please rephrase.
Done. We reformulated the whole paragraph, in response to your previous comment.

l 78: So more information about the physical model would be useful here. Is it truly a 3-layer model or are these subdivided into more layers? How is the model divided in the horizontal?
Some information about the physical model was indeed missing, as also noted by reviewer 1. The physical model comes from a simulation of the numerical model NEMO that have a 0.25° horizontal resolution and 75 vertical levels). The physical fields are then horizontally degraded to 1° horizontal resolution and depth-averaged in 3 vertical layers defined by the value of the euphotic depth (line 84). We give these precisions in the revised version (lines 96-101)

l 83: Why is "migrant-umeso" not abbreviated as "mumeso" and why is "meso" part of the name when they also migrate to the epipelagic? I think it would be beneficial to the reader to rethink the names. For example, given that the layers have just been introduced as z_1, z_2 and z_3, the names could include the indices of the layers they inhabit (the use of "nekton" is just a suggestion here): (1) epi -> nekton_1 (2) umeso -> nekton_2 (3) ummeso -> nekton_12 (4) lmeso -> nekton_3 (5) lmmeso -> nekton_23 (6) lhmmeso -> nekton_13
The name and abbreviations have been chosen to follow the official denomination from the CMEMS (Copernicus Marine Environment Monitoring Service). This service provides indeed a global reanalysis of mid-trophic levels, where the name and abbreviations are already "ummeso" …etc for the different functional groups. Here is the reference documentation:
http://resources.marine.copernicus.eu/documents/PUM/CMEMS-GLO-PUM-001-033.pdf.

l 90: Is this equivalent to reduction in the model resolution? Is the horizontal resolution that is used 1 degree?
We run SEAPODYM-MTL with 1°x1° forcing fields (temperature, currents velocity, primary production). All the forcing fields were previously degraded or interpolated if needed (this is particularly the case of the FREEGLORYS 0.25° ocean model).
We reformulated and better specified the model description section of the manuscript in response to your second general comment and to reviewer 1 specific comments.

l 107: It would be useful to know the height of each layer here. What if layer 1 is well stratified but deep enough that its average temperature does not differ much from T_2?

The height of each layer depends linearly on the euphotic depth, so it changes with space and time (line 84). But we now give an approximate averaged depth for each layer to get a feeling of the numbers (lines 84-85).

In practice as the first layer is generally no deeper than 50-100 m, its averaged temperature differs from the underlying layer. But even if the layer 1 would be deep and well stratified, it would not be a problem either because from the model construction, the micronekton is impacted by the vertically-averaged temperature of each layer. So, what really matters is the difference of *vertically-averaged* temperature between the different pelagic layers, regardless of the stratification in each layer.

Eq 6: '[1,N]' denotes an interval that contain real numbers, '{1,...,N}' would be the correct way to denote integers (see my comment about '[[' below). Furthermore, shouldn't the intersect of any two Gamma_k be empty? The current equation only states the weaker condition that the intersect of all Gamma_k is empty.
We indeed intended to mention an integer interval; we corrected it with "{1…N}" and leaved out the notation "[[1, N]]". The second comment is right too, this is indeed the intersection of any two Gamma_k that is empty and not only the intersection of all of them. We corrected the text accordingly.

l 124: It would not be difficult to express the results of a k-means clustering in words. I would recommend that the authors do that, so that some one without good knowledge of mathematical notation can understand the results.
We added a definition of the k-mean clustering in words: "The k-mean clustering method separate N values in a given number of cluster by minimizing the distance of each value to the mean (called the center) of each cluster." (Lines 131-132).

l 126: I don't think the double-bracket notation '[[ ]]' for integer ranges is very common (I have found it on the French wikipedia page but not the English, compare https://en.wikipedia.org/wiki/List_of_mathematical_symbols to https://fr.wikipedia.org/wiki/Table_de_symboles_math%C3%A9matiques.) I would suggest to either change it or briefly explain it.
We changed for the notation "{…}" instead.

l 124: "we explicit this dependence" -> "we make this dependence explicit"
Done

l 132: "the inverse model": What is the inverse model, this is the first time it is mentioned? Better explanation is required.
Due to reorganisation of section 2.3 in response to reviewer 1 specific comments, this mention does not appear anymore. Note that we now detail this section and added a figure (Figure 1) to further explain the OSSE configuration. The "inverse model" is the model that uses the MLE (cf. control run in Figure 1 in the revised version), but it would have been indeed more accurate in the sentence you mentioned to use "MLE" directly.

Eq 8: If alpha is constant here, I would suggest to abandon it and let gamma be uniformly distributed in '[-0.1,0.1]'.

Alpha is constant for most experiments except the ones in section 3.4.
We now mention it: "The amplitude alpha is set to 0.1 for all experiments except in section 3.4 where alpha varies" (line 164).

Eq 8: For a particularly small F, this could become negative.
Yes, this is generally not a problem (the current velocity can become negative and the current simply reverse direction, or the temperature can also become negative in extreme polar regions, as it is already the case for the native forcing fields). But we indeed ensured that the primary production is always positive.
We now mention it in the text: "For small values of F, this perturbation can induce a sign reversal of the forcing. This does not matter for the temperature or the currents velocities, primary production has however been constraint to positive values." (Lines 163-165 in the revised version).

l 230: "The temperature shows the presence of a strong bias is". Bias with regard to what? I would suggest to change to something like: "Temperatures are different between the two configurations."
We changed as suggested, note that this paragraph has also been further simplified.

l 233: "Therefore, it seems here that the difference observed in the temperature values of the two datasets has a stronger impact on the parameter estimation than the regime of currents." So far it has been demonstrated that both temperature and velocity differ between the two experiments/configurations. What is the evidence that differences in temperature have a stronger impact?
We show that low velocities give better estimations than high velocities. We show also that high temperatures give better estimation than low temperatures. But what if we now compare a configuration of low velocities and low temperatures with a configuration of high velocities and high temperatures? This is what experiment 1' and 1'' are showing. The configuration with high temperatures and high velocities give better estimation than the configuration with low temperature and low velocities. So it is as if the temperature governed the performance more than the velocities. This suggests thus that differences in temperature have a stronger impact.

However, this information was slightly beyond the scope of the point we wanted to make here. We thus removed it.

l 237: It would be good to get a feel for the numbers, do significant cross-correlations occur often, what is their proportion w.r.t. the total number of experiments?
Among the 26 possible experiments, 9 had a significant cross-correlation. We now specify it in the text (lines 271-272).

l 242: Fig 5 is referenced before Fig 4.
This is not the case anymore since we combined figures 2, 4, 6 and 7 in one figure 3.

l 258: "if the mean error on the estimated parameters were higher in average, the result does not change". I am not sure what is meant here, is the mean error higher on average? Please rephrase.
We rephrased the sentence as: "The same kind of experiments were carried out in a temperate

regime (not shown) and even though the mean error on the estimated parameters is higher on average, the result does not change: weak stratification always leads to a better estimation than strong stratification." (Lines 290-291 in the revised version).

l 267: Do you mean "Exp. 1a and 1b" here or 4a and 4b?
We meant Exp. 4a and 4b and corrected it in the text.

l 270: "Indeed, not only the temperature is higher but also the vertical gradient of temperature.": It is not fully clear what this sentence is referring to.
We rephrased it as: "Indeed, Exp. 4d (T_4 regime) has higher temperature than Exp. 4b (T_2 regime) but it has also a higher stratification index (S_3 regime for Exp. 4d and S_1 regime for Exp. 4b)" (Lines 303-304).

Eq 10: What is E_pp?
E_pp is the total energy transfer from the primary production to the mid-trophic level, all functional groups together. Its definition is given in the Appendix A, but we also recall it below equation 10 in the revised version.

Table 3: It would be nice to add the number of samples/observable points for each configuration.
We included this information in the Table 3. We also added a note in the caption to explain that even if the number of observable point differs from one configuration to another, the experiment were conducted with a constant number of observation points (400 synthetic observations).

Fig 1: Reference Table 2 in caption.
Done

Fig 1: I understand the intent of using transparency to indicate uncertainty but I doubt it is done correctly here. It appears like the colors are plotted on top each other in a predefined order, so even light orange colors in (b) will appear more orange than blue because the orange is plotted on top of the blue.
The idea was that even if orange were plotted on top of the blue, transparency would make the resulting colour neither orange nor blue but something in between. However, given the resolution of the figure and the very few point that are concerned, this information may be not relevant. We removed it.

Fig 2,4,6,7 can be combined into one, which would allow a nice comparison between the different configurations.
We agree and it is done so in the revised version (Figure 3).

Tracked Changes Version

Influence of oceanic conditions in the energy transfer efficiency estimation of a micronekton model

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Abstract. Micronekton – small marine pelagic organisms ~~mostly in the size range~~ around 1-10 cm in size – is a key component of the ocean ecosystem, as it constitutes the main source of forage for all larger predators. Moreover, the mesopelagic component of micronekton that undergoes Diel Vertical Migration (DVM) likely plays a key role in the transfer and storage of CO_2 in the deep ocean: ~~the so-called~~ this is known as the 'biological pump' ~~mechanism~~. SEAPODYM-MTL is a spatially explicit dynamical model of micronekton. It simulates six functional groups of ~~migrant~~ vertically migrant (DVM) and non-migrant (no DVM) micronekton, in the epipelagic and mesopelagic layers. Coefficients of energy transfer efficiency between primary production and each group are unknown ~~. But~~, but they are essential as they control the ~~predicted~~ production of micronekton biomass. Since these coefficients are not directly measurable, a data assimilation method is used to estimate them. In this study, Observing System Simulation Experiments (~~OSSE) in the framework of twin experiments are used to test various observation networks at a global scale~~ OSSEs) are used at a global scale to explore the response of oceanic regions regarding energy transfer coefficients estimation. ~~Observational networks~~ Sampling regions show a variety of performances. It appears that environmental conditions are crucial to determine ~~network efficiency~~ the optimal observing regions. According to our study, ideal sampling areas are warm ~~, non-dynamic~~ and productive waters associated with weak surface currents like the eastern side of tropical Oceans. These regions are found to reduce the error of estimated coefficients by 20% compared to cold and more dynamic sampling regions. The results are discussed in term of interactions between physical and biological processes.

1 Introduction

Micronekton organisms are at the mid-trophic level of the ocean ecosystem and have thus a central role, as prey of ~~all~~ larger predator species such as tunas, swordfish, turtles, sea birds or marine mammals, and as a potential new resource in the blue economy (St John et al., 2016). Diel Vertical ~~Migrations~~ Migration (DVM) characterizes a large biomass of the mesopelagic ~~component of micronekton~~ (inhabiting the twilight zone (200-1000 m) ~~of~~ component of micronekton of the world ocean. This migration of biomass occurs when organisms move up from a deep habitat during daytime to a shallower habitat at night. DVM is generally related to a trade-off between the need for food and predator avoidance (Benoit-Bird et al., 2009) and seem to be triggered by sunlight (Zaret and Suffern, 1976). Through these daily migrations, the mesopelagic micronekton potentially con-

tributes to a substantial transfer of atmospheric CO_2 to the deep ocean, after its metabolization by photosynthesis and export
25 through the food chain (Davison et al., 2013). The understanding and quantification of this mechanism, called the 'biological
pump', are crucial in the context of climate change ~~(Zaret and Suffern, 1976; Benoit-Bird et al., 2009; Davison et al., 2013; Giering et al., 2~~
(Zaret and Suffern, 1976; Volk and Hoffert, 1985; Benoit-Bird et al., 2009; Davison et al., 2013; Giering et al., 2014; Ariza et al., 2015)
. However, there is a lack of comprehensive ~~dataset~~ datasets at global scale to properly estimate micronekton biomass and com-
position. The few existing estimates of global biomass of mesopelagic micronekton vary considerably between less than 1 and
30 $\sim$ 20 Gt (Gjosaeter and Kawaguchi, 1980; Irigoien, 2014; Proud et al., 2018), so that micronekton has been compared to a
"dark hole" in the studies of marine ecosystems (St John et al., 2016). Therefore, a priority is to ~~develop the datasets,~~ collect
observations and develop methods and models needed to simulate and quantify the dynamics and functional roles of these
species' communities.

Observations and biomass estimations of micronekton rely traditionally on net sampling and active acoustic sampling (e.g.,
35 Handegard et al., 2009; Davison, 2011). Each method has limitations. Micronekton species can detect approaching fishing ~~gears~~
trawls and part of them can move away to avoid the net. This phenomenon leads to biomass underestimation from net trawling
(Kaartvedt et al., 2012). Conversely, acoustic signal intensity may overestimate biomass due to presence of organisms with
strong acoustic target strength, e.g. ~~many mesopelagic species but also siphonophores~~ species that have gas inclusion inducing
strong resonance (Davison, 2011; Proud et al., 2017). ~~Some organisms like squids, have both excellent skills to escape the~~
40 ~~trawl net and a low response to acoustic signal, making this component strongly underestimated with both methods. Progress~~
Progresses are expected in the coming years thanks to the ~~use of~~ combined use of different measurement techniques: multiple
acoustic frequencies~~associated to ,~~ traditional net sampling and optical techniques (Kloser et al., 2016; Davison et al., 2015).
~~More accurate biomass estimates should~~ The accuracy of biomass estimates is predicted to benefit from this combination of
techniques and the developments of algorithms that can attribute acoustic signal to biological groups.

45 While these techniques of ~~observation and methods of in situ~~ observational estimates of biomass are progressing, new
developments are also achieved in the modeling of ~~ocean ecosystem including micronekton components~~ the micronekton
components of the ocean ecosystem. SEAPODYM (Spatial Ecosystem And POpulation Dynamics Model) is an eulerian
ecosystem model that includes one lower- (zooplankton) and six mid-trophic (micronekton) functional groups, and detailed
~~target fish populations (Lehodey et al., 1998, 2008)~~fish populations (Lehodey et al., 1998, 2008, 2010). Given the structural
50 importance of DVM, the micronekton functional groups are defined based on the daily migration behavior of organisms be-
tween three broad epi- and meso-pelagic bio-acoustic layers (Lehodey et al., 2010, 2015). ~~The spatial~~ In addition to DVM,
the horizontal dynamics of biomass in each group is driven by ~~the ocean circulation~~ocean dynamics, while a diffusion co-
efficient ~~account~~ accounts for local random movements. The ~~time of development~~ recruitment time and the natural mortal-
ity of organisms ~~in the functional groups~~ are linked to the temperature in the vertical layers inhabited ~~during the~~ by each
55 functional group during day or night. These mechanisms are simulated with a system of advection-diffusion-reaction equations
(Lehodey et al., 2008). Primary production is the source of energy distributed to each group according to a coefficient of energy
transfer efficiency. Eleven parameters control the biological processes: a diffusion coefficient, six coefficients $(E'_i)_{i \in [\![1,6]\!]}$ of
energy transfer from primary production toward each mid-trophic functional group, and four parameters for the relationship

between water temperature and ~~time~~ times of development (mortality, recruitment) (Lehodey et al., 2010). The ~~later~~ latter four parameters were estimated from a compilation of data found in the scientific literature (Lehodey et al., 2010). Therefore, the largest uncertainty remains on the energy transfer efficiency coefficients, that control the total abundance of each functional group.

A method to estimate the model parameters has been developed using a Maximum Likelihood Estimation (MLE) approach (Senina et al., 2008). ~~Its implementation is based on an adjoint technique (Errico, 1997) to iteratively optimize a cost function that represents the discrepancy between model outputs and observations.~~ A first study has shown that this method can be used to estimate the parameters E'_i using relative ratios of observed acoustic signal and predicted biomass in the three vertical layers during daytime and nighttime (Lehodey et al., 2015). ~~A single acoustic transect was used, with the strong assumption that acoustic signal and predicted biomass were directly proportional~~However, this study was conducted for a single transect in the very idealized framework of twin experiments (the same run is used for observation generation and parameter estimation). While we can expect that improved estimates of micronekton biomass will become available in the coming years, ~~they~~ this will likely still require costly operations at sea. Therefore, it is ~~useful to use the model and its MLE approach to evaluate the potential that these observations contain for the model parameters estimation through~~ important to assess realistically how well observations can estimate parameters before deploying observational systems. For this purpose, we use Observing System Simulation Experiments (OSSE~~) (Arnold and Dey, 1986).~~, Arnold and Dey (1986)) at a global scale. This method allows for simulating synthetic observations in places where an observing system does not exist yet, and to see how useful the synthetic observations are for the estimation.

The objective of the present study is to characterize and identify ~~the~~ sampling regions, regarding oceanic variables, in which micronekton biomass observation gives the most useful information for the model energy transfer coefficients estimation. ~~For this purpose, we use OSSE based on twin experiments.~~ A set of synthetic observations is generated with SEAPODYM using a reference parameterization. Then, the set of parameter values is changed and an error is added to the forcing field in order to simulate more realistic conditions. The MLE is used to estimate the set of parameters from the set of synthetic observations. The difference between the reference and estimated parameters provides a metric to select the best sampling zones. A method based on the clustering (Jain et al., 1999) of oceanic variables (temperature, currents velocity, stratification and productivity) is presented to investigate the sensitivity of the parameters estimation to the oceanographic conditions of the observation regions. This method aims at determining which conditions are the most favorable for collecting observations in order to estimate the energy transfer efficiency coefficients.

The paper is organized as follows: Section 2 describes the model set-ups and forcings ~~. The~~ as well as the method developed to characterize regions of observations and the metrics used to evaluate the parameters estimation~~are detailed as well~~. Section 3 describes the outcome of the clustering method to define oceanographic regimes and synthesizes the main results of our estimation experiments. The results are then discussed in Section 4 in the light of biological and dynamical processes. Some applications and limitations of our study are also identified along with suggestions for possible future research.

2 Method

2.1 SEAPODYM-MTL and its configuration

SEAPODYM-MTL (Mid-Trophic Levels) models six functional groups of micronekton in the epi- and upper and lower mesopelagic layers at a global scale. These layers encompass the upper 1000 m of the ocean~~, as observed from acoustic detection and net sampling~~. The euphotic depth (z_{eu}) is used to define the depth boundaries of the vertical layers. These boundaries are defined as follows (an approximate average depth is given in brackets): $z_1(x,y,t) = 1.5 \times z_{eu}(x,y,t)$ ($\sim 50 - 100$ m), $z_2(x,y,t) = 4.5 \times z_{eu}(x,y,t)$ ($\sim 150 - 300$ m), $z_3(x,y,t) = \min(10.5 \times z_{eu}(x,y,t), 1000)$ ($\sim 350 - 700$m), where z_{eu} is given in meters. The six functional groups are called (1) epi (for ~~the~~ organisms inhabiting permanently the epipelagic layer); (2) umeso (for ~~the~~ organisms inhabiting permanently the upper mesopelagic layer); (3) ummeso (for migrant-umeso, ~~the~~ organisms inhabiting the upper mesopelagic layer at day and the epipelagic layer at night); (4) lmeso (for ~~the~~ organisms inhabiting permanently the lower mesopelagic layer); (5) lmmeso (for migrant-lmeso, ~~the~~ organisms inhabiting the lower mesopelagic layer at day and the upper mesopelagic layer at night) and (6) lhmmeso (for highly migrant lmeso, ~~the~~ organisms inhabiting the lower mesopelagic layer at day and the epipelagic layer at night). The model is forced by current velocities, temperature and net primary production (see Appendix A for detailed equations).

This work is based on a ten-year (2006-2015) simulation of SEAPODYM-MTL, called hereafter the ~~TRUTH simulation. Due to high computational demand, the original resolution of forcing fields (0.25°×week)has been degraded to 1°×month~~nature run (NR). Euphotic depth, horizontal velocity and temperature fields come from the ocean dynamical simulation FREEGLORYS2V4 produced by Mercator-Ocean[1]. ~~Temperature and horizontal velocity fields are depth-averaged over the water column of each three trophic layers ending with a three-layers forcings field set. Net .~~ FREEGLORYS2V4 is the global, non-assimilated version of GLORYS2V4[1] simulation that aims at generating a synthetic mean state of the ocean and its variability for oceanic variables (temperature, salinity, sea surface height, currents speed, sea-ice coverage). It is produced using the numerical model NEMO[2] with the ORCA025 configuration (eddy-permitting grid with 0.25° horizontal resolution and 75 vertical levels, see Barnier et al. (2006)) and forced with the ERA-Interim atmospheric reanalysis from the ECMWF[3]. The net primary production is estimated using the Vertically Generalized Production Model (VGPM) of Behrenfeld and Falkowski (1997) with satellite derived ~~chlorophyll a~~ chlorophyll-a concentration. This product is available at Ocean Productivity Home Page of the Oregon State University[4]. Due to high computational demand, the original resolution of the simulation 0.25°×week has been degraded to 1°×month. Temperature, horizontal velocity and primary production fields are depth-averaged over the water column of each three layers defined by z_1, z_2 and z_3, ending with a set of three-layered forcings fields. Initial conditions of SEAPODYM-MTL come from a ~~two-years~~ two-year spin-up based on a monthly ~~based climatology simulationin order to reach equilibrium~~climatology simulation. Reference values of SEAPODYM-MTL parameters ~~in the TRUTH simulation~~ are

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[1] http://resources.marine.copernicus.eu/documents/QUID/CMEMS-GLO-QUID-001-025.pdf
[2] https://www.nemo-ocean.eu/
[3] https://www.ecmwf.int/
[4] http://www.science.oregonstate.edu/ocean.productivity/

those published in Lehodey et al. (2010). Overall the simulation reproduces the dynamics of the ocean well, but due to the low 1° horizontal resolution, meso-scale features like eddies are not represented. The simulation captures the main temporal variability with a seasonal cycle in primary production and DVM cycle for micronekton.

2.2 Clustering approach to characterize potential sampling regions

In this section we describe the method we ~~use to select different observation sets~~ used to select the different observation regions for OSSE, based on environmental characteristics. We define the spatio-temporal discrete observable space Ω as the set of the $1° \times 1°$ grid points belonging to SEAPODYM-MTL discrete domain. The characterization of each observation point relies on four indicators defined from the environmental variables: the depth-averaged temperature $\mathcal{T}$, a stratification index $\mathcal{S}$, the surface velocity norm $\mathcal{V}$ and a bloom index $\mathcal{B}$, for which different regimes of intensity are defined. The averaged temperature $\mathcal{T}$ over the water-column is defined as:

$$\mathcal{T}(x,y,t) = \frac{1}{3}(T_1(x,y,t) + T_2(x,y,t) + T_3(x,y,t)), \tag{1}$$

where T_k is the depth-averaged temperature over the kth trophic layer of the model. The stratification index $\mathcal{S}$ is defined as the absolute difference of temperature between the surface and subsurface layers:

$$\mathcal{S}(x,y,t) = |T_{21}(x,y,t) - T_{12}(x,y,t)|. \tag{2}$$

The surface velocity norm $\mathcal{V}$ is defined as:

$$\mathcal{V}(x,y,t) = \sqrt{u_1^2(x,y,t) + v_1^2(x,y,t)}, \tag{3}$$

where u_1 and v_1 are ~~respectively~~ the zonal and meridional components of the depth-averaged velocity respectively, in the first layer of the model. The phytoplankton bloom index $\mathcal{B}$ is defined following Siegel et al. (2002) and Henson and Thomas (2007) as a Boolean: 1 for bloom regions and 0 for no bloom regions according to temporal variation relative to annual median threshold overshooting. More precisely, we define:

$$\mathcal{B}(x,y) = \begin{cases} 1 & \text{if there exists } t \text{ such that} \quad |PP(x,y,t) - \widetilde{PP}(x,y)| > 0.05 \times \widetilde{PP}(x,y), \\ 0 & \text{elsewhere.} \end{cases} \tag{4}$$

where $\widetilde{PP}(x,y)$ is the temporal median of the primary production $PP(x,y,t)$ at point (x,y). Note that contrary to the previous indicator variables, the bloom index does not depend on time. For each indicator variable $\mathcal{G} \in \{\mathcal{T}, \mathcal{S}, \mathcal{V}, \mathcal{B}\}$ we define several ordered value-based *regimes*. The number of regimes ~~together with regime~~ and regimes boundary values are obtained by partitioning the set G_N of the values of the indicator variable $\mathcal{G}$ at N observable locations constituting an ensemble $S_N \subset \Omega$.

$$G_N = \{g_i = \mathcal{G}(X_i) \quad X_i \in S_N\}_{1 \leq i \leq N}. \tag{5}$$

The partition of G_N is computed using a k-mean clustering ~~method (Kanungo et al., 2002)and the~~ (Kanungo et al., 2002). The k-mean clustering method separates N values in a given number of cluster by minimizing the distance of each value to the mean

150   (called the center) of each cluster. The number of clusters is chosen according to the Elbow score (Kodinariya and Makwana, 2013; Tibshirani et al., 2001). The k-mean method leads to n clusters $(\Gamma_k)_{k \in \{1...n\}}$ (called indicator variable regimes), that satisfy the following properties:

$$
\begin{cases}
\bigcup_{k=1}^{n} \Gamma_k = G_N \quad \text{and} \quad \forall i, j \in \{1...n\}, i \neq j, \quad \Gamma_i \bigcap \Gamma_j = \emptyset \\
\text{and} \\
\forall i \in \{1...N\}, g_i \in \Gamma_k \quad \text{if} \quad k = \underset{l \in \{1...n\}}{\operatorname{argmin}} \|g_i - \mu_l\|,
\end{cases}
\tag{6}
$$

where μ_l is the mean of values in Γ_l. Note that Γ_k depends on the variable $\mathcal{G}$. In the following, we ~~explicit this dependence~~

155   make this dependence explicit by denoting $\Gamma_k(\mathcal{G})$. The k-mean clustering allows for size-varying class compared to more classical statistical analysis that would consist for example to define the regimes as the quantile of the variables distributions. This latter could lead to under or over estimation of some regimes. The same kind of problem would arise from a classification defined by traditional eco-regions (Longhurst, 1995; Sutton et al., 2017), which would not account for the specificity of our forcing fields. This is why performing a clustering on the set of forcing fields used seems a more rigorous approach here.

160   We define a *configuration* as the intersection of a selection of regimes of given indicator variables. For ~~$i \in [\![1, n_\mathcal{T}]\!], j \in [\![1, n_\mathcal{S}]\!], k \in [\![1, n_\mathcal{V}]\!]$ and $l \in [\![1, n_\mathcal{B}]\!]$~~ $i \in \{1...n_\mathcal{T}\}, j \in \{1...n_\mathcal{S}\}, k \in \{1...n_\mathcal{V}\}$ and $l \in \{1...n_\mathcal{B}\}$, the configuration C is defined as:

$$
C = \mathcal{T}_i \otimes \mathcal{S}_j \otimes \mathcal{V}_k \otimes \mathcal{B}_l = \Gamma_i(\mathcal{T}) \bigcap \Gamma_j(\mathcal{S}) \bigcap \Gamma_k(\mathcal{V}) \bigcap \Gamma_l(\mathcal{B}),
\tag{7}
$$

where $n_\mathcal{G}$ is the number of clusters for the indicator variable $\mathcal{G}$. For the sake of simplicity we may also say that an observation point belongs to a configuration when the values of the indicator variables at this point belong to the corresponding regimes of

165   the configuration. Each configuration corresponds to a subset $S_M \subset S_N$ of observable points.

2.3   ~~Twin experiments~~OSSE system configuration

~~In this paper,~~ The implementation of OSSE requires to follow a precise protocol (Hoffman and Atlas, 2016). Here, we describe the different steps. A scheme summarizing the OSSE methodology is given in Figure 1.

2.3.1   Nature run

170   The nature run (NR) used to perform the OSSE is generated using the ~~inverse model and MLE are used in the framework of twin experiments as in (Lehodey et al., 2015). A reference simulation (TRUTH) is generated from the~~ reference configuration of SEAPODYM-MTL described in section 2.1. The reference simulation is used to compute synthetic observations. The goal is to retrieve back the reference energy transfer coefficients of the six micronekton functional groups E'_i by assimilating the synthetic observations into a ~~twin simulation of SEAPODYM. However, contrary to Lehodey 2015, an error is introduced~~

175   different simulation of SEAPODYM-MTL, called the control run.

2.3.2   Control run

The control run (CR) used to perform the parameter estimate is generated using perturbed forcing fields (Figure 1). A perturbation is added to the reference forcing fields ~~as input of the twin simulation. This is~~ in order to consider more real-istically the discrepancy between the real state of the ocean (represented here by the ~~TRUTH simulation) during data collection~~

180 NR) and the simplified representation of ~~these conditions by the ocean circulation model used for the parameter optimization. The twin simulation (TWIN) differs thus from the reference simulation (TRUTH) by the forcing fields and the coefficients E'_i. The reference forcing fields~~ this state by numerical models. The reference forcing fields are perturbed with a white noise whose maximal amplitude is a fraction of the averaged fields. Let F be the considered forcing field and let $\overline{F}$ be its global average (in space and time), we define the perturbed field as:

185 $$\widetilde{F}(x,y,t) = F(x,y,t) + \gamma(\alpha\overline{F}), \tag{8}$$

where $\alpha \in [0,1]$ is the amplitude of the perturbation and $\gamma \in [-1,1]$ is a uniformly distributed random number. The amplitude α is set to 0.1 for all experiments ~~. The~~ except in section 3.4 where α varies. For small values of F, this perturbation can induce a sign reversal of the forcing. This does not matter for the temperature or the currents velocities, primary production has however been constraint to positive values. White noise has been preferred to more realistic perturbation to avoid any geographical

190 bias pattern. The implications of this choice are further discussed in section 4.3. Its amplitude, fixed to 10% of error, is however representative of the mean error estimated for ocean circulation models (Lellouche et al., 2012; Ferry et al., 2012). The parameters E'_i are randomly sampled between 0 and 1. This *first guess* is used as initialization of the optimization scheme. We run each experiment several times with different random sampled first guess in order to ensure that the inverse model is not sensitive to the initial parameters. The set-up of the ~~TRUTH and TWIN~~ NR and CR simulations are summarized in Table 1.

195 2.3.3 Assimilation module

A MLE is used as an assimilation module. Its implementation is based on an adjoint technique (Errico, 1997) to iteratively optimize a cost function that represents the discrepancy between model outputs and observations. This approach conforms to current practices. More details about the implementation of this approach in SEAPODYM can be found in Senina et al. (2008) and Lehodey et al. (2015).

200 2.3.4 Synthetic observations

In the framework of OSSE, we perform estimation experiments with different sets of ~~fixed number~~ ($N_e = 400$ ~~) of~~ synthetic observation points. The synthetic observations are sampled in the different configurations constructed as explained in the previous section. Let M be the number of points in a given configuration. If $M < N_e$, we consider that the configuration is too singular to be relevant for our study and is ignored. If $M > N_e$ we randomly extract a sub-sample $S_{N_e} \subset S_M$ of observation

205 points. In order to study the influence of one indicator at a time, we compare experiments for which the regime of the studied indicator varies and the regime of the other indicator variables remain fixed. In the following we call *primary variable* the studied indicator variable and *secondary variables* the ones whose regimes are fixed. For a given group of experiments, we check that the configurations are statistically comparable ~~between~~ to each others by ensuring that the distribution of secondary

variables are close enough between configurations (cf. marginal distribution plots in Section 3). If this not the case, they are not presented. reported. A random sampling of observations within each configuration is preferred to a more realistic observation network to avoid any geographical bias. But this choice is discussed in section 3.4, where realistic networks are tested. The coverage in terms of observation numbers is however quite realistic. We assume 400 observations, which at the resolution of the model (1°×1 month) corresponds for example to the deployment of six moorings during five years.

2.4 Estimation OSSE system evaluation metrics

The estimation experiments are evaluated using three metrics: (i) the performance of the estimation, (ii) its accuracy and (iii) its convergence speed.

(i) The performance is measured with the mean relative error between the estimated coefficients and the reference coefficients as defined in Lehodey et al. (2015) (Eq. 9:).

$$E_r = \frac{1}{6} \sum_{i=1}^{6} \left| \frac{\widehat{E_i'} - E_i'}{E_i'} \right|. \tag{9}$$

(ii) The accuracy is measured by the residual value of the likelihood which provides a good estimate of the discrepancy between the estimated and the observed biomass.

(iii) The convergence speed is measured by the iterations number of the optimization scheme.

The residual likelihood and iterations number metrics are provided by the Automatic Differentiation Model Builder (ADMB) algorithm (Fournier et al., 2012) that implements is used to implement the MLE. Each metric provides different and independent information. For example, it is possible to obtain good performance and bad accuracy with an experiment that estimates correctly the energy transfer parameters for the different functional groups but over- or under-estimates the total amount of biomass. The performance is generally used to discriminate the different experiments since the aim of the study is to find the networks that better estimate energy transfer coefficients and thus directly minimize the error E_r (Eq. 9). However, the accuracy and precision of the experiment are discussed. The convergence is necessary to ensure that the optimization problem is well defined.

3 Results

3.1 Environmental regimes clustering

The number of points by regime per regime, obtained from the clustering (Section 2.2) and defined for each environmental variable (Table 2), shows a large variability. Some regimes present represent a larger amount of observable points. For instance, the tropical temperature regime covers 31% of the observable points. Almost 50% of the observable points show a weak stratification and only 10% of them have a positive bloom index or high velocities. When they are shown on a map (Figure 2) these regimes reproduce classical spatial patterns described in the scientific literature (Fieux and Webster, 2017). The regimes of the

temperature variable ($\mathcal{T}$) show a latitudinal distribution. The polar regime ($\mathcal{T}_1$) is located south of the Polar front (Southern hemisphere) and in the Arctic Ocean. The subpolar regime is located between the Polar front and the South Tropical front (Southern Ocean), in the ~~Labrador and Greenland Seas~~ Subpolar gyre region (North Atlantic) and in the Bering Sea (North Pacific). The temperate regime covers the subtropical zones of the Southern Atlantic, Indian and Pacific Oceans, located north of the South Tropical front, and extends as well in the eastern part of the Atlantic and Pacific Ocean. The tropical regime covers most of the tropical ocean and the Indian ocean. The regimes of the stratification variable ($\mathcal{S}$) are also structured according to the latitude, as stratification depends on the temperature. The stratification decreases from the tropical oceans (where the surface waters are warm compared to the deep waters) to the pole (where the surface waters are almost as cold as the deep waters). The regimes of the ~~velocity variable~~ surface velocity norm ($\mathcal{V}$) highlight the main energetic structures of the oceanic circulation. The high surface currents regime thus covers the intense jet-structured equatorial currents, the western boundary currents (the Gulf Stream in the Atlantic and the Kuroshio in the Pacific), the Agulhas current along the South Africa coast and the Antarctic Circumpolar Current in the Southern Ocean. The regimes of bloom index ($\mathcal{B}$) separate mostly the productive regions (North Atlantic and North Pacific, Southern Ocean, Eastern side of Tropical Atlantic, along the African coast) from the non productive regions (center of subtropical gyres mostly, as well as coastal regions of Arctic and Antarctic).

Based on ~~this result~~ these results, we construct ~~and select configurations~~ ~~to conduct the OSSE (section 2.2).~~ all possible configurations, using the methodology described in subsection 2.2. Then the configurations are selected to perform the OSSEs presented in subsection 2.3. The choice of the configuration is limited by the number of observation points available in each of them. Among the 48 possible configurations, ~~22~~ 21 of them are ~~considered non-existent because they have~~ near-empty intersection and contain less than 0.5% of all observable points. They are thus considered as non-existent. In addition, we study the influence of the primary variable by selecting only groups of configurations whose distributions along secondary variables are similar. This leads to a selection of 7 groups of experiments (Table 3). The first three groups of Experiments 1a-b, 1c-d and 1e-f are meant to study the influence of the velocity regimes $\mathcal{V}_1$ and $\mathcal{V}_2$. The group of Experiments 2a-d will be used to study the influence of the temperature regimes $\mathcal{T}_1$, $\mathcal{T}_2$, $\mathcal{T}_3$ and $\mathcal{T}_4$. The group Experiments 3a-c will be used to investigate the influence of the stratification index regimes $\mathcal{S}_1$, $\mathcal{S}_2$ and $\mathcal{S}_3$. Finally, Experiments 4a-b and 4c-d are used for the study the influence of the bloom index regimes $\mathcal{B}_1$ and $\mathcal{B}_2$.

3.2 Estimation performance with respect to environmental conditions

Table 3 shows the selected configurations for each experiment as well as their evaluation metrics. All experiments converged after 16 to 28 iterations. This confirms that the optimization problem is well defined. Since the number of iterations is partially dependent on the random initial first guess, it is not used as a criterion of discrimination between experiments.

3.2.1 Influence of the horizontal currents velocity

The influence of the ~~currents~~ current velocity regimes (high ~~currents~~ current velocity system or low ~~currents~~ current velocity system) on the performance of the parameters estimation is studied considering three groups of experiments (Table 3, Exp. 1a

to 1f). The observation points are randomly sampled in a subset of the considered configuration for which the primary variable is the currents velocity norm $\mathcal{V}$.

From these sets of experiments, it appears that the performance ~~on the estimation of parameters decreases with the~~ of the parameters estimation decreases with higher currents velocity at the observation ~~point~~points. This conclusion is valid ~~whatever~~ regardless of the regime of the secondary variables: either low or high temperatures, positive or null bloom index and weak or strong stratification (Table 3). Lower velocity reduces the error on the estimated energy transfer coefficients for functional groups that are impacted by currents in the epipelagic and upper mesopelagic layers. The currents decrease with depth and are almost uniform over the different regions in the lower mesopelagic layer (not shown). Consequently, the estimate of the parameters for the non migrant lower mesopelagic (lmeso) group is not sensitive to the regime of currents (Figure ~~??~~3a). Conversely, the estimation is the most sensitive for the epipelagic group, whose dynamics is entirely driven by the surface currents.

Note that the influence of low and high velocities is not explored for all secondary variable fixed regimes. Indeed, even ~~with~~ within fixed regimes, the secondary variables distribution along observation points might not be statistically comparable between two experiments. This could lead to a potential bias introduced by a secondary variable, which is not the target of the study. For instance, the influence of velocity in a polar temperature regime can be investigated by comparing the configurations $C' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$ (low velocity) and $C'' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_2$ (high velocity). The corresponding ~~twin~~ estimation experiments Exp. 1' ~~(observations sampled in C')~~ and Exp. 1" ~~(observations sampled in C")~~ estimate two sets of parameters ~~whose relative distances to the target parameters are~~ give relative errors of 48% and 10% respectively. ~~Before concluding that observations in very cold (polar regimes) and highly dynamics waters improve the performance of the estimation, it is necessary to check the~~ This result seems contradictory with Exps. 1a-f. But looking at the distributions of the observations along the secondary variables.~~The temperature shows the presence of a strong bias is (Figure 4). Therefore, despite~~, we can notice that the temperatures are different between the two configurations. Despite this, it has been fixed to the "polar regime", the temperature in configuration C' is on average lower ($-0.7°$C) than the temperature of configuration C" ($2.1°$C) ~~. Thus Experiments~~ (Figure 4). Thus Exps. 1' and 1" measure ~~correlatively the influence of the velocity and of the~~ the combined effect of both velocity and temperature. The lower velocities are coupled with lower temperatures and the higher velocities with higher temperatures. Therefore, it ~~seems here that the difference observed in the temperature values of the two datasets has a stronger impact on the parameter estimation than the regime of currents.~~ is not possible to conclude on the influence of the velocity on the parameters estimation from these experiments.

In the following, although distribution along secondary variables are not always shown, they have always been used in the analysis to check that the ~~results of twin experiments~~ OSSE results are not biased by this type of difference between the distributions of randomly selected datasets. Experiments with such cross-correlation between indicator variables are not presented, this concerns 9 out of the 26 possible experiments.

3.2.2 Influence of ~~the~~ temperature

In experiments 2a to 2d (Table 3), temperature is the primary variable, ranging from polar regime (Exp. 2a), to subpolar (Exp. 2b), temperate (Exp. 2c) and tropical (Exp. 2d) regimes. All other indicator variables (stratification, velocity and bloom index) are secondary variables that are set to weak, low and 1 respectively. Figure 5 shows that the distributions along the secondary variables of each configuration are close enough for the experiments to be compared, avoiding any risk of cross-correlation. The performance of the estimation increases with the temperature (Figure ~~??~~3b). The mean error on the parameter estimates decreases respectively from polar (Exp. 2a; 9.1%) to subpolar (Exp. 2b; 7%), temperate (Exp. 2c; 3%) and tropical (Exp. 2d; 1.4%) configurations (Table 3).

3.2.3 Influence of ~~the vertical gradient of temperature~~stratification

The influence of ~~the stratification is~~ stratification is first investigated with a ~~first~~ set of three configurations combining tropical temperature regime, low velocity regime, null bloom index regime and three regimes of weak (Exp. 3a); intermediate (Exp. 3b) and strong (Exp. 3c) stratification. A marginal distribution plot of observation sets for all experiments (not shown) indicates that the three ~~data sets~~ datasets differ only along the stratification variable (primary variable). The observation points display a temperature between $14°C$ and $17°C$, a velocity between 0 and 0.07 m s^{-1} and a null bloom index for each experiments. The performance decreases with the intensity of stratification (Figure ~~??~~ 3c and Table 3). The mean error is: 3.5% for a weak stratification and a vertical gradient of about $0.4°C$ (Exp. 3a), 5.9% for an intermediate stratification with a gradient of about $5.9°C$ (Exp. 3b) and 8% for a strong stratification, around $11.7°C$ (Exp. 3c). A strong stratification seems to deteriorate the estimate for all migrant groups (Figure ~~??~~3c). These results are not specific to the choice of regimes for the secondary variables. The same kind of experiments were carried out in a temperate regime (not shown) and ~~if~~ even though the mean error on the estimated parameters ~~were higher in~~ is higher on average, the result does not change: ~~a~~ weak stratification always leads to a better estimation than ~~a~~ strong stratification. The comparison was not fully possible in other temperature or velocity regimes because these configurations are not sufficiently ~~well represented(see Section 3.2.1).~~ represented.

3.2.4 Influence of ~~the~~ primary production

In order to investigate the influence of ~~the~~ primary production on the performance of the estimation, we compare the results of estimation in configurations with different bloom index regimes (primary variable). Temperature, stratification index and velocity have been fixed (secondary variables) to subpolar, weak and low regimes respectively (Exp. 4a and 4b) and to tropical, strong and low for Exp. 4c and 4d. Distributions of the observation points along the secondary variables indicate that the experiments are not biased by secondary variables, as the distributions present similar modes centered at $5°C$ for the temperature, at $0.5°C$ for the stratification index and at 0.04 m s^{-1} for the velocity (Exp. ~~1a and 1b~~4a and 4b) and at $15.5°C$, $11°C$ and 0.05 m s^{-1} respectively for Exp. 4c and 4d (not shown).

Both Exp. 4a and 4b result ~~both~~ in an averaged error of 7% on the estimated parameters (Table 3). Exp. 4d (averaged error of 8%) gives a similar value as Exp. 4b. Indeed, ~~not only the temperature is higher but also the vertical gradient of~~

~~temperature . As we concluded it~~ Exp. 4d ($\mathcal{T}_4$ regime) has higher temperature than Exp. 4b ($\mathcal{T}_2$ regime) but it has also a higher strafication index ($\mathcal{S}_3$ regime for Exp. 4d and $\mathcal{S}_1$ regime for Exp. 4b). Following conclusions from the two previous sections, ~~the temperature improves the performance of the estimation when increasing and the gradient deteriorates the performance when increasing~~ better performance is achieved when temperature increases, though increasing stratification has the opposite effect. So, the two effects might compensate in this case and result in a similar estimation. However, when considering bloom regions (Exp. 4c), the estimation error falls to 1.5% ~~in~~ on average. In addition, this experiment estimates the energy transfer coefficients for migrant micronekton groups with less than 1% error (Figure ~~??~~3d).

3.3 Global map of parameters estimation errors

When considering all possible experiments, and given the fact that all these configurations are associated to specific locations and times, it is possible to represent a global map of averaged estimation ~~error~~ errors (Eq. 9). This map (Figure 6) shows that on average, the error increases from the equator towards the poles ~~(Figure 6)~~. The lowest performances (errors $> 40\%$) are mostly found in the Arctic and Southern Ocean. Low performances are also found at some specific locations ~~along the veins of the main currents~~ (e.g. along the main currents). The signature of the Antarctic Circumpolar Current ~~can be~~ is found in the Southern Ocean with error over 10%. Similarly, the signature of the North Atlantic Drift can be seen with a patch of high errors between Canada and Ireland (Figure 2c and 6). The patch of high errors in the North Pacific Ocean ~~is however~~, however, is difficult to interpret. The equatorial regions show interesting patterns that are similar across the three oceans. In the vicinity of the equator, good performances are observed (mean error 2%). On both northern and southern sides of this low error band, the performance is ~~degraded~~ decreased with errors reaching about 8%. The equatorial regions are characterized by strong currents and warm surface waters. As ~~demonstrated~~ described above, these environmental features have ~~antagonistic~~ opposite effects on the performance of the estimation. Therefore, a possible explanation of this distribution of errors is that water temperature is high enough to overcome the effect of currents ~~velocity~~ in the equatorial band, but when moving poleward, the temperature decreases cannot compensate anymore for the negative effect of currents which is still quite strong. It is to note that the map presented in Figure 6 has been obtained for a given set of forcing fields (temperature, velocity, primary production). It is thus dependent on the simulation that is used. The regime-dependence of the estimation performance is however independent of the simulation.

3.4 Testing realistic networks

The above experiments are based on random selection of observation points within a large subset. This technique was chosen to avoid any bias related to the temporal or spatial potential ~~correlation~~ auto-correlation of observation networks. However, sampling at sea is rarely randomly distributed and can generate correlations. To relax this strong assumption, we ~~made twin~~ perform experiments based on positions from real acoustic transects (underways ship measurements). Two regions are compared using positions data ~~collected during the maintenance cruises~~ of the PIRATA ~~network of moorings~~ cruises in the Equatorial Atlantic

Ocean (PIRATA[5]) and during research) and cruises of the British Antarctic Survey in Antarctic peninsula region (BAS[5]) (Figure 7).

The same forcing, method and initial parameterization were used with a random noise amplitude (α) increasing from 0 to 0.2. Subsets of $N_e = 400$ observations were selected along the transects to run the experiments. The resulting averaged relative error on the coefficients is shown as a function of the amplitude of perturbation (Figure 8a) for both networks. It appears that the estimation error increases with the amplitude of the error introduced on the forcing field. Also, whatever the perturbation, the estimation error is always lower when using PIRATA observation networks than BAS observation networks. These results are fully consistent with the previous results indicating that networks located in tropical warm waters, as for PIRATA, give better estimates than the ones located in cold waters, as for the BAS (Figure 8b). The This should give confidence in the fact that our results are robust when the "random sampling" hypothesis used in the previous section is relaxed and that more realistic sampling designs are considered. Here in particular, the temporal auto-correlation of the different samplings is very strong since PIRATA and BAS are both underway ship measurements taken from 2-month cruises, repeated annually. The results seem much less dependent to the exact design of the samplings and the seasonality of the measurements than to their actual geographical location. Oceanic conditions of the observations (correlated to their geographical location) are the first order of sensitivity. In this sense, the PIRATA network is thus a very promising observatory for the micronekton, especially since it already includes a complete set of various physical and biogeochemical parameters measurements (Foltz et al., 2019).

4 Discussion

The modeling of micronekton in SEAPODYM-MTL relies on relatively simple mechanisms with a few parameters and three fundamental environmental forcing variables: temperature, horizontal currents and primary production, that influence the dynamics of the model. They also influence the skills of the MLE to estimate its parameters, assuming that a reasonable set of accurate micronekton biomass values can be collected at sea. This study allowed characterizing oceanic configurations based on the four variables used to drive the model. Given the definition of micronekton functional groups based on the DVM behavior between vertical layers, the stratification can effectively result in important changes in the dynamics of micronekton and the resulting biomass distribution. Once defined with the clustering method, the configurations were used to run twin experiments allowing to identify which associated environmental conditions were the most favorable to the estimation of energy transfer efficiency coefficients of the model. We found that observations from warm temperature regions (such as temperate or tropical regions) were more effective than those from cold regions. The presence of a bloom at the location of observation also improves the performance of the estimation (especially in warm environment). Conversely, high temperature stratification and high intensity of currents are both found to deteriorate the estimation. Thus, at global scale, we found that the better conditions for the estimation of energy transfer coefficient are warm waters, low currents, low vertical temperature gradients and seasonally high primary production In the following, we will discuss a possible theoretical interpretation of the

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4.1 An interpretation of the performance in term of observability

The differences in the performance of parameter estimation can be interpreted in ~~regard~~ the light of the characteristic times of physical and biological processes. The parameters we want to estimate (E'_i) control the energy transfer efficiency between the primary production (PP) and micronekton production (P) (Eq. A3; Appendix A). These parameters are thus directly related to the relative amount of P at age $\tau = 0$ in each functional group and we have:

$$E'_i = \frac{P_i(\tau = 0)}{cE_{pp} \int PP dz} \tag{10}$$

where E_{pp} is the total energy transfer from the primary production to the mid-trophic level, all functional groups together and c a conversion coefficient (see Appendix A). It is possible to rewrite the initial condition (Eq. A3) as a system of six equations involving the energy transfer coefficients.

$$
\begin{cases}
\rho_{1,d}(P_{|\tau=0}) = E'_1 \\
\rho_{1,n}(P_{|\tau=0}) = E'_1 + E'_3 + E'_6 \\
\rho_{2,d}(P_{|\tau=0}) = E'_2 + E'_3 \\
\rho_{2,n}(P_{|\tau=0}) = E'_2 + E'_4 \\
\rho_{3,d}(P_{|\tau=0}) = E'_4 + E'_5 + E'_6 \\
\rho_{3,n}(P_{|\tau=0}) = E'_4
\end{cases}
\tag{11}
$$

where $\rho_{K,\omega}(P_{|\tau=0})$ is the ratio of age 0 potential micronekton production in the layer $K \in \{1,2,3\}$, at the time of the day $\omega \in \{\text{day}, \text{night}\}$.

The ~~micronekton predicted biomass in~~ predicted micronekton biomass at a given time and ~~place~~ location (grid cell) results from two main mechanisms. First, the potential production (P) evolves in time from age $\tau = 0$, and is redistributed by advection and diffusion until the recruitment time τ_r when it is transferred into biomass (B). Then, the biomass is built by the accumulation of recruitment over time in each grid cell and is lost due to a ~~temperature~~ temperature-dependent mortality rate, while the currents redistribute the biomass spatially. The observations are the relative amount of biomass in each layer, i.e. the ratios of biomass $\rho_{K,\omega}(B_{|t=t^o})$ (Eq. A5), where t^o is the time at which the observation is collected. Therefore, the observation will be as close as the energy transfer parameters we want to estimate if $\rho_{K,\omega}(B_{|t=t^o})$ is close to $\rho_{K,\omega}(P_{|\tau=0})$. This requires that the integrated mixing of biomass during the elapsed time between the age 0 of potential production and the time of observation (i.e. at least the recruitment time) ~~being~~ is as weak as possible. This can be achieved in ~~different~~ two ways: (i) either the currents are weak so that the advective mixing is also weak (but ~~still~~ the diffusive mixing will still remain); (ii) Or the temperature is high, leading to a short recruitment time with reduced period of transport and biomass redistribution. These two mechanisms can explain why warm temperatures and weak currents were found to improve the estimations compared to cold

temperatures and high velocities (Sections 3.2.1 and 3.2.2). An additional effect of warm temperature is to induce a higher mortality rate. When warm waters are combined with high primary production (e.g. the equatorial upwelling region), there is a rapid turnover of biomass and the relative ratios of biomass by layer are closer to the initial ratio of production and thus to the energy transfer efficiency coefficients. Conversely, at cold temperature, the mortality rate is lower; biomass is accumulated from recruitment events and carries with it the integrated mixing and the perturbed ratio structures. This can explain why, at warm temperature, high productivity is needed for a better estimation (section 3.2.4). A side effect is that if temperature is not homogeneous across layers, then the mortality rate λ will differ for each functional group, depending on the layers it inhabits. This will be an additional driver of perturbation on the observed ratios of biomass. This is consistent with the result that a strong thermal stratification degrades the performance of estimation (section 3.2.3).

An observation will thus be the most effective for the estimation of parameters if it carries the information of the initial distribution of primary production into functional groups. This is the case if the biomass is renewed quickly enough compared to the time it takes for the currents and diffusive coefficient to mix it. This condition can be seen in terms of equilibrium between the biological processes (production, recruitment and mortality) and the physical processes (advection and diffusion). For an observation to be the most useful to the parameter estimation, it is necessary that the characteristics time governing biological processes (τ_β) is shorter than the one governing physical processes (τ_ϕ) at the location of the observation : $\tau_\beta \ll \tau_\phi$.

This interpretation highlights the problem of observability of the parameters E_i' from the measurements $\rho_{K,\Omega}(B)$. The parameters are directly observable at the age $\tau = 0$ of the primary production, but the measurements and the information we can get on the system are available only after a time τ_r. The observability will then be the better if the observable variables have not changed too much during the time τ_r (short τ_r, slow ocean dynamics). This is intrinsically linked to governing equations of the system (Eq. A1-A3) and therefore should not be dependent of the framework of the study.

4.2 Towards eco-regionalization ?

The clustering approach we propose allowed identifying oceanic regions that provide optimal oceanic characteristics for our parameters estimation by separating regions where the distribution of biomass is driven by physical processes from regions where it is driven by biological processes. It gives essential information about the optimal regions for implementing observational networks. This could be seen as a new definition of eco-regions based on similar ecosystem structuring dynamics. The definition of ocean eco-regions has been proposed based on various criteria (Emery, 1986; Longhurst, 1995; Spalding et al., 2012; Fay and McKinley, 2014; Sutton et al., 2017; Proud et al., 2017). A convergence of these different approaches to identify regions characterized by homogeneous mesopelagic species communities would be of great interest to facilitate the modeling and biomass estimate of the mesopelagic components. Acoustic observation models could be developed and validated at the scale of these regions. Then, the observation models integrated to ecosystem and micronekton models as the one used here, would serve to convert their predicted biomass into acoustic signal to be directly compared to all acoustic observations collected in the selected region. This approach would allow

to account for (and estimate) the sources of biases and errors linked to acoustic observations directly in the data assimilation scheme.

4.3 Limitations and perspectives

460 We have chosen to model the error between the true state of the ocean and the ~~twin simulation~~ modelled state by adding a white noise perturbation to the forcings ~~. This method has been chosen to introduce a spatial homogeneous error to avoid any bias. A random noise ensures that the results obtained in different location are directly comparable. Nevertheless,~~ of the NR as input of the CR. The realism of this approach is questionable, as it does not take into account the possible spatial distribution of uncertainty and errors of ocean models, and other approaches would be interesting to explore. For instance,

465 implementing an error proportional to the deviation of the climatological field should be more realistic because it would be based on the natural and intrinsic variability of the ocean. Indeed, we expect forcing fields to be less accurate where the ocean has strong variability. However, for the purpose of our study, a spatial homogeneous error was preferable to avoid introducing any bias. Random noise ensures that the results obtained in different locations are directly comparable. Sensitivity study with respect to the choice of forcing errors modelling was beyond the scope of this study. In addition to the uncertainty on ocean

470 models outputs, other sources of uncertainties remain to be explored to progress toward more realistic estimation experiments. For instance, we considered that the observation operator (Eq. A5) is perfect but field observations are always tainted by errors. The micronekton biomass estimates at sea require a chain of extrapolation and corrections to account for the sampling gear selectivity and the portion of water layer sampled. For acoustic data, many factors need to be considered sources of potential error: the correction with depth, the target strength of species, the intercalibration between instruments and the signal

475 processing methods (Handegard et al., 2009, 2012; Kaartvedt et al., 2012; Proud et al., 2018). This is an important research domain that requires to combine multiple observation systems, including new emerging technologies as broadband acoustic, optical imagery and environmental DNA to reduce overall bias in estimates of micronekton biomass (e.g., Kloser et al., 2016) and use those estimates to assess, initiate and assimilate into ecosystem models. Finally, the results of the clustering approach need to be confirmed with other ocean circulation model outputs, especially at higher resolution to check the impact of the

480 mesoscale activity on the definition of optimal regions for energy transfer efficiency estimation. In a future study, in addition to test the impact of introducing noises in the observations, the same approach could be used to directly estimate also the model parameters that control the relationship between the water temperature and the time of development of micronekton organisms. Other perspectives may include a study of the sensitivity to the design of the samplings (the impact of moored instruments in comparison with underway measurements), in the continuity of the work of Lehodey et al. (2015).

485 5 Conclusions

Understanding and modelling marine ecosystem dynamics is considerably challenging. It generally requires sophisticated models relying on a certain number of parameterized physical and biological processes. SEAPODYM-MTL provides a parsimonious approach with only a few parameters and ~~a~~ an MLE to estimates these parameters from observations. ~~The~~ Among

them, the energy transfer efficiency coefficients are of great importance because they directly control the biomass of micronek-
ton functional groups, including those that undergo DVM and contribute to the sequestration of carbon dioxide into the deep
ocean (Davison et al., 2013; Giering et al., 2014; Ariza et al., 2015). Therefore, a correct assessment of energy transfer coeffi-
cients is crucial for climate studies. Given the high cost of observation at sea, the design of optimal ~~observation~~ observational
networks through simulation experiments (~~OSSE~~OSSEs) is a valuable approach before the deployment of ~~observing platforms.~~
such platforms. Our objective was different from most OSSEs studies designed to correct outputs of operational models, e.g.,
for weather and physical oceanography forecast systems (Fujii et al., 2019). Here the objective was to search for the optimal
observations to estimate the set of invariant fundamental parameters of the model. This study provides ~~a methodology~~ insights
for implementing such ~~an observation network~~observations, based on the definition of oceanic regions using only four vari-
ables: the depth-averaged temperature, a thermal stratification index, the surface ~~currents~~ current velocity norm and a bloom
index. ~~Twin experiments~~ Experiments that were conducted in these regions with random sampling or based on realistic exist-
ing networks have shown that the quality of the ~~estimation of~~ MLE for the energy transfer efficiency coefficients is mainly
linked to environmental conditions. ~~The~~ We found that observations from warm temperature regions (such as temperate or
tropical regions) were more effective than those from cold regions. The presence of a bloom at the location of observation also
improves the performance of the estimation (especially in warm environment). Conversely, high temperature stratification and
high intensity of currents are both found to deteriorate the estimate. Thus, an optimal combination of environmental factors
is found at a global scale for productive, warm and moderately stratified waters, with weak dynamics, such as the eastern
side of the tropical Oceans. ~~An interpretation~~ The main limitation in this study is certainly the absence of realistic modelling
of the different sources of errors: the error between the modelled and the true state of the ocean have been modelled with a
white noise perturbation that does not allow for spatially inhomogeneous errors. And the observations have been assumed to
be directly proportional to biomass. The absence of a realistic observation model converting the acoustic signal into biomass
(Jech et al., 2015) prevents to account for the different types of observation errors. Future studies should include these missing
components. An interpretation of the results in term of balance between characteristic times of biological and physical pro-
cesses has been proposed~~to explain these results. In a future study~~, ~~in addition to test the impact of introducing noises in~~
~~the observations, the same approach could be used to directly estimate also the model parameters~~~~that control the relationship~~
~~between the water temperature and the time of development of micronekton organisms.~~, pointing out a mathematical problem of
observability. Hopefully this study will help in the next development of observing networks for micronekton and more generally
will provide a useful methodology for future research aiming at investigating the influence of environmental conditions on the
observability of some parameters. In any cases, we believe it is a next step in the modeling of mid-trophic ecosystems and its
implications ranking from fisheries management to climate studies.

Appendix A: SEAPODYM-MTL underlying equations

SEAPODYM-MTL is based on a system of advection-diffusion-reaction equations for each functional group i, $i \in [\![1,6]\!]$, involving two state variables: the potential production P_i (expressed in ~~gramm~~ gram of wet weight by squared meters by day, $\mathrm{gWWm^{-2}d^{-1}}$) and the biomass B_i (expressed in gramm of wet weight by squared meters, $\mathrm{gWWm^{-2}}$):

$$\frac{\partial B_i}{\partial t} = -\left(\frac{\partial}{\partial x}(uB_i) + \frac{\partial}{\partial y}(vB_i)\right) + D\left(\frac{\partial^2 B_i}{\partial x^2} + \frac{\partial^2 B_i}{\partial y^2}\right) - \lambda(T)B_i + P_i(\tau_r(T)), \tag{A1}$$

$$\frac{\partial P_i}{\partial t} = -\left(\frac{\partial}{\partial x}(uP_i) + \frac{\partial}{\partial y}(vP_i)\right) + D\left(\frac{\partial^2 P_i}{\partial x^2} + \frac{\partial^2 P_i}{\partial y^2}\right) - \frac{\partial P_i}{\partial \tau}, \tag{A2}$$

where x, y, t and τ are the variables for space, time and age respectively. u, v $(\mathrm{ms^{-1}})$ and T (°C) are the currents velocities and temperature respectively. These variables are integrated over each layer K, $K \in [\![1,3]\!]$ and weighted by the time each functional group i spends in the layer. D is the diffusion coefficient accounting for both the physical diffusion and the ability of micronekton organisms to swim short distances. τ_r (days) is the recruitment coefficient corresponding to the age for which the potential production converts into biomass of micronekton. λ $(\mathrm{days^{-1}})$ is the mortality coefficient which accounts for natural mortality. Note that these two last parameters depend on the temperature.

The initial conditions for this system are :

$$B_i(t=0) = B_0, \quad P_i(t=0) = P_0, \tag{A3}$$

$$P_i(\tau=0) = cE_i'E_{pp} \int_{z_3}^{0} PP\, dz, \tag{A4}$$

where B_0 and P_0 are obtained by spinup, PP (in milimol of carbon per cubic meters per day, $\mathrm{mmolCm^{-3}d^{-1}}$) is the net primary production, E_{pp} (adimensional) is the total energy transfer from the primary production to the mid-trophic level, E_i' (adimensional) is the distribution of this energy into the different functional groups, c is the conversion coefficient between mmolC and gWW and $z_3 = min(10.5 \times z_{eu}, 1000)$, z_{eu} the euphotic depth (in meters).

A module estimates SEAPODYM-MTL parameters by a variational data assimilation method : a Maximum Likelihood Estimation (MLE) (Senina et al., 2008). This method minimizes a cost function (the likelihood) that measures the distance between the biomass predicted by the model and the observed biomass. As the model outputs and the observations are not directly comparable, they are transformed with an observation model operator $\mathcal{H}$. $\mathcal{H}$ is defined for each layer K as:

$$\mathcal{H} \quad : \quad B \quad \mapsto \quad \rho_{K,\omega} = \frac{\sum_{i|K(i,\omega)=K} B_i}{\sum_{i=1}^{6} B_i} \tag{A5}$$

where $K(i,\omega)$ denotes the layer that the functional group number i occupies at the time of the day ω. $\mathcal{H}$ gives for each layer the relative amount of biomass that we call *ratio* (Lehodey et al., 2015).

The gradient of the likelihood function is computed using the adjoint state method. The parameters are then estimated using a quasi-Newton algorithm implemented by the Automatic Differenciation Model Builder (ADMB) algorithm (Fournier et al., 2012). SEAPODYM-MTL and the exact formulation of the cost function are described in detail in Lehodey et al. (2015).

550 *Author contributions.* All authors contributed to the design of the study. AD developed the method, conducted the experiments, analyzed the results and wrote the original manuscript. AC and OT contributed to the development of the parameter estimation component of SEAPODYM-MTL. OT prepared the forcing fields and contributed to the revision of the manuscript. PL coordinated the AtlantOS activity at CLS and contributed to the analysis of results and the revision of the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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Table 1. SEAPODYM-MTL parameters used for the two different ~~simulation TRUTH~~ simulations: the nature run (NR) and ~~TWIN~~the control run (CR). E is the energy transferred by net primary production to intermediate trophic levels, λ is the mortality coefficient, τ_r is the minimum age to be recruited in the mid-trophic functional population, D is the diffusion rate that models the random dispersal movement of organisms. $E'_i, i \in [\![1,6]\!]$ are the redistribution energy transfer coefficients to the 6 components of the micronekton population. The parametrization of the ~~TRUTH simulation~~ NR is called the reference parametrization and is taken from Lehodey et al. (2010).

Simulation	$1/\lambda$ (d)	τ_r (d)	D (NM^{2}d^{-1})	E	E_1	E'_2	E'_3	E'_4	E'_5	E'_6	Forcing
~~TRUTH~~ NR	2109	527	15	0.0042	0.17	0.10	0.22	0.18	0.13	0.20	F
~~TWIN~~ CR	2109	527	15	0.0042	——————— first guess ———————						$\widetilde{F}$ (Eq. 8)

Table 2. Outcome of the clustering method (Section 2.2). For each indicator variable (Temperature $\mathcal{T}$, Stratification $\mathcal{S}$, Velocity $\mathcal{V}$ and Bloom Index $\mathcal{B}$), the number n of clusters, the center and size (# observable) of each cluster (regimes) are given, as well as the proportion of all observable point it represents.

	Temperature ($\mathcal{T}$; $n = 4$)				Stratification ($\mathcal{S}$; $n = 3$)			Velocity ($\mathcal{V}$; $n = 2$)		Bloom Index ($\mathcal{B}$; $n = 2$)	
Regimes	$\mathcal{T}_1$	$\mathcal{T}_2$	$\mathcal{T}_3$	$\mathcal{T}_4$	$\mathcal{S}_1$	$\mathcal{S}_2$	$\mathcal{S}_3$	$\mathcal{V}_1$	$\mathcal{V}_2$	$\mathcal{B}_1$	$\mathcal{B}_2$
Regime names of $\Gamma_k(\mathcal{G})$, $k \in [\![1, n]\!]$	**polar**	**subpolar**	**temperate**	**tropical**	**weak**	**inter.**	**strong**	**low**	**high**	**bloom**	**no bloom**
Cluster center	$0.4°$C	$6.4°$C	$12.6°$C	$16.3°$C	$0.4°$C	$5.9°$C	$11.7°$C	0.05 ms^{-1}	0.3 ms^{-1}	74.6 mmolCm^{-2}d^{-1}	18.4 mmolCm^{-2}d^{-1}
# Observable in cluster	1106695	658105	1115102	1300298	2084302	1212945	882949	3698826	481367	449545	3730655
Proportion	26.5%	15.7%	26.7%	31.1%	49.8%	29.0%	21.1%	88.5%	11.5%	10.8%	89.2%

Table 3. Experiment table. List of conducted experiments, their corresponding configurations and the evaluation diagnostics: mean relative error on the coefficients, residual likelihood and number of iterations. The ~~section~~ tested regime (primary variable) is specified in ~~which~~ the first column, the number of observale belonging to each configuration is indicated in the fourth column, with their relative proportion in brackets. Note that even if the number of ~~these~~ observable differ for each configuration, the experiments were conducted with 400 observations randomly chosen among the ones belonging to the configuration. The section that describes each experiment is ~~discribed is given~~ mentioned in the last column.

	Experiment	Configuration	# Observable	E_r (Eq. 9)	Residual Likelihood	# Iterations	Section
Velocity ($\mathcal{V}$)	1a	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	317695 (7.6%)	7.0%	0.9	28	3.2.1
	1b	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_2$	54343 (1.3%)	9.7%	0.5	21	
	1c	$\mathcal{T}_3 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	112865 (2.7%)	3.1%	0.5	24	
	1d	$\mathcal{T}_3 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_1$	397119 (9.5%)	8.3%	1.5	23	
	1e	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	401299 (9.6%)	1.5%	1.1	16	
	1f	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_2 \otimes \mathcal{B}_1$	146307 (3.5%)	8.5%	1.2	18	
Temperature ($\mathcal{T}$)	2a	$\mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	982347 (23.5%)	9.1%	1.7	19	3.2.2
	2b	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	175568 (4.2%)	7.0%	0.6	26	
	2c	$\mathcal{T}_3 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	112865 (2.7%)	3.1%	1.3	20	
	2d	$\mathcal{T}_4 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	58522 (1.4%)	1.4%	0.6	22	
Stratification ($\mathcal{S}$)	3a	$\mathcal{T}_4 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	75244 (1.8%)	3.5%	0.7	21	3.2.3
	3b	$\mathcal{T}_4 \otimes \mathcal{S}_2 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	91964 (2.2%)	5.9%	0.8	25	
	3c	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	40130 (0.9%)	8.0%	1.1	21	
Bloom Index ($\mathcal{B}$)	4a	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	175568 (4.2%)	7.0%	0.6	26	3.2.4
	4b	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	317695 (7.6%)	7.0%	0.9	28	
	4c	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	401299 (9.6%)	1.5%	0.6	22	
	4d	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	40130 (0.9%)	8.0%	0.8	21	
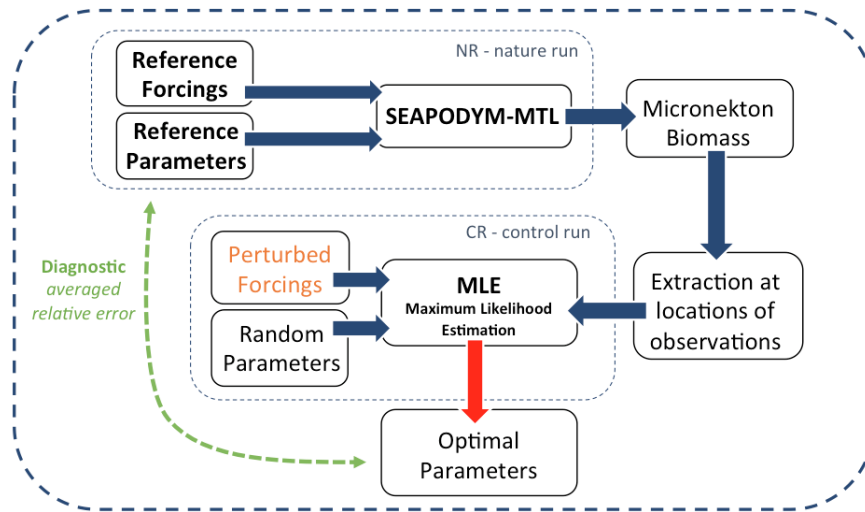
Figure 1. ~~Spatial division~~ A schematic view of the ~~different regimes~~OSSE system. ~~(a) **Temperature** : polar (pale blue), subpolar (yellow), temperate (gray), tropical (red). (b) **Stratification** : weak (dark blue), intermediate (purple), strong (magenta). (c) **Currents Velocities** : low (blue), high (orange). (d) **Bloom Index** : bloom (green), no bloom (beige). Each point of~~ The synthetic observations are generated using the ~~subset S_N has been plotted at its spatial location~~ simulation with ~~a color corresponding to~~ the ~~regime it belongs to~~reference configuration (nature run). ~~A transparency factor has been applied in order~~ The control run is used to ~~account for~~perform the ~~temporal fluctuation of regimes (a given point may belongs to different regimes over time)~~estimation experiments. The ~~resulting color on~~ evaluation of the ~~map corresponds to~~ OSSE is done by comparing the ~~most frequent regime~~ estimated parameters with the ~~corresponding point belongs to~~reference parameters.
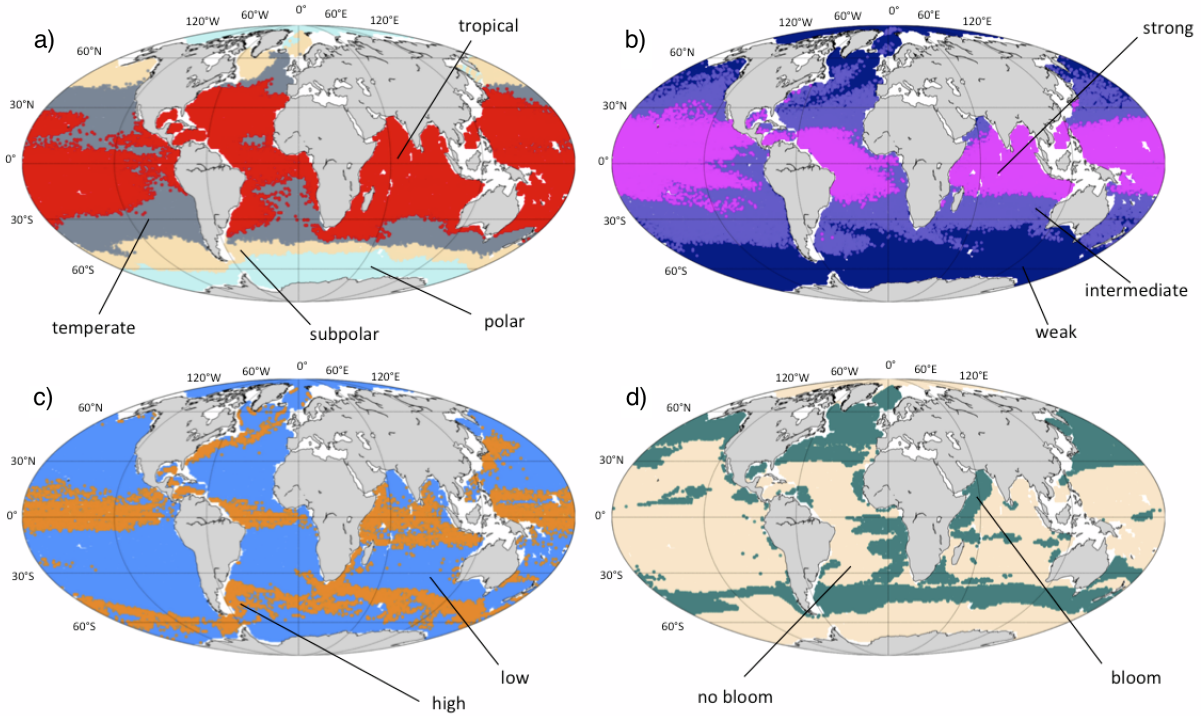
Figure 2. Spatial division of the different regimes as defined in Table 2. **(a) Temperature** : polar (pale blue), subpolar (yellow), temperate (gray), tropical (red). **(b) Stratification** : weak (dark blue), intermediate (purple), strong (magenta). **(c) Currents Velocities** : low (blue), high (orange). **(d) Bloom Index** : bloom (green), no bloom (beige). Each point of the subset S_N has been plotted at its spatial location with a color corresponding to the regime it belongs to.
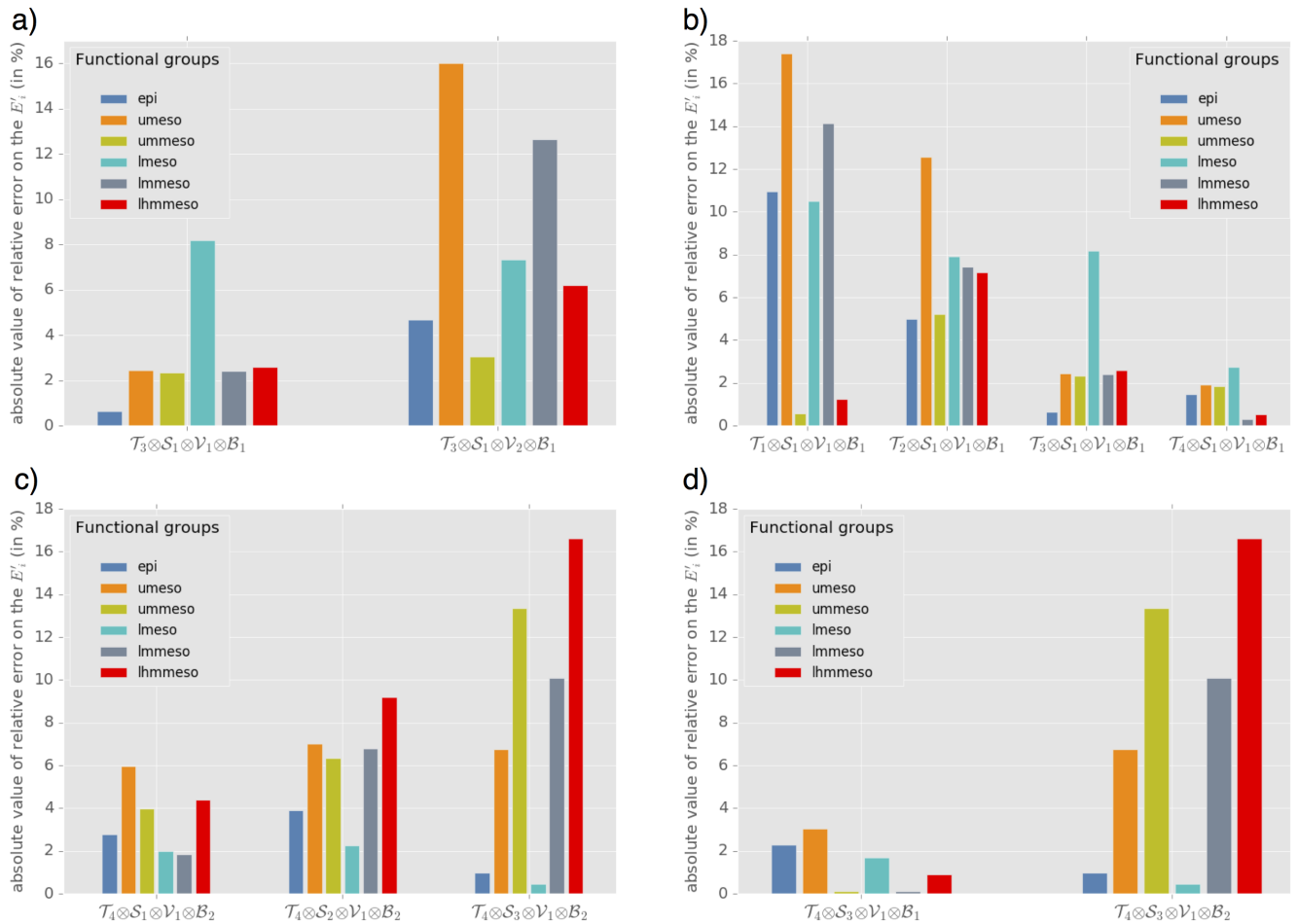
Figure 3. Mean relative error (E_r in %, Eq. 9) on each E_i' coefficients ~~–~~for (a) Exp. 1c and 1d, which present the following tested regimes: high ~~vs~~ versus low velocities in temperate temperatures, weak stratification and bloom regimes; (b) Exp. 2a, 2b, 2c and 2d which compares polar, subpolar, temperate and tropical temperatures in weak stratification, low velocity and bloom regimes; (c) Exp. 3a, 3b and 3c which compares weak, intermediate and high stratification in tropical temperatures, low velocity and no bloom regimes; and (d) Exp. 4c and 4d: bloom versus no bloom regimes in tropical temperatures, strong stratification and low velocities.
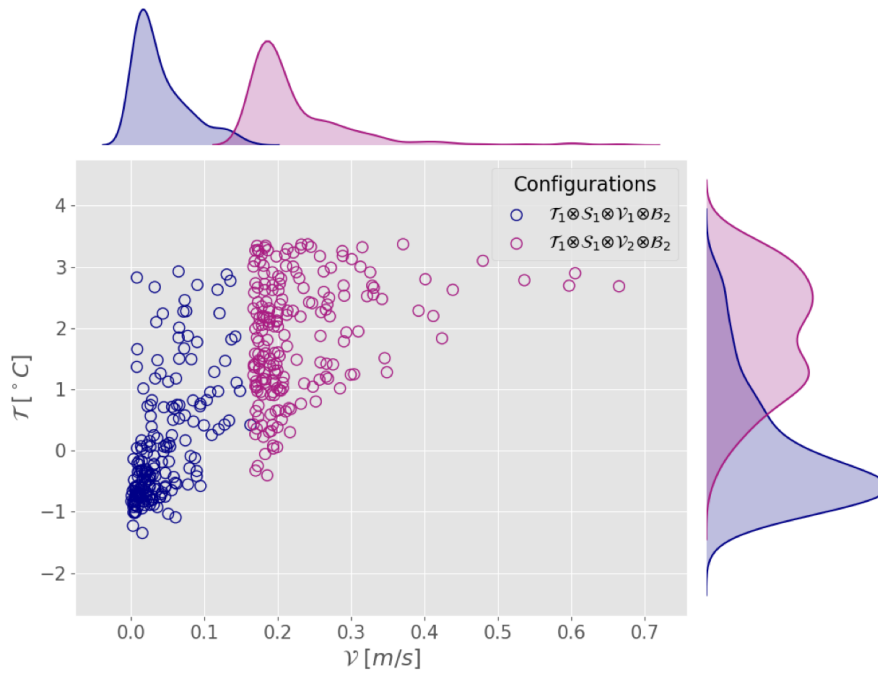
Figure 4. Scatter plot and marginal distribution from kernel density estimation (Silverman, 2018) in the plane $(\mathcal{V}, \mathcal{T})$ of observation points used in Exp. 1' and 1" generated by random sampling in configurations $C' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$ and $C'' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_2$.

Mean relative error (E_r in %, Eq. 9) on each E'_i coefficients for Exp. 2a, 2b, 2c and 2d : polar vs subpolar vs temperate vs tropical temperatures in weak stratification, low velocity and bloom regimes.
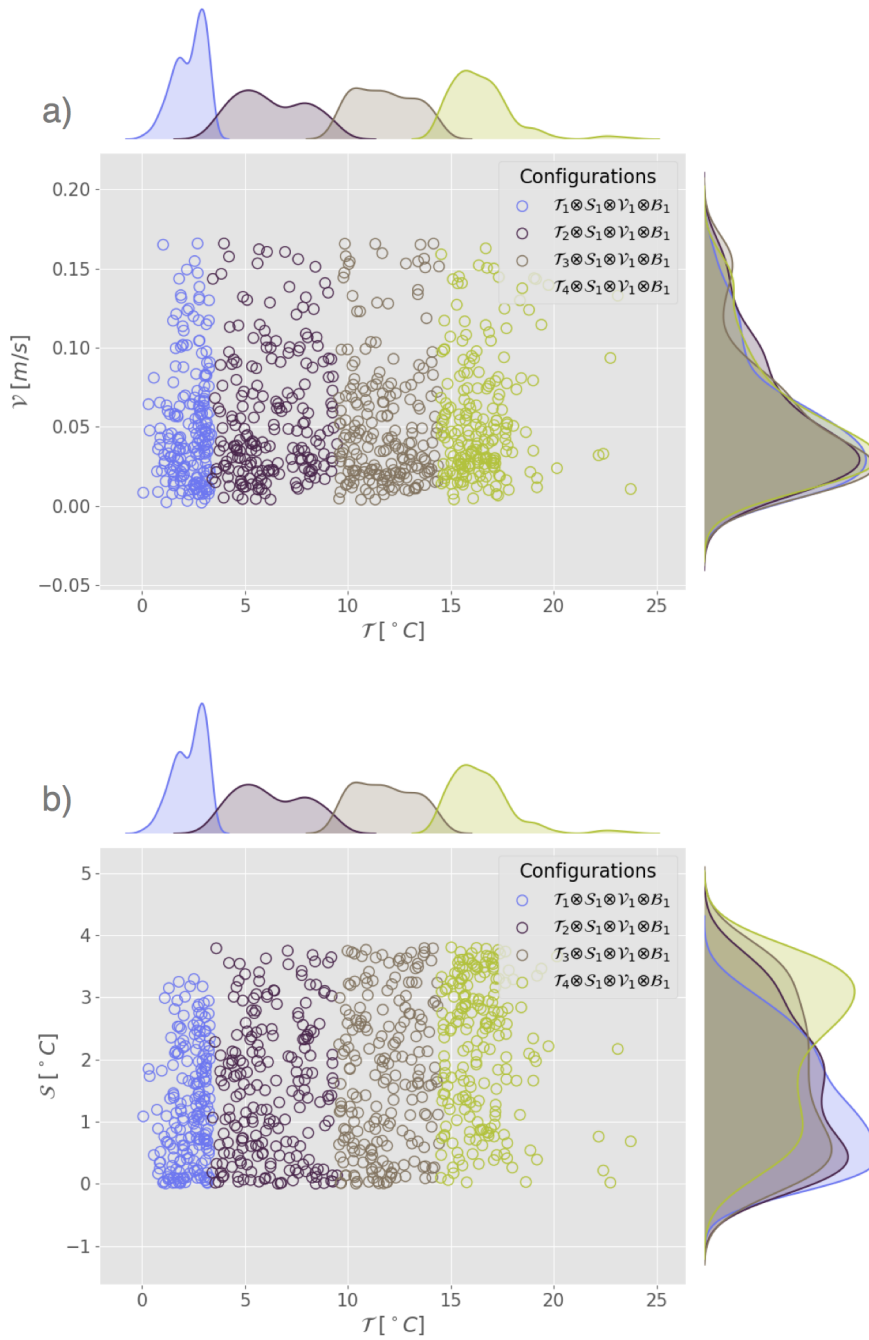
Figure 5. Scatter plot and marginal distribution from kernel density estimation in the plane (a) $(\mathcal{T},\mathcal{V})$ and (b) $(\mathcal{T},\mathcal{S})$ for the configurations corresponding to Exp. 3a, 3b, 3c and 3d from table 3.

655 ~~Mean relative error (E_r in %, Eq. 9) on each E_i' coefficients for Exp. 3a, 3b and 3c : comparison of weak, intermediate and high stratification in tropical temperatures, low velocity and no bloom regimes.~~

Mean relative error (E_r in %, Eq. 9) on each E'_i coefficients for Exp. 4c and 4d : bloom (4c) vs no bloom (4d) regimes in tropical temperatures, strong stratification and low velocities.
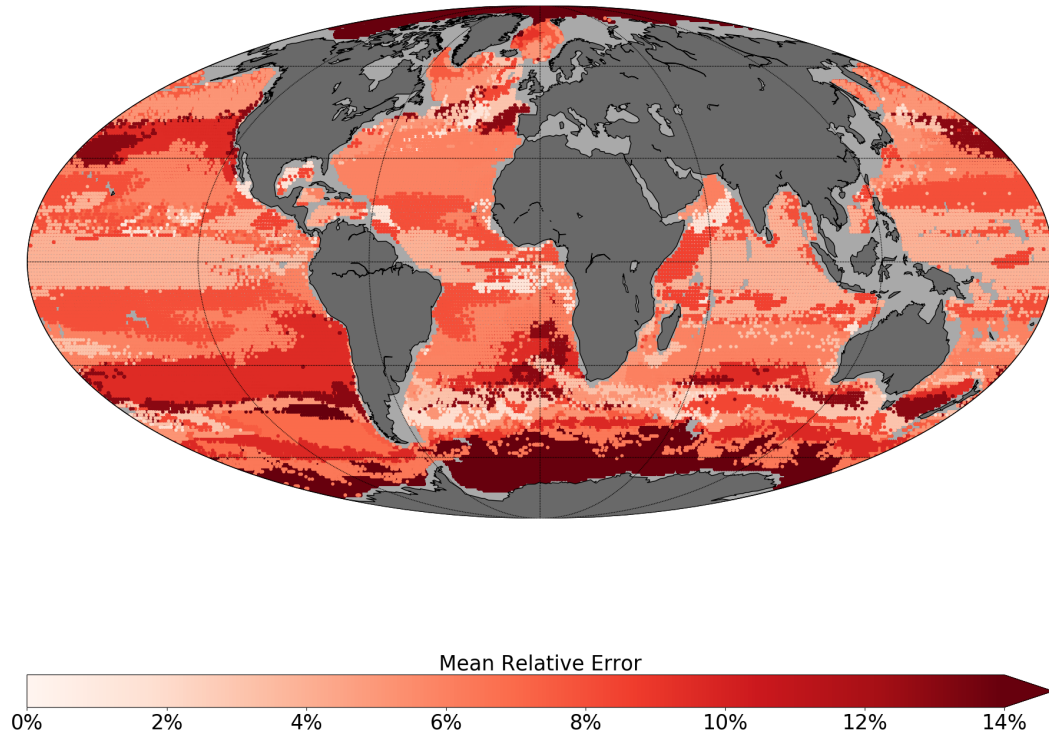
Figure 6. Averaged absolute value of relative error (E_r in %, Eq. 9) between the estimated and the target energy transfer parameters (E_i') according to the location of the chosen observation points~~in~~, associated to the ~~twin experiment framework~~forcing fields descrbed in section 2.1. Cells with no data have been shaded in grey.
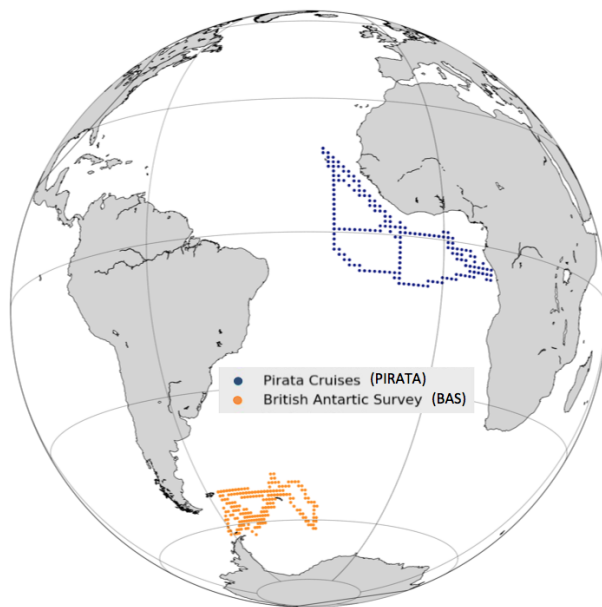
Figure 7. Map of PIRATA and BAS ship transects for the years 2013-2015.
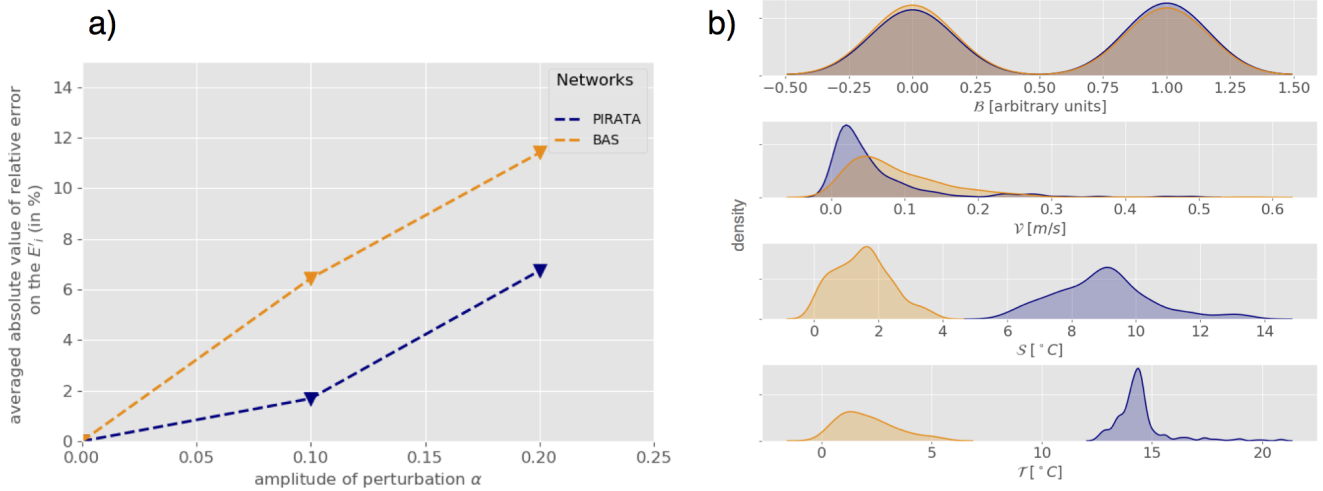
Figure 8. (a) Mean relative error on the coefficients E_r (in %, Eq. 9) as a function of the perturbation amplitude α (Eq. 8) for PIRATA (blue) and BAS (orange) observation networks. (b) Statistical distribution of all PIRATA (blue) and BAS (orange) observation location indicator variables : Bloom Index ($\mathcal{B}$), velocity norm ($\mathcal{V}$), stratification index ($\mathcal{S}$) and temperature ($\mathcal{T}$) estimated using kernel density estimation (Silverman, 2018).

Annotated Draft – Reviewer 1

Influence of oceanic conditions in the energy transfer efficiency estimation of a micronekton model

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Abstract. Micronekton – small marine pelagic organisms mostly in the size range 1-10 cm– is a key component of the ocean ecosystem, as it constitutes the main source of forage for all larger predators. Moreover, the mesopelagic component of micronekton that undergoes Diel Vertical Migration (DVM) likely plays a key role in the transfer and storage of CO_2 in the deep ocean: the so-called 'biological pump' mechanism. SEAPODYM-MTL is a spatially explicit dynamical model of micronekton. It simulates six functional groups of migrant and non-migrant micronekton, in the epipelagic and mesopelagic layers. Coefficients of energy transfer efficiency between primary production and each group are unknown but they are essential as they control ~~the predicted~~ biomass. Since these coefficients are not directly measurable, a data assimilation method is used ~~to estimate them~~. In this study, Observing System Simulation Experiments (OSSE) in the framework of twin experiments are used to test various observation networks at a global scale regarding energy transfer coefficients estimation. Observational networks show a variety of performances. It appears that environmental conditions are crucial to determine ~~network efficiency~~. According to our study, ideal sampling areas are warm, ~~non-dynamic~~ and productive with like the eastern side of tropical Oceans. These regions are found to reduce the error of estimated coefficients by 20% compared to cold and dynamic sampling regions. The results are discussed in term of interactions between physical and biological processes.

1 Introduction

Micronekton organisms are at the mid-trophic level of the ocean ecosystem and have thus a central role, as prey of all larger predator species and as a potential new resource in the blue economy (St John et al., 2016). Diel Vertical Migrations (DVM) characterizes a large biomass of the mesopelagic component of micronekton inhabiting the twilight zone (200-1000 m) of the world ocean. Through these daily migrations, the mesopelagic micronekton potentially contributes to a substantial transfer of atmospheric CO_2 to the deep ocean after its metabolization by photosynthesis and export through the food chain. The understanding and quantification of this mechanism, called the 'biological pump', are crucial in the context of climate change (Zaret and Suffern, 1976; Benoit-Bird et al., 2009; Davison et al., 2013; Giering et al., 2014; Ariza et al., 2015). However, there is a lack of comprehensive dataset at global scale to properly estimate micronekton biomass and composition. The few existing estimates of global biomass of mesopelagic micronekton vary considerably between less than 1 and ∼ 20 Gt (Gjosaeter and

Kawaguchi, 1980; Irigoien, 2014; Proud et al., 2018), so that micronekton has been compared to a "dark hole" in the studies
25   of marine ecosystems (St John et al., 2016). Therefore, a priority is to develop the datasets, methods and models needed to
simulate and quantify the dynamics and functional roles of these species' communities.

Observations and biomass estimations of micronekton rely traditionally on net sampling and active acoustic sampling (e.g.,
Handegard et al., 2009; Davison, 2011). Each method has limitations. Micronekton species can detect approaching fishing
gears and part of them can move away to avoid the net. This phenomenon leads to biomass underestimation from net trawling
30   (Kaartvedt et al., 2012). Conversely, acoustic signal intensity may overestimate biomass due to presence of organisms with
strong acoustic target strength, e.g. many mesopelagic species but also siphonophores that have gas inclusion inducing strong
resonance (Davison, 2011; Proud et al., 2017). Some organisms like squids, have both excellent skills to escape the trawl net and
a low response to acoustic signal, making this component strongly underestimated with both methods. Progress are expected in
the coming years thanks to the use of multiple acoustic frequencies associated to traditional net sampling and optical techniques
35   (Kloser et al., 2016; Davison et al., 2015). More accurate biomass estimates should benefit from this combination of techniques
and the developments of algorithms that can attribute acoustic signal to biological groups.

While these techniques of observation and methods of in situ estimates of biomass are progressing, new developments are
also achieved in the modeling of ocean ecosystem including micronekton components. SEAPODYM (Spatial Ecosystem And
POpulation Dynamics Model) is an eulerian ecosystem model that includes one lower- (zooplankton) and six mid-trophic (mi-
40   cronekton) functional groups, and detailed target fish populations (Lehodey et al., 1998, 2008). Given the structural importance
of DVM, the functional groups are defined based on the daily migration behavior of organisms between three broad epi- and
meso-pelagic bio-acoustic layers (Lehodey et al., 2010, 2015). The spatial dynamics of biomass in each group is driven by the
ocean circulation, while a diffusion coefficient account for local random movements. The time of development and the natural
mortality of organisms in the functional groups are linked to the temperature in the vertical layer inhabited during the day
45   or night. These mechanisms are simulated with a system of advection-diffusion-reaction equations. Primary production is the
source of energy distributed to each group according to a coefficient of transfer efficiency. Eleven parameters control the bio-
logical processes: a diffusion coefficient, six coefficients $(E'_i)_{i\in[\![1,6]\!]}$ of energy transfer from primary production toward each
mid-trophic functional group and four parameters for the relationship between water temperature and time of development
(mortality, recruitment) (Lehodey et al., 2010). The later four parameters were estimated from a compilation of data found
50   in the scientific literature (Lehodey et al., 2010). Therefore, the largest uncertainty remains on the energy transfer efficiency
coefficients, that control the total abundance of each functional group.

A method to estimate the model parameters has been developed using a Maximum Likelihood Estimation (MLE) approach
(Senina et al., 2008). Its implementation is based on an adjoint technique (Errico, 1997) to iteratively optimize a cost function
that represents the discrepancy between model outputs and observations. A first study has shown that this method can be used
55   to estimate the parameters E'_i using relative ratios of observed acoustic signal and predicted biomass in the three vertical layers
during daytime and nighttime (Lehodey et al., 2015). A single acoustic transect was used, with the strong assumption that
acoustic signal and predicted biomass were directly proportional. While we can expect that improved estimates of micronekton
biomass become available in the coming years, they will likely still require costly operations at sea. Therefore, it is useful to use

model and its MLE approach to evaluate the potential that these observations contain for the model parameters estimation
60   through Observing System Simulation Experiments (OSSE) (Arnold and Dey, 1986).

     The objective of the present study is to characterize and identify the sampling regions, regarding oceanic variables, in which micronekton biomass observation gives the most useful information for the model energy transfer coefficients estimation. For this purpose, we use OSSE based on twin experiments. A set of synthetic observations is generated with SEAPODYM using a reference parameterization. Then, the set of parameter values is changed and an error is added to the forcing field in order to

65   simulate more realistic conditions. The MLE is used to estimate the set of parameters from the set of synthetic observations. The difference between the reference and estimated parameters provides a metric to select the best sampling zones. A method based on the clustering (Jain et al., 1999) of oceanic variables (temperature, currents velocity, stratification and productivity) is presented to investigate the sensitivity of the parameters estimation to the oceanographic conditions of the observation regions. This method aims at determining which conditions are the most favorable for collecting observations in order to estimate the

70   energy transfer efficiency coefficients.

     The paper is organized as follows: Section 2 describes the model set-ups and forcings. The method developed to characterize regions of observations and the metrics used to evaluate the parameters estimation are detailed as well. Section 3 describes the outcome of the clustering method to define oceanographic regimes and synthesizes the main results of our estimation experiments. The results are then discussed in Section 4 in the light of biological and dynamical processes. Some applications

75   and limitations of our study are also identified along with suggestions for possible future research.

2   Method

2.1   SEAPODYM-MTL and its configuration

SEAPODYM-M models six functional groups of micronekton in the epi- and upper and lower mesopelagic layers at a global scale. These layers encompass the upper 1000 m of the ocean, as observed from acoustic detection and net sampling.

80   The euphotic depth (z_{eu}) is used to define the depth boundaries of the vertical layers. These boundaries are defined as follows: $z_1(x,y,t) = 1.5 \times z_{eu}(x,y,t)$, $z_2(x,y,t) = 4.5 \times z_{eu}(x,y,t)$, $z_3(x,y,t) = \min(10.5 \times z_{eu}(x,y,t), 1000)$, where z_{eu} is given in meters. The six functional groups are called (1) epi (for the organisms inhabiting permanently the epipelagic layer); (2) umeso (for the organisms inhabiting permanently the upper mesopelagic layer); (3) ummeso (for migrant-umeso, the organisms inhabiting the upper mesopelagic layer at day and the epipelagic layer at night); (4) lmeso (for the organisms inhabiting

85   permanently the lower mesopelagic layer); (5) lmmeso (for migrant-lmeso, the organisms inhabiting the lower mesopelagic layer at day and the upper mesopelagic layer at night) and (6) lhmmeso (for highly migrant lmeso, the organisms inhabiting the lower mesopelagic layer at day and the epipelagic layer at night). The model is forced by current velocities, temperature and net primary production (see Appendix A for detailed equations).

     This work is based on a ten-year (2006-2015) simulation of SEAPODYM-MTL, called hereafter the TRUTH simulation.

90   Due to high computational demand, the original resolution of forcing fields (0.25°×week) has been degraded to 1°×month. Euphotic depth, horizontal velocity and temperature fields come from the ocean dynamical simulation FREEGL S2V4

produced by Mercator-Ocean[1]. Temperature and horizontal velocity fields are depth-averaged over the water column of each three trophic layers ending with a three-layers forcings field set. Net primary production is estimated using the Vertically Generalized Production Model (VGPM) of Behrenfeld and Falkowski (1997) with satellite derived chlorophyll a concentration.

95 This product is available at Ocean Productivity Home Page of the Oregon State University[2]. Initial conditions of SEAPODYM-MTL come from a two-years spin-up based on a monthly based climatology simulation in order to reach equilibrium. Reference values of SEAPODYM-MTL parameters in the TRUTH simulation are those published in Lehodey et al. (2010).

2.2 Clustering approach to characterize potential sampling regions

In this section we describe the method we use to select different observation sets for OSSE, based on environmental character-
100 istics. We define the spatio-temporal discrete observable space Ω as the set of the $1° \times 1°$ grid points belonging to SEAPODYM-MTL discrete domain. The characterization of each observation point relies on four indicators defined from the environmental variables: the depth-averaged temperature $\mathcal{T}$, a stratification index $\mathcal{S}$, the surface velocity norm $\mathcal{V}$ and a bloom index $\mathcal{B}$, for which different regimes of intensity are defined. The averaged temperature $\mathcal{T}$ over the water-column is defined as:

$$\mathcal{T}(x,y,t) = \frac{1}{3}(T_1(x,y,t) + T_2(x,y,t) + T_3(x,y,t)), \tag{1}$$

105 where T_k is the depth-averaged temperature over the kth trophic layer of the model. The stratification index $\mathcal{S}$ is defined as the absolute difference of temperature between the surface and subsurface layers:

$$\mathcal{S}(x,y,t) = |T_2(x,y,t) - T_1(x,y,t)|. \tag{2}$$

The surface velocity norm $\mathcal{V}$ is defined as:

$$\mathcal{V}(x,y,t) = \sqrt{u_1^2(x,y,t) + v_1^2(x,y,t)}, \tag{3}$$

110 where u_1 and v_1 are respectively the zonal and meridional components of the depth-averaged velocity in the first layer of the model. The phytoplankton bloom index $\mathcal{B}$ is defined following Siegel et al. (2002) and Henson and Thomas (2007) as a Boolean: 1 for bloom regions and 0 for no bloom regions according to temporal variation relative to annual median threshold overshooting. More precisely, we define:

$$\mathcal{B}(x,y) = \begin{cases} 1 & \text{if there exists } t \text{ such that} \quad |PP(x,y,t) - \widetilde{PP}(x,y)| > 0.05 \times \widetilde{PP}(x,y), \\ 0 & \text{elsewhere.} \end{cases} \tag{4}$$

115 where $\widetilde{PP}(x,y)$ is the temporal median of the primary production $PP(x,y,t)$ at point (x,y). Note that contrary to the previous indicator variables, the bloom index does not depend on time. For each indicator variable $\mathcal{G} \in \{\mathcal{T},\mathcal{S},\mathcal{V},\mathcal{B}\}$ we define several ordered value-based *regimes*. The number of regimes together with regime boundary values are obtained by partitioning the set G_N of the values of the indicator variable $\mathcal{G}$ at N observable locations constituting an ensemble $S_N \subset \Omega$.

$$G_N = \{g_i = \mathcal{G}(X_i) \quad X_i \in S_N\}_{1 \le i \le N}. \tag{5}$$

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[1]https://www.mercator-ocean.fr/
[2]http://www.science.oregonstate.edu/ocean.productivity/

120 The partition of G_N is computed using a k-mean clustering method (Kanungo et al., 2002) and the number of clusters is chosen according to the Elbow score (Kodinariya and Makwana, 2013; Tibshirani et al., 2001). The k-mean method leads to n clusters $(\Gamma_k)_{k \in [\![1,n]\!]}$ (called indicator variable regimes), that satisfy the following properties:

$$
\begin{cases}
\bigcup_{k=1}^{n} \Gamma_k = G_N \quad \text{and} \quad \bigcap_{k=1}^{n} \Gamma_k = \emptyset \\
\text{and} \\
\forall i \in [1,N], g_i \in \Gamma_k \quad \text{if} \quad k = \underset{l \in [1,n]}{\operatorname{argmin}} \|g_i - \mu_l\|,
\end{cases}
\tag{6}
$$

where μ_l is the mean of values in Γ_l. Note that Γ_k depends on the variable $\mathcal{G}$. In the following, we explicit this dependence

125 by denoting $\Gamma_k(\mathcal{G})$. We define a *configuration* as the intersection of a selection of regimes of given indicator variables. For $i \in [\![1,n_{\mathcal{T}}]\!]$, $j \in [\![1,n_{\mathcal{S}}]\!]$, $k \in [\![1,n_{\mathcal{V}}]\!]$ and $l \in [\![1,n_{\mathcal{B}}]\!]$, the configuration C is defined as:

$$
C = \mathcal{T}_i \otimes \mathcal{S}_j \otimes \mathcal{V}_k \otimes \mathcal{B}_l = \Gamma_i(\mathcal{T}) \cap \Gamma_j(\mathcal{S}) \cap \Gamma_k(\mathcal{V}) \cap \Gamma_l(\mathcal{B}),
\tag{7}
$$

where $n_{\mathcal{G}}$ is the number of clusters for the indicator variable $\mathcal{G}$. For sake of simplicity we may also say that an observation point belongs to a configuration when the values of the indicator variables at this point belong to the corresponding regimes of

130 the configuration. Each configuration corresponds to a subset $S_M \subset S_N$ of observable points.

2.3 Twin experiment

In this paper, the inverse model and MLE are used in the framework of twin experiments as in (Lehodey et al., 2015). A reference simulation (TRUTH) is generated from the reference configuration. The reference simulation is used to compute synthetic observations. The goal is to retrieve back the reference energy transfer coefficients of the six micronekton functional

135 groups E'_i by assimilating the synthetic observations into a twin simulation of SEAPODYM. However, contrary to Lehodey 2015, an error is introduced to the reference forcing fields as input of the twin simulation. This is to consider more realistically the discrepancy between the real state of the ocean (represented here by the TRUTH simulation) during data collection and the simplified representation of these conditions by the ocean circulation model used for the parameter optimization. The twin simulation (TWIN) differs thus from the reference simulation (TRUTH) by the forcing fields and the coefficients E'_i. The

140 reference forcing fields are perturbed with a white noise whose maximal amplitude is a fraction of the averaged fields. Let F be the considered forcing field and let $\overline{F}$ be its global average (in space and time), we define the perturbed field as

$$
\widetilde{F}(x,y,t) = F(x,y,t) + \gamma(\alpha\overline{F}),
\tag{8}
$$

where $\alpha \in [0,1]$ is the amplitude of the perturbation and $\gamma \in [-1,1]$ is a uniformly distributed random number. The amplitude α is set to 0.1 for all experiments. The parameters E'_i are randomly sampled between 0 and 1. This *first guess* is used as initial-

145 ization of the optimization scheme. We run each experiment several times with different random sampled first guess in order to ensure that the inverse model is not sensitive to the initial parameters. The set-up of the TRUTH and TWIN simulations are summarized in Table 1.

(cc) (i)

In the framework of OSSE, we perform estimation experiments with different sets of fixed number ($N_e = 400$) of synthetic
observation points. The synthetic observations are sampled in the different configurations constructed as explained in the
previous section. Let M be the number of points in a given configuration. If $M < N_e$, we consider that the configuration is too
singular to be relevant for our study and is ignored. If $M > N_e$ we randomly extract a sub-sample $S_{N_e} \subset S_M$ of observation
points. In order to study the influence of one indicator at a time, we compare experiments for which the regime of the studied
indicator varies and the regime of the other indicator variables remain fixed. In the following we call *primary variable* the
studied indicator variable and *secondary variables* the ones whose regimes are fixed. For a given group of experiments, we
check that the configurations are statistically comparable between each others by ensuring that the distribution of secondary
variables are close enough between configurations (cf. marginal distribution plots in Section 3). If this not the case, they are
not presented.

2.4 Estimation evaluation me

The estimation experiments are evaluated using three metrics: (i) the performance of the estimation, (ii) its accuracy and (iii)
its convergence speed.

(i) The performance is measured with the mean relative error between the estimated coefficients and the reference coefficients
as defined in Eq. 9:

$$E_r = \frac{1}{6} \sum_{i=1}^{6} \left| \frac{\widehat{E_i'} - E_i'}{E_i'} \right|. \tag{9}$$

(ii) The accuracy is measured by the residual value of the likelihood which provides a good estimate of the discrepancy
between the estimated and observed biomass.

(iii) The convergence speed is measured by the iterations number of the optimization scheme.

The residual likelihood and iterations number metrics are provided by the Automatic Differentiation Model Builder (ADMB)
algorithm (Fournier et al., 2012) that implements the MLE. Each metric provides different and independent information.
For example, it is possible to obtain good performance and bad accuracy with an experiment that estimates correctly the
energy transfer parameters for the different functional groups but over- or under-estimates the total amount of biomass. The
performance is generally used to discriminate the different experiments since the aim of the study is to find the networks that
better estimate energy transfer coefficients and thus directly minimize the error E_r (Eq. 9). However, the accuracy and precision
of the experiment are discussed. The convergence is necessary to ensure that the optimization problem is well defined.

3 Results

3.1 Environmental regimes clustering

The number of points by regime defined for each environmental variable (Table 2) shows a large variability. Some regimes present a larger amount of observable points. For instance, the tropical temperature regime covers 31% of the observable points. Almost 50% of the observable show a weak stratification and only 10% of them have a positive bloom index or high velocities. When they are shown on a map (Figure 1) these regimes reproduce classical spatial patterns described in the scientific literature (Fieux and Webster, 2017). The regimes of the temperature variable ($\mathcal{T}$) show a latitudinal distribution. The polar regime ($\mathcal{T}_1$) is located south of the Polar front (Southern hemisphere) and in the Arctic Ocean. The subpolar regime is located between the Polar front and the South Tropical front (Southern Ocean), in the Labrador and Greenland Seas (North Atlantic) and in the Bering Sea (North Pacific). The temperate regime covers the subtropical zones of the Southern Atlantic, Indian and Pacific Oceans, located north of the South Tropical front, and extends as well in the eastern part of the Atlantic and Pacific Ocean. The tropical regime covers most of the tropical ocean and the Indian ocean. The regimes of the stratification variable ($\mathcal{S}$) are also structured according to the latitude as stratification depends on the temperature. The stratification decreases from the tropical oceans (where the surface waters are warm compared to the deep waters) to the pole (where the surface waters are almost as cold as the deep waters). The regimes of the velocity variable ($\mathcal{V}$) highlight the main energetic structures of the oceanic circulation. The high currents regime thus covers the intense jet-structured equatorial currents, the western boundary currents (the Gulf Stream in the Atlantic and the Kuroshio in the Pacific), the Agulhas current along the South Africa coast and the Antarctic Circumpolar Current in the Southern Ocean. The regimes of bloom index ($\mathcal{B}$) separate mostly the productive regions (North Atlantic and North Pacific, Southern Ocean, Eastern side of Tropical Atlantic, along the African coast) from the non productive regions (center of subtropical gyres mostly, as well as coastal regions of Arctic and Antarctic).

Based on this result, we construct select configurations to constrain the OSSE (section 2.2). The choice of the configuration is limited by the number of observation points available in each of them. Among the 48 possible configurations, 22 of them are considered non-existent because they have less than 0.5% all observable points. In addition, we study the influence of the primary variable by selecting only groups of configurations whose distributions along secondary variables are similar. This leads to a selection of 7 groups of experiments (Table 3). The first three groups of Experiments 1a-b, 1c-d and 1e-f are meant to study the influence of the velocity regimes $\mathcal{V}_1$ and $\mathcal{V}_2$. The group of Experiments 2a-d will be used to study the influence of the temperature regimes $\mathcal{T}_1$, $\mathcal{T}_2$, $\mathcal{T}_3$ and $\mathcal{T}_4$. The group Experiments 3a-c will be used to investigate the influence of the stratification index regimes $\mathcal{S}_1$, $\mathcal{S}_2$ and $\mathcal{S}_3$. Finally, Experiments 4a-b and 4c-d are used for the study the influence of the bloom index regimes $\mathcal{B}_1$ and $\mathcal{B}_2$.

3.2   Esti on performance with respect to environmental conditions

Table 3 shows the selected configurations for each experiment as well as their evaluation metrics. All experiments converged after 16 to 28 iterations. This confirms that the optimization problem is well defined. Since the number of iterations is partially dependent on the random initial first guess, it is not used as a criterion of discrimination between experiments.

210   3.2.1   Influence of the horizontal currents velocity

The influence of the currents velocity regimes (high currents system or low currents system) on the performance of the parameters estimation is studied considering three groups of experiments (Table 3, Exp. 1a to 1f). The observation points are randomly sampled in a subset of the considered configuration for which the primary variable is the currents velocity norm $\mathcal{V}$. In these sets of experiments, it appears that the performance on the estimation of parameters decreases with the cur-

215   rents velocity at the observation point. This conclusion is valid whatever the regime of the secondary variables: either low or high temperatures, positive or null bloom index and weak or strong stratification (Table 3). Lower velocity reduces the error on the estimated energy transfer coefficients for functional groups that are impacted by currents in the epipelagic and upper mesopelagic layers. The currents decrease with depth and are almost uniform over the different regions in the lower mesopelagic layer (not shown). Consequently, the estimate of the parameters for the non migrant lower mesopelagic (lmeso)

220   group is not sensitive to the regime of currents (Figure 2). Conversely, the estimation is the most sensitive for the epipelagic group, whose dynamics is entirely driven by the surface currents.

Note that the influence of low and high velocities is not explored for all secondary variable fixed regimes. Indeed, even with fixed regimes, the secondary variables distribution along observation points might not be statistically comparable between two experiments. This could lead to a potential bias introduced by a secondary variable, which is not the target of the study.

225   For instance, the influence of velocity in a polar temperature regime can be investigated by comparing the configurations $C' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$ and $C'' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_2$. The corresponding ~~twin experiments Exp. 1~~' (observations sampled in C') and Exp. 1" (observations sampled in C") estimate two sets of parameters whose relative distances to the target parameters are 48% and 10% respectively. Before concluding that observations in very cold (polar regimes) and highly dynamics waters improve the performance of the estimation, it is necessary to check the distributions of the observations along the secondary

230   variables. The temperature shows the presence of a strong bias is (Figure 3). Therefore, despite it has been fixed to "polar regime", the temperature in configuration C' is on average lower ($-0.7°C$) than the temperature of configuration C" ($2.1°C$). Thus Experiments 1' and 1" measure correlatively the influence of the velocity and ~~of the~~ temperature. The lower velocities are coupled with lower temperatures and the higher velocities with higher temperatures. Therefore, it seems here that the difference observed in the temperature values of the two datasets has a stronger impact on the parameter estimation than the regime of

235   currents.

In the following, although distribution along secondary variables are not always shown, they have always been used in the analysis to check that the results of ~~twin experiments~~ are not biased by this type of difference between the distributions of randomly selected datasets. Experiments with such cross-correlation between indicator variables are not presented.

3.2.2 Influence of the temperature

240 In experiments 2a to 2d (Table 3), temperature is the primary variable, ranging from polar regime (Exp. 2a), to subpolar (Exp. 2b), temperate (Exp. 2c) and tropical (Exp. 2d) regimes. All other indicator variables (stratification, velocity and bloom index) are secondary variables that are set to weak, low and 1 respectively. Figure 5 shows that the distributions along the secondary variables of each configuration are close enough for the experiments to be compared, avoiding any risk of cross-correlation. The performance of the estimation increases with the temperature (Figure 4). The mean error on the parameter

245 estimates decreases respectively from polar (Exp. 2a; 9.1%) to subpolar (Exp. 2b; 7%), temperate (Exp. 2c; 3%) and tropical (Exp. 2d; 1.4%) configurations (Table 3).

3.2.3 Influence of the vertical gradient of temperature

The influence of the stratification is investigated with a first set of three configurations combining tropical temperature regime, low velocity regime, null bloom index regime and three regimes of weak (Exp. 3a); intermediate (Exp. 3b) and strong (Exp. 3c)

250 stratification. A marginal distribution plot of observation sets for all experiments (not shown) indicates that the three data sets differ only along the stratification variable (primary variable). The observation points display a temperature between $14°C$ and $17°C$, a velocity between 0 and 0.07 m s^{-1} and a null bloom index for each experiments. The performance decreases with the intensity of stratification (Figure 6 and Table 3). The mean error is: 3.5% for a weak stratification and a vertical gradient of about $0.4°C$ (Exp. 3a), 5.9% for an intermediate stratification with a gradient of about $5.9°C$ (Exp. 3b) and 8% for

255 a strong stratification, around $11.7°C$ (Exp. 3c). A strong stratification seems to deteriorate the estimate for all migrant groups (Figure 6). These results are not specific to the choice of regimes for the secondary variables. The same kind of experiments were carried out in a temperate regime (not shown) and if the mean error on the estimated parameters were higher in average, the result does not change: a weak stratification always leads to a better estimation than a strong stratification. The comparison was not fully possible in other temperature or velocity regimes because these configurations are not sufficiently well represented

260 ~~(see Section 3.2.1 §2)~~.

3.2.4 Influence of the primary production

In order to investigate the influence of the primary production on the performance of the estimation, we compare the results of estimation in configurations with different bloom index regimes (primary variable). Temperature, stratification index and velocity have been fixed (secondary variables) to subpolar, weak and low regimes respectively (Exp. 4a and 4b) and to tropical,

265 strong and low for Exp. 4c and 4d. Distributions of the observation points along the secondary variables indicate that the experiments are not biased by secondary variables as the distributions present similar modes centered at $5°C$ for the temperature, at $0.5°C$ for the stratification index and at 0.04 m s^{-1} for the velocity (Exp. 1a and 1b) and at $15.5°C$, $11°$ and 0.05 m s^{-1} respectively for Exp. 4c and 4d (not shown).

Exp. 4a and 4b result ~~both~~ in an averaged error of 7% on the estimated parameters (Table 3). ~~Exp.~~ 4d (averaged error of 8%)

270 gives a similar value as ~~Exp. 4b~~. Indeed, not only the temperature is higher but also the vertical gradient of temperature. ~~As~~

we concluded it from the two previous sections, the temperature improves performance of the estimation when increasing and the gradient deteriorates the performance when increasing. So, the two effects might compensate in this case and result in a similar estimation. However, when considering bloom regions (Exp. 4c), the estimation error falls .5% in average. In addition, this experiment estimates the energy transfer coefficients for migrant micronekton groups with less than 1% error (Figure 7).

3.3 Global map of parameters estimation errors

When considering all possible experiments, and given the fact that all these configurations are associated to specific locations and times, it is possible to represent a global map of averaged estimation error (Eq. 9). This map shows that on average, the error increases from the equator towards the poles (Figure 8). The lowest performances (errors $> 40\%$) are mostly found in the Arctic and Southern Ocean. Low performances are also found at some specific locations along the veins of the main currents. The signature of the Antarctic Circumpolar Current are found in the Southern Ocean with error over 10%. Similarly, the signature of the North Atlantic Drift can be seen with a patch of high errors between Canada and Ireland (Figure 1c and 8). The patch of high errors in the North Pacific Ocean is however difficult to interpret. The equatorial regions show interesting patterns that are similar across the three oceans. In the vicinity of the equator, good performances are observed (mean error 2%). On both northern and southern sides of this low error band, the performance is degraded with errors reaching about 8%. The equatorial regions are characterized by strong currents and warm waters. As demonstrated above, these environmental features have antagonistic effects on the performance of the estimation. Therefore, a possible explanation of this distribution of errors is that water temperature is high enough to overcome the effect of currents velocity in the equatorial band, but when moving poleward, the temperature decreases cannot compensate anymore for the negative effect of currents which is still quite strong.

3.4 Testing realistic networks

The above experiments are based on random selection of observation points within a large subset. This technique was chosen to avoid any bias related to the temporal or spatial potential correlation of observation networks. However, sampling at sea is rarely randomly distributed and can generate correlations. To relax this strong assumption, we made twin experiments based on positions from real acoustic transects. Two regions are compared using positions data collected during the maintenance cruises of the PIRATA network of moorings in the Equatorial Atlantic Ocean (PIRATA[3]) and during research cruises of the British Antarctic Survey in Antarctic peninsula region (BAS[4]) (Figure 9).

The same forcing, method and initial parameterization were used with a random noise amplitude (α) increasing from 0 to 0.2. Subsets of $N_e = 400$ observations were selected along the transects to run the experiments. The resulting averaged relative error on the coefficients is shown as a function of the amplitude of perturbation (Figure 10a) for both networks. It appears that the estimation error increases with the amplitude of the error introduced on the forcing field. Also, whatever the

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[3]http://www.brest.ird.fr/pirata/pirata
[4]https://www.bas.ac.uk/projects-wcb

perturbation, the estimation error is always lower when using PIRATA observation networks than BAS observation networks. These results are fully consistent with the previous results indicating that networks located in tropical warm waters, as for PIRATA, give better estimates than the ones located in cold waters, as for the BAS (Figure 10b). The PIRATA network is thus

305 a very promising observatory for the micronekton, especially since it already includes a complete set of various physical and biogeochemical parameters measurements (Foltz et al., 2019).

4 Discussion

The modeling of micronekton in SEAPODYM-MTL relies on relatively simple mechanisms with a few parameters and three fundamental environmental forcing variables: temperature, horizontal currents and primary production, that influence the dy-

310 namics of the model. They also influence the skills of the MLE to estimate its parameters, assuming that a reasonable set of accurate micronekton biomass values can be collected at sea. This study allowed characterizing oceanic configurations based on the four variables used to drive the model. Given the definition of micronekton functional groups based on the DVM behavior between vertical layers, the stratification can effectively result in important changes in the dynamics of micronekton and the resulting biomass distribution. Once defined with the clustering method, the configurations were used to run twin experiments

315 allowing to identify which associated environmental conditions were the most favorable to the estimation of energy transfer efficiency coefficients of the model. We found that observations from warm temperature regions (such as temperate or tropical regions) were more effective than those from cold regions. The presence of a bloom at the location of observation also improves the performance of the estimation (especially in warm environment). Conversely, high temperature stratification and high intensity of currents are both found to deteriorate the estimation. Thus, at global scale, we found that the better conditions for the

320 estimation of energy transfer coefficient are warm waters, low currents, low vertical temperature gradients and seasonally high primary production.

4.1 An interpretation of the performance in term of observability

The differences in the performance of parameter estimation can be interpreted in terms of the characteristic times of physical and biological processes. The parameters we want to estimate (E_i') control the energy transfer efficiency between the primary

325 production (PP) and micronekton production (P) (Eq. A3; Appendix A). These parameters are thus directly related to the relative amount of P at age $\tau = 0$ in each functional group and we have:

$$E_i' = \frac{P_i(\tau = 0)}{c E_{pp} \int PP dz} \tag{10}$$

(cc)

It is possible to rewrite the initial condition (Eq. A3) as a system of six equations involving the energy transfer coefficients.

$$
\begin{cases}
\rho_{1,d}(P_{|\tau=0}) = E'_1 \\
\rho_{1,n}(P_{|\tau=0}) = E'_1 + E'_3 + E'_6 \\
\rho_{2,d}(P_{|\tau=0}) = E'_2 + E'_3 \\
\rho_{2,n}(P_{|\tau=0}) = E'_2 + E'_4 \\
\rho_{3,d}(P_{|\tau=0}) = E'_4 + E'_5 + E'_6 \\
\rho_{3,n}(P_{|\tau=0}) = E'_4
\end{cases}
\tag{11}
$$

330   where $\rho_{K,\omega}(P_{|\tau=0})$ is the ratio of age 0 potential micronekton production in the layer $K \in \{1,2,3\}$, at the time of the day $\omega \in \{\text{day}, \text{night}\}$.

The micronekton predicted biomass in a given time and place (grid cell) results from two main mechanisms. First, the potential production evolves in time from age $\tau = 0$, and is redistributed by advection and diffusion until the recruitment time τ_r when it is transferred into biomass (B). Then, the biomass is built by accumulation of recruitment over time in each

335   grid cell and is lost due to a temperature mortality rate, while the currents redistribute the biomass. The observations are the relative amount of biomass in each layer, i.e. the ratios of biomass $\rho_{K,\omega}(B_{|t=t^o})$ (Eq. A5), where t^o is the time at which the observation is collected. Therefore, the observation will be as close as the energy transfer parameters we want to estimate if $\rho_{K,\omega}(B_{|t=t^o})$ is close to $\rho_{K,\omega}(P_{|\tau=0})$. This requires the integrated mixing of biomass during the elapsed time between the age of potential production and the time of observation (i.e. at least the recruitment time) be as weak as possible.

340   This can be achieved in different ways: (i) either the currents are weak so that the advective mixing is also weak (but still the diffusive mixing will remain); (ii) Or the temperature is high, leading to a short recruitment time with reduced period of transport and redistribution. These two mechanisms can explain why warm temperatures and weak currents were found to improve the estimations compared to cold temperatures or high velocities (Sections 3.2.1 and 3.2.2). An additional effect of warm temperature is to induce a higher mortality rate. When warm waters are combined with high primary production (e.g. the

345   equatorial upwelling region), there is a rapid turnover of biomass and relative ratios of biomass by layer closer to the initial ratio of energy transfer efficiency coefficients. Conversely, at cold temperature, the mortality rate is lower; biomass is accumulated from recruitment events with a more distant origin and carries with it the integrated mixing and the perturbed ratio structures. This can explain why, at warm temperature, high productivity is needed for a better estimation (section 3.2.4). A side effect is that if temperature is not homogeneous across layers, then the mortality rate λ will differ for each functional group, depending

350   on the layers it inhabits. This will be an additional driver of perturbation on the observed ratios of biomass. This is consistent with the result that a strong thermal stratification degrades the performance of estimation (section 3.2.3).

An observation will thus be the most effective for the estimation of parameters if it carries the information of the initial distribution of primary production into functional groups. This is the case if the biomass is renewed quickly enough compared to the time it takes for the currents and diffusive coefficient to mix it. This condition can be seen in terms of equilibrium between

355   the biological processes (production, recruitment and mortality) and the physical processes (advection and diffusion). In other words, for an observation to be effective for the estimation and not to introduce errors, it is necessary that the characteristics

time governing biological processes (τ_β) is shorter than the one governing physical processes (τ_ϕ) at the location of the observation : $\tau_\beta \ll \tau_\phi$.

This interpretation highlights the problem of observability of the parameters E'_i from the measurements $\rho_{K,\Omega}(B)$. The param-
360 eters are directly observable at the age $\tau = 0$ of the primary production, but the measurements and the information we can get on the system are available only after a time τ_r. The observability will then be the better if the observable variables have not changed too much during the time τ_r (short τ_r, slow ocean dynamics). This is intrinsically linked to governing equations of the system (Eq. A1-A3) and therefore should not be dependent of the framework of the study.

4.2 Towards eco-regionalization ?

365 The clustering approach we propose allowed identifying oceanic regions that provide optimal oceanic characteristics for our parameters estimation by discriminating regions where the distribution of biomass is driven by physical processes from regions where it is driven by biological processes. It gives an essential information on the optimal regions for implementing observation networks. This could be seen as a new definition of eco-regions based on similar ecosystem structuring dynamics. The definition of ocean eco-regions has been proposed based on various criteria (Emery, 1986; Longhurst, 1995; Spalding et al., 2012; Fay and
370 McKinley, 2014; Sutton et al., 2017; Proud et al., 2017). A convergence from these different approaches to identify regions characterized by homogeneous mesopelagic species communities would be of great interest to facilitate the modeling and biomass estimate of these components. Acoustic observation models could be developed and validated at the scale of these regions. Then, the observation models integrated to ecosystem and micronekton models as the one used here, would serve to convert their predicted biomass into acoustic signal to be directly compared to all acoustic observations collected in the
375 selected region. This approach would allow to account for (and estimate) the sources of biases and errors linked to acoustic observations directly in the data assimilation scheme.

4.3 Limitations and perspectives

We have chosen to model the error between the true state of the ocean and the twin simulation by adding a white noise perturbation to the forcings. This method has been chosen to introduce a spatial homogeneous error to avoid any bias. A
380 random noise ensures that the results obtained in different location are directly comparable. Nevertheless, other approaches would be interesting to explore. For instance, implementing an error proportional to the deviation of the climatological field should be more realistic because it would be based on the natural and intrinsic variability of the ocean. In addition to the uncertainty on ocean models outputs, other sources of uncertainties remain to be explored to progress toward more realistic estimation experiments. For instance, we considered that the observation operator (Eq. A5) is perfect but field observations
385 are always tainted by errors. The micronekton biomass estimates at sea require a chain of extrapolation and corrections to account for the sampling gear selectivity and the portion of water layer sampled. For acoustic data, many factors need to be considered sources of potential error: the correction with depth, the target strength of species, the intercalibration between instruments and the signal processing methods (Handegard et al., 2009, 2012; Kaartvedt et al., 2012; Proud et al., 2018). This is an important research domain that requires to combine multiple observation systems, including new emerging technologies

390   as broadband acoustic, optical imagery and environmental DNA to reduce overall bias in estimates of micronekton biomass (e.g., Kloser et al., 2016) and use those estimates to assess, initiate and assimilate into ecosystem models. Finally, the results of the clustering approach need to be confirmed with other ocean circulation model outputs, especially at higher resolution to check the impact of the mesoscale activity on the definition of optimal regions for energy transfer efficiency estimation.

5   Conclusions

395   Understanding and modelling marine ecosystem dynamics is considerably challenging. It generally requires sophisticated models relying on a certain number of parameterized physical and biological processes. SEAPODYM-MTL provides a parsimonious approach with only a few parameters and a MLE to estimates these parameters from observations. The energy transfer efficiency coefficients directly control the biomass of micronekton functional groups, including those that undergo DVM and contribute to the sequestration of carbon dioxide into the deep ocean (Davison et al., 2013; Giering et al., 2014;

400   Ariza et al., 2015). Therefore, a correct assessment of energy transfer coefficients is crucial for climate studies. ~~Given the high cost of observation at sea, the design of optimal observation networks through simulation experiments (OSSE) is a valuable approach before the deployment of observing platforms.~~ This study provides ~~a methodology~~ for implementing such an observation network, based on the definition of oceanic regions using only four variables: the depth-averaged temperature, a thermal stratification index, the surface currents velocity norm and a bloom index. Twin experiments that were conducted in

405   these regions with random sampling or based on realistic existing networks have shown that the quality of the estimation of the energy transfer efficiency coefficients is mainly linked to environmental conditions. The optimal combination of environmental factors is found for productive, warm and moderately stratified waters, with weak dynamics, such as the eastern side of the tropical Oceans. An interpretation in terms of balance between characteristic times of biological and physical processes has been proposed to explain these results. In a future study, in addition to test the impact of introducing noises in the observations,

410   the same approach could be used to directly estimate also the model parameters that control the relationship between the water temperature and the time of development of micronekton organisms.

Appendix A: SEAPODYM-MTL underlying equations

SEAPODYM-MTL is based on a system of advection-diffusion-reaction equations for each functional group i, $i \in [\![1,6]\!]$, involving two state variables: the potential production P_i (expressed in gramm of wet weight by squared meters by day,

415    $\mathrm{gWWm^{-2}d^{-1}}$) and the biomass B_i (expressed in gramm of wet weight by squared meters, $\mathrm{gWWm^{-2}}$):

$$\frac{\partial B_i}{\partial t} = -\left(\frac{\partial}{\partial x}(uB_i) + \frac{\partial}{\partial y}(vB_i)\right) + D\left(\frac{\partial^2 B_i}{\partial x^2} + \frac{\partial^2 B_i}{\partial y^2}\right) - \lambda(T)B_i + P_i(\tau_r(T)), \tag{A1}$$

$$\frac{\partial P_i}{\partial t} = -\left(\frac{\partial}{\partial x}(uP_i) + \frac{\partial}{\partial y}(vP_i)\right) + D\left(\frac{\partial^2 P_i}{\partial x^2} + \frac{\partial^2 P_i}{\partial y^2}\right) - \frac{\partial P_i}{\partial \tau}, \tag{A2}$$

where x, y, t and τ are the variables for space, time and age respectively. u, v (ms^{-1}) and T $(^{\circ}\mathrm{C})$ are the currents velocities and temperature respectively. These variables are integrated over each layer K, $K \in [\![1,3]\!]$ and weighted by the time each

420   functional group i spends in the layer. D is the diffusion coefficient accounting for both the physical diffusion and the ability of micronekton organisms to swim short distances. τ_r (days) is the recruitment coefficient corresponding to the age for which the potential production converts into biomass of micronekton. λ (days^{-1}) is the mortality coefficient which accounts for natural mortality. Note that these two last parameters depend on the temperature.

The initial conditions for this system are :

425   $$B_i(t=0) = B_0, \quad P_i(t=0) = P_0, \tag{A3}$$

$$P_i(\tau=0) = cE_i'E_{pp}\int_{z_3}^{0} PP\,dz, \tag{A4}$$

where B_0 and P_0 are obtained by spinup, PP (in milimol of carbon per cubic meters per day, $\mathrm{mmolCm}^{-3}\mathrm{d}^{-1}$) is the net primary production, E_{pp} (adimensional) is the total energy transfer from the primary production to the mid-trophic level, E_i' (adimensional) is the distribution of this energy into the different functional groups, c is the conversion coefficient between

430   mmolC and gWW and $z_3 = min(10.5 \times z_{eu}, 1000)$, z_{eu} the euphotic depth (in meters).

A module estimates SEAPODYM-MTL parameters by a variational data assimilation method : a Maximum Likelihood Estimation (MLE) (Senina et al., 2008). This method minimizes a cost function (the likelihood) that measures the distance between the biomass predicted by the model and the observed biomass. As the model outputs and the observations are not

435   directly comparable, they are transformed with an observation model operator $\mathcal{H}$. $\mathcal{H}$ is defined for each layer K as :

$$\mathcal{H} \quad : \quad B \quad \mapsto \quad \rho_{K,\omega} = \frac{\sum_{i|K(i,\omega)=K} B_i}{\sum_{i=1}^{6} B_i} \tag{A5}$$

where $K(i,\omega)$ denotes the layer that the functional group number i occupies at the time of the day ω. $\mathcal{H}$ gives for each layer the relative amount of biomass that we call *ratio* (Lehodey et al., 2015).

The gradient of the likelihood function is computed using the adjoint state method. The parameters are then estimated using

440   a quasi-Newton algorithm implemented by the Automatic Differenciation Model Builder (ADMB) algorithm (Fournier et al., 2012). SEAPODYM-MTL and the exact formulation of the cost function are described in detail in Lehodey et al. (2015).

Author contributions. AD designed the method, conducted the study ,analyzed the results and wrote the original manuscript. AC and OT contributed to the development of the parameter estimation component of SEAPODYM-MTL and helped designing the method. OT prepared the forcing fields, provided a technical support and a redaction support. PL coordinated the AtlantOS activity at CLS and contributed to the

445   design of the study, the analysis of results and the redaction.

Competing interests. The authors declare that they have no conflict of interest.

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Table 1. SEAPODYM-MTL parameters used for the two different simulation TRUTH and TWIN. E is the energy transferred by net primary production to intermediate trophic levels, λ is the mortality coefficient, τ_r is the minimum age to be recruited in the mid-trophic functional population, D is the diffusion rate that models the random dispersal movement of organisms. $E_i', i \in [\![1,6]\!]$ are the redistribution energy transfer coefficients to the 6 components of the micronekton population. The parametrization of the TRUTH simulation is called the reference parametrization and is taken from Lehodey et al. (2010).

Simulation	$1/\lambda$ (d)	τ_r (d)	D (NM^{2}d^{-1})	E	E_1	E_2'	E_3'	E_4'	E_5'	E_6'	Forcing
TRUTH	2109	527	15	0.0042	0.17	0.10	0.22	0.18	0.13	0.20	F
TWIN	2109	527	15	0.0042	———— first guess ————						$\widetilde{F}$ (Eq. 8)

Table 2. Outcome of the clustering method (Section 2.2). For each indicator variable (Temperature $\mathcal{T}$, Stratification $\mathcal{S}$, Velocity $\mathcal{V}$ and Bloom Index $\mathcal{B}$), the number n of clusters, the center and size (# observable) of each cluster (regimes) are given, as well as the proportion of all observable point it represents.

Regimes	Temperature ($\mathcal{T}$; $n=4$)				Stratification ($\mathcal{S}$; $n=3$)			Velocity ($\mathcal{V}$; $n=2$)		Bloom Index ($\mathcal{B}$; $n=2$)	
	$\mathcal{T}_1$	$\mathcal{T}_2$	$\mathcal{T}_3$	$\mathcal{T}_4$	$\mathcal{S}_1$	$\mathcal{S}_2$	$\mathcal{S}_3$	$\mathcal{V}_1$	$\mathcal{V}_2$	$\mathcal{B}_1$	$\mathcal{B}_2$
Regime names of $\Gamma_k(\mathcal{G})$, $k \in [\![1,n]\!]$	**polar**	**subpolar**	**temperate**	**tropical**	**weak**	**inter.**	**strong**	**low**	**high**	**bloom**	**no bloom**
Cluster center	0.4°C	6.4°C	12.6°C	16.3°C	0.4°C	5.9°C	11.7°C	0.05 $\mathrm{ms^{-1}}$	0.3 $\mathrm{ms^{-1}}$	74.6 $\mathrm{mmolCm^{-2}d^{-1}}$	18.4 $\mathrm{mmolCm^{-2}d^{-1}}$
# Observable in cluster	1106695	658105	1115102	1300298	2084302	1212945	882949	3698826	481367	449545	3730655
Proportion	26.5%	15.7%	26.7%	31.1%	49.8%	29.0%	21.1%	88.5%	11.5%	10.8%	89.2%

Table 3. Experiment table. List of ex~~per~~~~ents, their corresponding configura~~tions and the evaluation diagnostics: mean relative error on ~~the coefficients, residual likelihood and number of iteration~~s. The section in ~~each of these experiment is discribed is given in the last~~ ~~column.~~

Experiment	Configuration	E_r (Eq. 9)	Residual Likelihood	# Iterations	Section
1a	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	7.0%	0.9	28	3.2.1
1b	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_2$	9.7%	0.5	21	
1c	$\mathcal{T}_3 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	3.1%	0.5	24	
1d	$\mathcal{T}_3 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_1$	8.3%	1.5	23	
1e	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	1.5%	1.1	16	
1f	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_2 \otimes \mathcal{B}_1$	8.5%	1.2	18	
2a	$\mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	9.1%	1.7	19	3.2.2
2b	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	7.0%	0.6	26	
2c	$\mathcal{T}_3 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	3.1%	1.3	20	
2d	$\mathcal{T}_4 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	1.4%	0.6	22	
3a	$\mathcal{T}_4 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	3.5%	0.7	21	3.2.3
3b	$\mathcal{T}_4 \otimes \mathcal{S}_2 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	5.9%	0.8	25	
3c	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	8.0%	1.1	21	
4a	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	7.0%	0.6	26	3.2.4
4b	$\mathcal{T}_2 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	7.0%	0.9	28	
4c	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_1$	1.5%	0.6	22	
4d	$\mathcal{T}_4 \otimes \mathcal{S}_3 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$	8.0%	0.8	21	
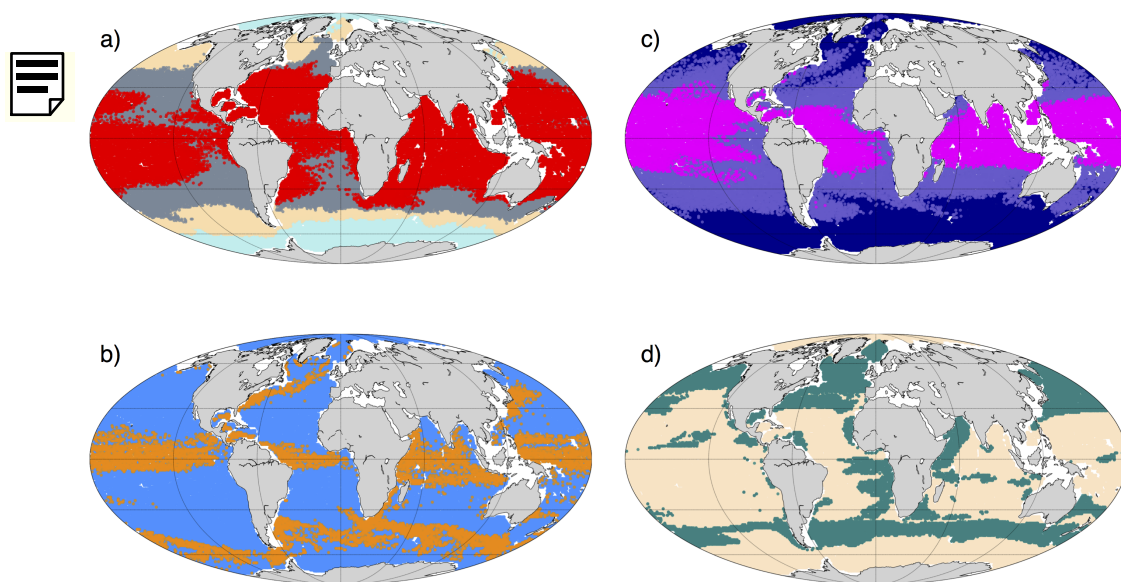
Figure 1. Spatial division of the different regimes. **(a) Temperature** : polar (pale blue), subpolar (yellow), temperate (gray), tropical (red). **(b) Stratification** : weak (dark blue), intermediate (purple), strong (magenta). **(c) Currents Velocities** : low (blue), high (orange). **(d) Bloom Index** : bloom (green), no bloom (beige). Each point of the subset S_N has been plotted at its spatial location with a color corresponding to the regime it belongs to. A transparency factor has been applied in order to account for the temporal fluctuation of regimes (a given point may belongs to different regimes over time). The resulting color on the map corresponds to the most frequent regime the corresponding point belongs to.
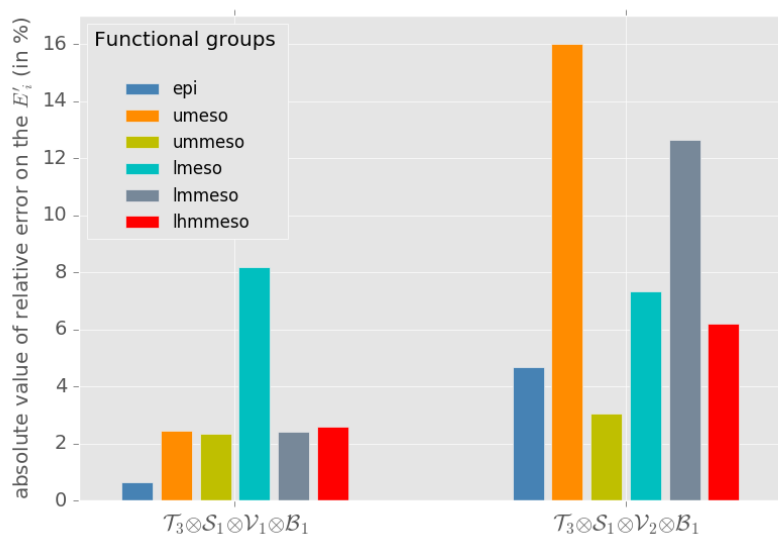
Figure 2. Mean relative error (E_r in %, Eq. 9) on each E'_i coefficients. ~~Exp. 1c and 1d :~~ high vs low velocities in temperate temperatures, weak stratification and bloom regimes.
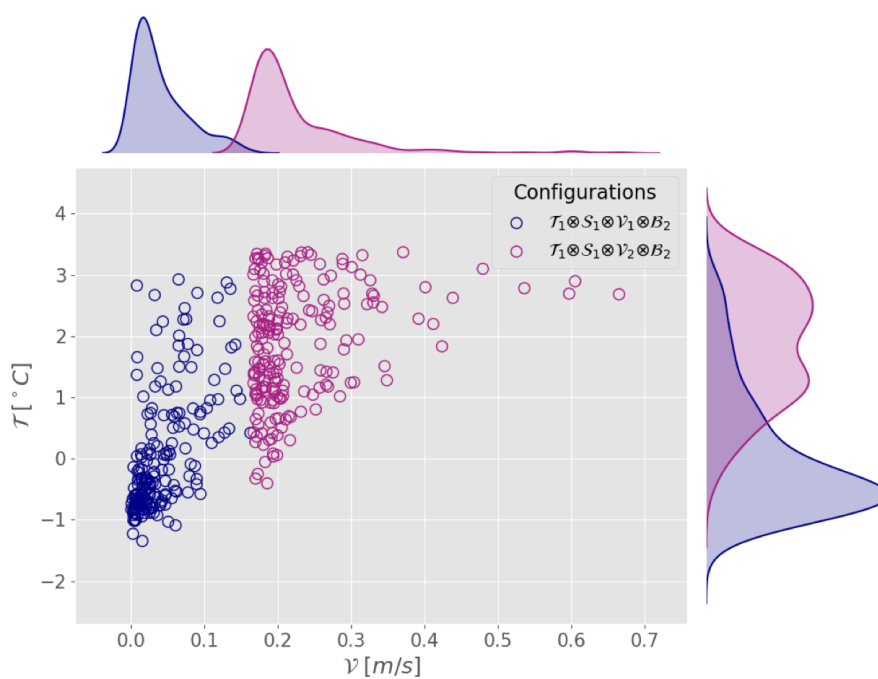
Figure 3. Scatter plot and marginal distribution from kernel density estimation (Silverman, 2018) in the plane $(\mathcal{V},\mathcal{T})$ of observation points used in Exp. 1' and 1" generated by random sampling in configurations $C' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_1 \otimes \mathcal{B}_2$ and $C'' = \mathcal{T}_1 \otimes \mathcal{S}_1 \otimes \mathcal{V}_2 \otimes \mathcal{B}_2$.
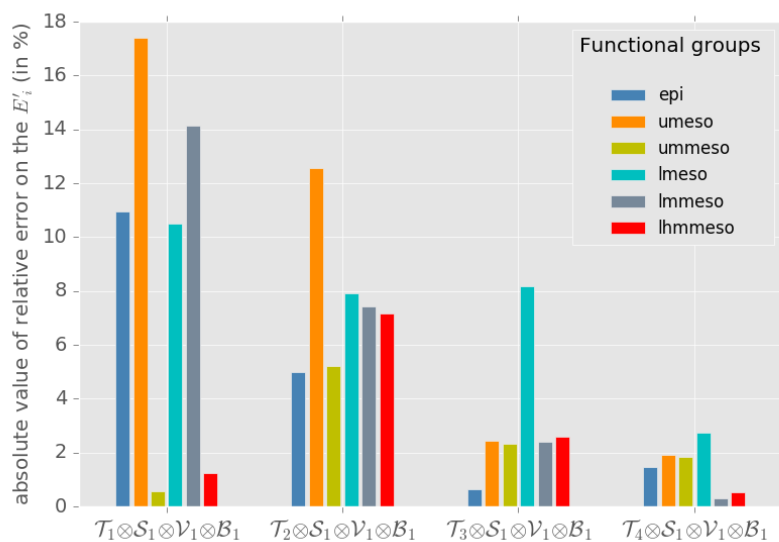
Figure 4. Mean relative error (E_r in %, Eq. 9) on each E'_i coefficients for Exp. 2a, 2b, 2c and 2d : polar vs subpolar vs temperate vs tropical temperatures in weak stratification, low velocity and bloom regimes.
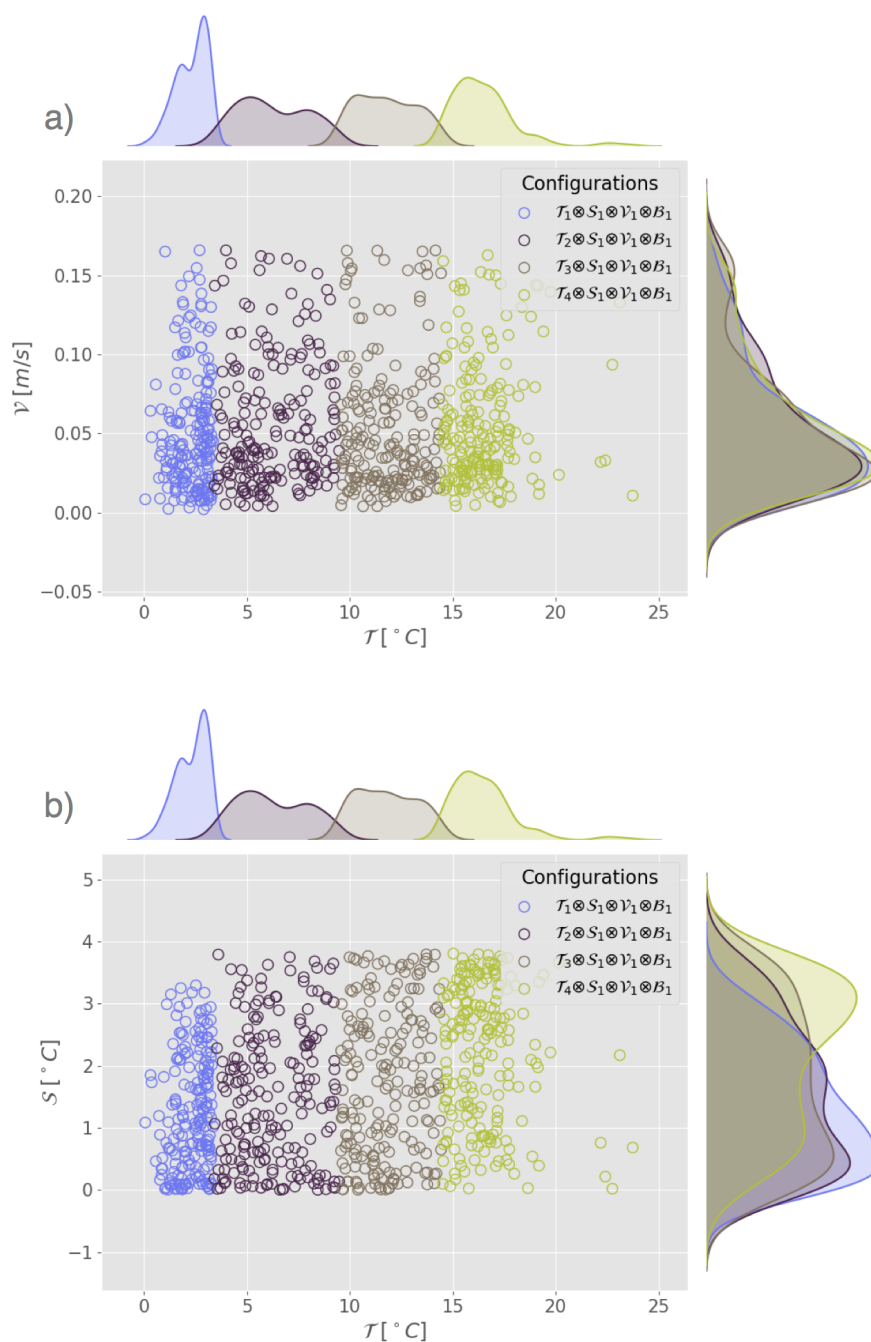
Figure 5. Scatter plot and marginal distribution from kernel density estimation in the plane (a) ($\mathcal{T}$,$\mathcal{V}$) and (b) ($\mathcal{T}$,$\mathcal{S}$) for the configurations corresponding to Exp. 3a, 3b, 3c and 3d from table 3.
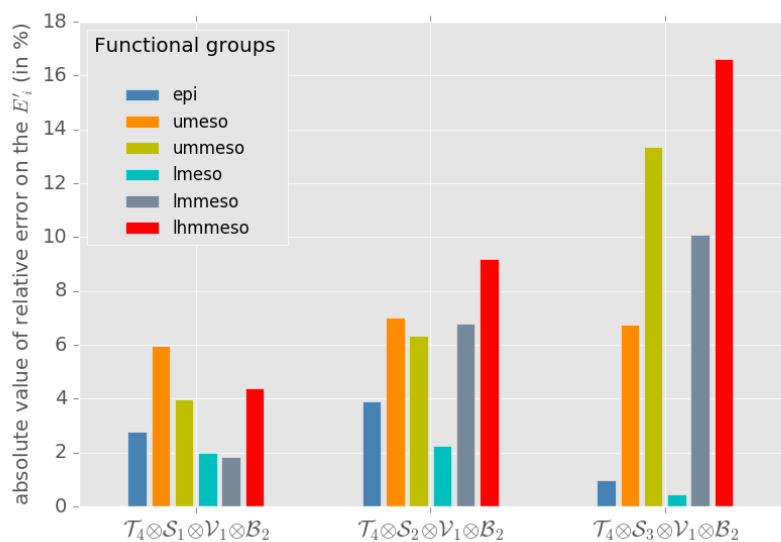
Figure 6. Mean relative error (E_r in %, Eq. 9) on each E'_i coefficients for Ex 3b and 3c : comparison of weak, intermediate and high stratification in tropical temperatures, low velocity and no bloom regimes.
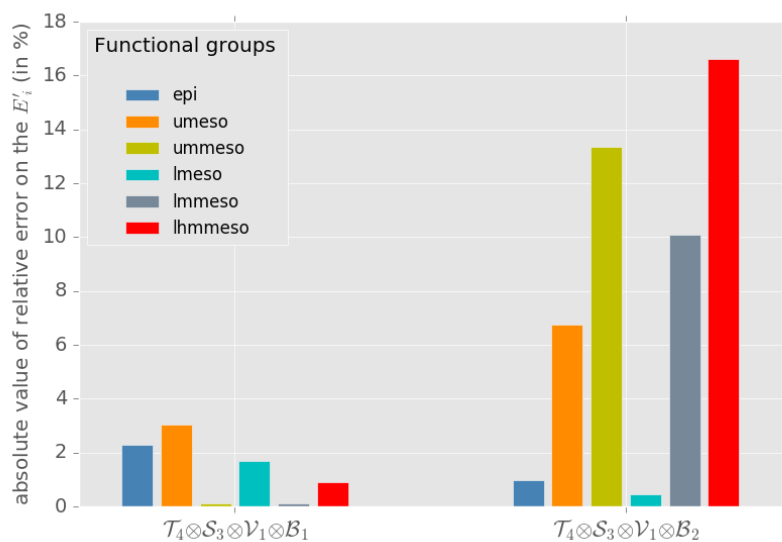
Figure 7. Mean relative error (E_r in %, Eq. 9) on each E_i' coefficients for Exp. d 4d : bloom (4c) vs no bloom (4d) regimes in tropical temperatures, strong stratification and low velocities.
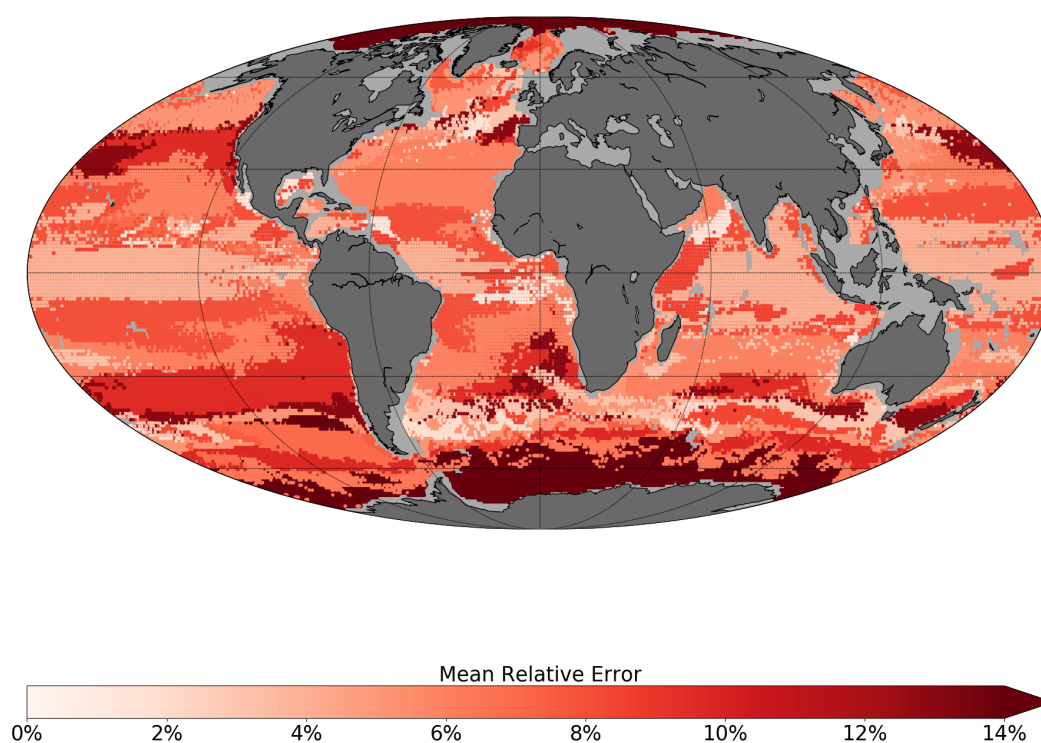
Figure 8. Averaged absolute value of relative error (E_r in %, Eq. 9) between the estimated and the target energy transfer parameters (E_i') according to the location of the chosen observation points in the twin experiment framework. Cells with no data have been shaded in grey.
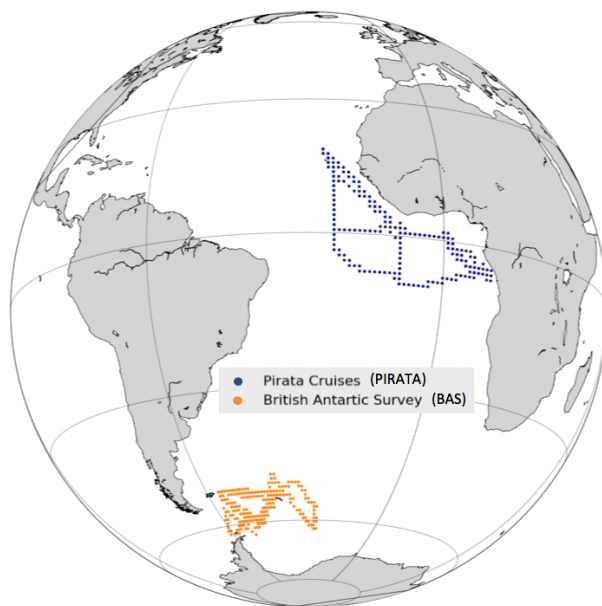
Figure 9. Map of PIRATA and BAS ship transects for the years 2013-2015.
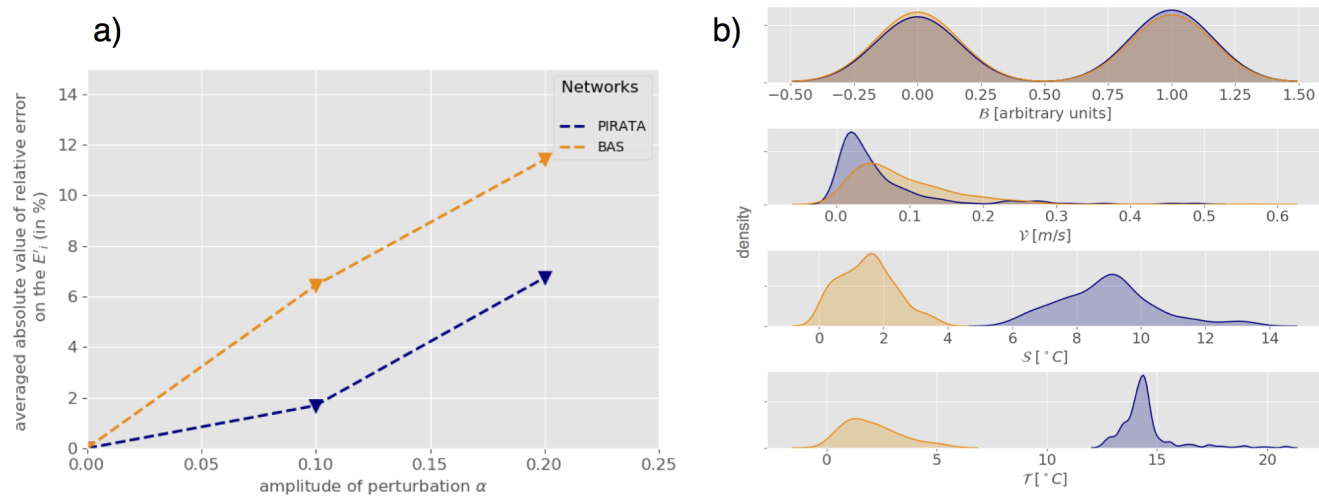
Figure 10. (a) Mean relative error on the coefficients E_r (in %, Eq. 9) as a function of the perturbation amplitude α (Eq. 8) for PIRATA (blue) and BAS (orange) observation networks. (b) Statistical distribution of all PIRATA (blue) and BAS (orange) observation location indicator variables : Bloom Index ($\mathcal{B}$), velocity norm ($\mathcal{V}$), stratification index ($\mathcal{S}$) and temperature ($\mathcal{T}$) estimated using kernel density estimation (Silverman, 2018).