Project	AtlantOS – 633211
Deliverable number	D5.5
Deliverable title	Optimal design of ecosystem module
Description	Within Task 5.3 "Regional Observing system simulation experiments and process modelling"; CLS is in charge of improving an ecosystem module for the ocean mid-trophic levels (i.e. micronekton) that utilizes multiple in-situ and satellite data as input to derive predictions for different trophic levels including fish [D5.5] and has the potential to be implemented into the routine services supported by a future IAOOS. With physical and biogeochemical variables becoming available in real-time, the real-time monitoring of marine resources relying on the development of ecosystem models is envisaged. Optimal design of acoustic sampling to calibrate the model parameters is investigated and the ecosystem module prepared for integration into the operational system in support of Task 8.7.
Work Package number	WP5
Work Package title	Integrated regional observing system
Lead beneficiary	
Lead authors	Patrick Lehodey; Olivier Titaud; Audrey Delpech; Anna Conchon
Contributors	
Submission date	5 Dec 2018
Due date	31 Oct 2018
Comments	Due to a reorganization of all departments in CLS, the ecosystem modelling team in charge of this task has been reduced in 2018.

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement n° 633211.

Stakeholder engagement relating to this task*

WHO are your most important stakeholders?	☐ Private company If yes, is it an SME ☐ or a large company ☐? ☐ National governmental body ☒ International organization ☐ NGO ☒ others Please give the name(s) of the stakeholder(s): - Western Central Pacific Fisheries Commission (INT) - Secretariat of the Pacific Community (INT) - ICCAT albacore working group (INT) - Duke University, USA - Azores IMAR (POR)
WHERE is/are the company(ies) or organization(s) from?	☒ Your own country ☒ Another country in the EU ☒ Another country outside the EU Please name the country(ies): - New Caledonia and Pacific Island Countries (SPC /WCPFC), USA, France, Portugal (Azores)
Is this deliverable a success story? If yes, why? If not, why?	☒ Yes, because the zooplankton and micronekton products are used to develop habitats and population dynamics models of top predators, both exploited (tunas) and protected (cetaceans) ☐ No, because …..
Will this deliverable be used? If yes, who will use it? If not, why will it not be used?	☐ Yes, by CLS, SPC (/WCPFC) for tuna modelling; by Duke University and IMAR for cetaceans habitat modelling ☐ No, because …

NOTE: This information is being collected for the following purposes:

1. To make a list of all companies/organizations with which AtlantOS partners have had contact. This is important to demonstrate the extent of industry and public-sector collaboration in the obs community. Please note that we will only publish one aggregated list of companies and not mention specific partnerships.
2. To better report success stories from the AtlantOS community on how observing delivers concrete value to society.

*For ideas about relations with stakeholders you are invited to consult D10.5 Best Practices in Stakeholder Engagement, Data Dissemination and Exploitation.

Contents

1. Summary

Micronekton -- a group of small organisms able to swim short distances -- is a key link in the oceanic trophic chain. It constitutes the main forage source for top predators and plays an important role in the biological pump. SEAPODYM-MTL is a spatially explicit dynamical model of micronekton. It models six functional groups defined according to their diel vertical migration behaviour. As Energy transfer efficiency from primary production to micronekton functional groups is not directly measurable, a data assimilation framework has been developed to estimate these parameters. In this report, several observation networks are tested regarding energy transfer coefficient estimation. Observing system simulation experiments (with perturbed forcing fields) are used to test them. Results indicate that the typology of environmental conditions are crucial to determine a network efficiency. The optimal sampling environment is predicted in warm, quiet to moderately dynamic and productive waters (e.g., eastern equatorial Atlantic Ocean).

2. Introduction

While the Marine Copernicus programme provides historical reanalyses and operational real time distributions of key physical and biogeochemical parameters, there is still a gap to fill in to deliver the complete set of parameters needed for studies on marine resources and ocean ecosystem modelling. This gap corresponds to the low and mid-trophic functional groups (LMTL) of the ocean food web, that are zooplankton and micronekton. They are key explanatory variables to understand and model the distributions and dynamics of most large marine species, the mechanisms of fish recruitment, the behaviour and habitats of large fishes and other marine animals like sea turtles, seabirds, whales and other marine mammals. More recently, the vertically migrant mesopelagic components of the micronekton has received increasing attention for the economic interest that a large exploitable biomass of some mesopelagic species could represent (e.g., St John et al., 2016). In the same time these vertically migrant mesopelagics have been identified as potential key players in the “biological pump” mechanism that transfers CO2 from the atmosphere to the deep ocean, thereby providing a significant ecosystemic service in the mitigation of climate change impacts (Davison et al., 2013; St John et al., 2016). Observing and modelling these micronekton groups is thus becoming a priority.

Observations rely traditionally on net sampling and active acoustic sampling. Each method has limitations. Even if they are small size organisms (mostly below 10 cm) mesopelagic species seem to detect approaching fishing gears and thus can move away to avoid the net. This phenomenon leads to underestimated biomass estimates 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. siphonophore that have gas inclusion inducing strong resonance (Proud et al., 2018). For other organisms like squids, that have excellent skills to escape the trawl net and a low response to acoustic signal, biomass estimates are underestimated with both methods. To solve this problem, acoustic observation models are needed, based on theoretical developments describing the acoustic responses of different species or groups of species, if possible, using several frequencies (Davison et al., 2015) and trawl net sampling to inform the model on the species composition.

While these acoustic observation models are developed, progresses are also achieved in the development of ocean ecosystem including mesopelagic organisms. This study uses the mid-trophic level component of the SEAPODYM model (Lehodey et al., 1998; 2008; 2010) that simulates production and biomass of six different functional groups of micronekton inhabiting the epipelagic and upper and lower mesopelagic vertical layers. It is an Eulerian modelling framework based on a system of advection-diffusion-reaction equations. It simulates the dynamics of these groups at global scale. The model accounts for the diel vertical behaviour of mesopelagic organisms (i.e., migrant or resident) and link the time of development of these organisms to their ambient water temperature. The source of energy for the functional groups is the primary production, characterized by transfer efficiency coefficients. The spatial dynamics is controlled by the ocean circulation, while a diffusion coefficient account for local random movements. Thus, the model is driven by primary production, temperature and horizontal currents. The euphotic depth is also needed to define the depth boundaries between epipelagic, upper mesopelagic and lower mesopelagic vertical layers. These variables

are now provided with more and more accuracy due to the large progress achieved in ocean operational modelling and data assimilation of satellite and in situ observations.

The mid-trophic model has eleven parameters to control the biological processes: a global coefficient of energy transfer efficiency (*E*) from primary production to all mid-trophic level groups; a matrix of energy transfer coefficients associated to the *n* functional groups (*E'n*); four parameters defining two temperature related decreasing exponential relationships for mortality and recruitment; and a diffusion coefficient. A method to estimate the model parameters has been developed using adjoint technique and Maximum Likelihood Estimation (MLE) (Senina et al 2008). A first study has shown that this method can be used to estimate the matrix of *E'n* parameters using relative ratios of observed acoustic signal and predicted biomass in the three vertical layers during daytime and nighttime (Lehodey et al., 2015). For the sake of simplicity, this approach was developed based on the strong assumption that acoustic signal and predicted biomass were directly proportional, despite that there are many potential biases to consider when converting acoustic signal into biomass (cf. above). Hopefully, improved estimates of mesopelagic biomass should become easier to obtain in the coming years and it is useful to revise the approach previously proposed to use this information.

More importantly, given the high cost of in situ observation at Sea to collect both acoustic and trawl net sampling data, it is also extremely useful to evaluate their potential through Observing System Simulation Experiments (OSSE). Here, the objective is to optimize the design of sampling to collect the most useful information for the model parameter estimation. Thus, in that case, OSSEs correspond to "twin experiments". A set of pseudo-observations (biomass of the six micronekton groups) is generated with the model using a reference (target) parameterization. Then the set of parameter values are changed and the inverse model with the MLE are used to test how close the model can approach the original parameterization used to produce the pseudo-observations. The difference between the target and new estimated parameters provides a metric to select the best sampling designs.

In this study, a method is presented to investigate the sensitivity of the model to retrieve the target parameter values from selected datasets of pseudo-observations. Two series of experiment are conducted: the first one based on real sampling profiles of acoustic data, from which micronekton biomass is assumed to be correctly estimated. The pseudo-observations are generated at the time and location where real observation data are available. This help discriminating the optimality of our dataset for the estimation of parameters. Then, a series of geographical boxes characterising different eco-regions is used for the generation of pseudo-observations: the time and location of the pseudo-observations are sampled randomly within each box. In both cases, the pseudo-observations are generated with the reference configuration of the model and used in the inverse model, after introducing noise in the forcing fields to mimic the discrepancy between the real state of the ocean and the model simulation environment.

3. Material and method

3.1. SEAPODYM model reference configuration

Based on first macro-ecological principles, SEAPODYM simulates six functional groups of micronekton for the oceanic epi- and mesopelagic layers (Lehodey et al., 1998; 2010; 2015). The model predicts the spatial and temporal dynamics of production and biomass with a system of advection-diffusion-reaction equations. The functional groups are defined based on vertical migration between three broad epi- and meso-pelagic zones between surface and ~ 800 m as observed from acoustic detection and net sampling and acoustic data (Figure 1). This model is driven by ocean temperature, horizontal currents, primary production and euphotic depth. The currents and temperature in the vertical layer inhabited by the organisms during day and night periods impact both their distributions and their time of development and natural mortality rates. The euphotic depth Z_{eu} is used to define the depth boundaries of the vertical layers, i.e., 1.5,4.5 and 10.5 x Z_{eu} (Figure 1). There are eleven parameters to control the biological processes for micronekton groups: a coefficient of transfer efficiency from primary production toward this mid-trophic level, a matrix of energy transfer distribution between functional groups, three parameters defining decreasing exponential relationships

between water temperature and age of recruitment and time of development (mortality, recruitment), and a diffusion coefficient.

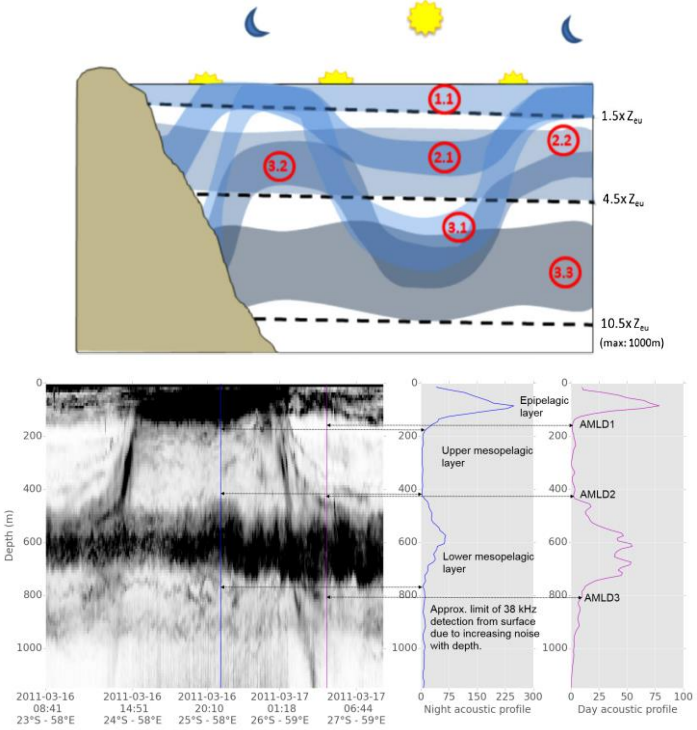

Figure 1: SEAPODYM-LMTL definition of micronekton functional groups. Redrawn from Lehodey et al (2015).

Top: Conceptual model (from Lehodey et al. (2015) with Identification of MTL functional groups: 1.1: Epipelagic; 2.1: migrant upper mesopelagic; 2.2: upper mesopelagic; 3.1: highly migrant lower mesopelagic; 3.2: migrant lower mesopelagic; 3.3: lower mesopelagic.

Bottom: Example of an acoustic transect showing bio-acoustic layers and the depth limits between them.

One initial parameterization has been achieved from the existing information available in the literature (Lehodey et al. 2010). It is used as the reference configuration in this study (Figure 2). The simulation has a monthly one-degree square resolution and spans a 10-year period over 2006-2015 in the global domain. The physical forcing variables are temperature and currents from ECCO reanalysis (GECCO2) interpolated fields on a regular 1x1° grid (available at www.ecco-group.org). Primary production and euphotic depth are computed using the VGPM model of Behrenfeld and Falkowski (1997) and available from the Ocean Productivity web site (www.science.oregonstate.edu/ocean.productivity/).

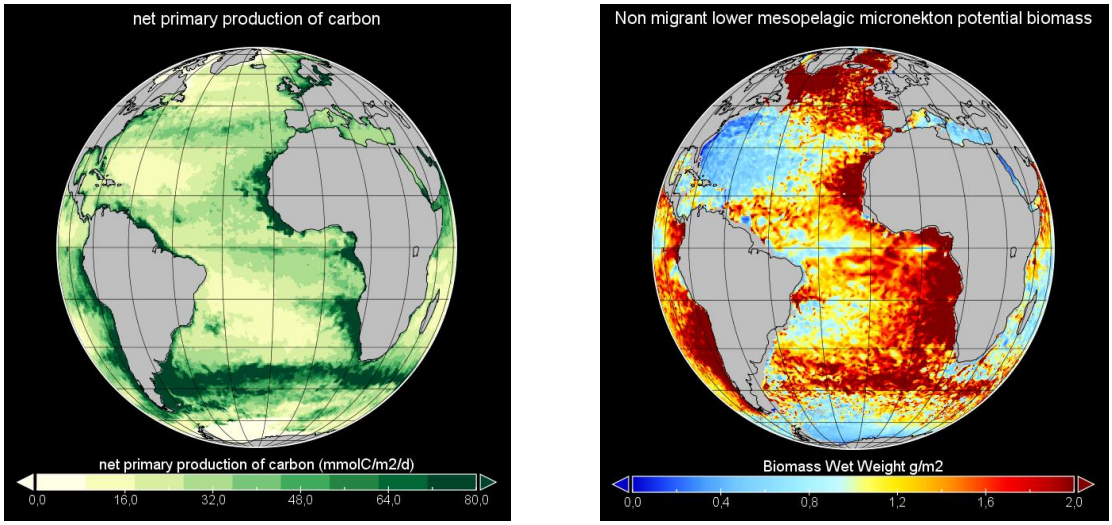

Figure 2: Snapshots (last week of 2015) showing the distribution of (left) satellite derived primary production (VGPM model) and (right) the biomass distribution of the lower resident mesopelagic micronekton functional group predicted by the SEAPODYM-MTL model.

3.2. Simulation experiments and metrics

The performance of the optimisation experiments uses metrics measuring how the new parameter estimates are close from the reference (target) values that generated the pseudo-observation dataset. With θ^t the target reference parameter value and θ^o the new estimated value, these metrics are:

- The relative error e between the optimal coefficients and the target coefficients:

$$e(\theta^o) = \left| \frac{\theta^o - \theta^t}{\theta^t} \right|$$

- The root mean square error for the estimated biomass given by the optimal parametrization at the location of observation compared to the targeted biomass:

$$\mathrm{RMSE}(\theta^o) = \sqrt{\mathbb{E}((\theta^o - \theta^t)^2)}$$

Before running simulation experiments (Figure 3), the noise in the forcing fields (Figure 4) was generated with:

- a linear perturbation with respect to the mean state of the ocean variable:

$$\forall (x,y) \in \Omega^2, \forall t \in [t_0, t_f], \quad \tilde{F}(x,y,t,\alpha) = \overline{F}(x,y) + \alpha(F^R(x,y,t) - \overline{F}(x,y))$$

α : perturbation parameter, $\alpha \in [0,1]$.

$\tilde{F}(\alpha = 1) = F^R(x,y,t)$ reference forcing fields
$\tilde{F}(\alpha = 0) = \overline{F}(x,y)$ climatology

- a white noise perturbation accounting for the intrinsic variability of the ocean:

$$\forall (x,y) \in \Omega^2, \forall t \in [t_0, t_f], \quad \tilde{F}(x,y,t) = F^R(x,y,t) + \beta\gamma\overline{F}$$

$\beta \in [0,1]$ amplitude of the perturbation
$\gamma \in [-1,1]$ random number, white noise

The linear perturbation is consistent with the geographical location and time of observations but does not allow a strict comparison between different regions and associated sampling networks. For such comparison the white noise approach is more appropriate.

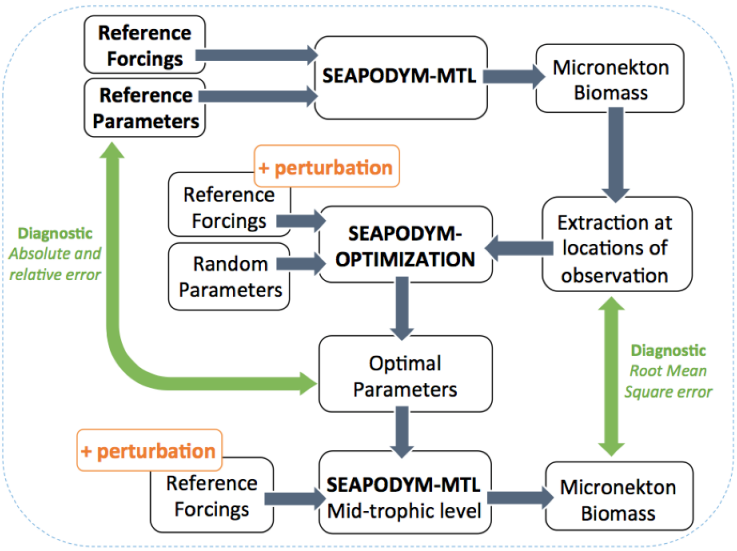

Figure 3. Scheme of twin experiment protocol.

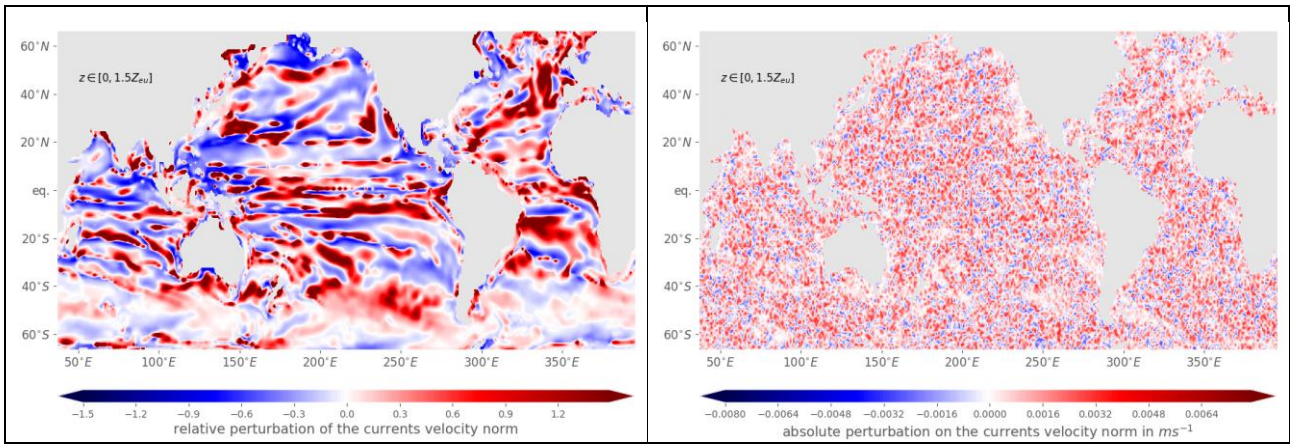

Figure 4: Example of perturbations introduced in the current velocity forcing fields. Left: with a linear perturbation (the perturbation introduced is a fraction of the mean field). Right: with a white noise perturbation (the perturbation introduced is a random value in a selected range).

3.3. Generating datasets of observations

Based on existing sampling programmes in the Atlantic Ocean, four types of annual surveys with vessels equipped with echo sounders are tested. They are:

- **PIRATA** (PIlot Research moored Array in the Tropical Atlantic): This network of tropical oceanographic moorings is maintained through a joint effort between Brazil, France and the USA. Acoustic data are recorded during maintenance cruises between moorings.
- **AMT** (Atlantic Meridional Transects): A multidisciplinary programme which undertakes biological, chemical and physical oceanographic research during an annual voyage between the UK and destinations in the South Atlantic. http://www.amt-uk.org/
- **BAS** (British Antarctic Survey): Oceanographic cruises conducted every year between the Falklands, South Georgia and the Antarctica peninsula.
- **MarEco**: A mooring at the Mid-Atlantic ridge (position 51°31.6 N – 30°19.9 W) equipped with an upside-down echo-sounder deployed during 11-month.

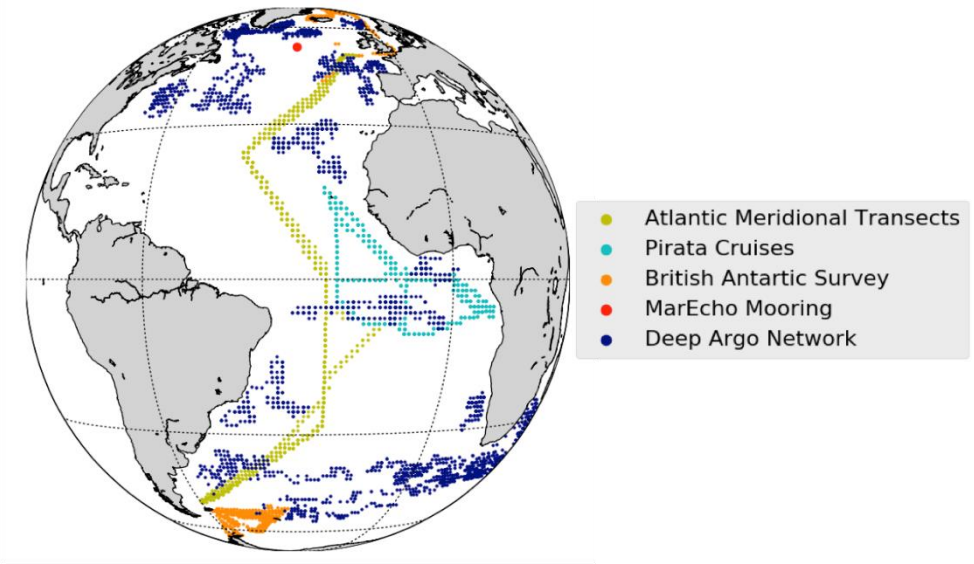

Figure 5: Reference networks used to generate micronekton biomass observations.

4. Results

4.1. Optimization experiments with existing networks

4.1.1. Twin experiments without perturbation

Twin experiments are first performed for each artificial observation dataset using the reference forcing fields without perturbation from noise. In these cases, the optimisation process works very well, the target coefficients are retrieved without errors (or errors less than 0.1%) whatever the observation network. This is not surprising since the observations used for the assimilation were produced with the same model and forcing. However, this is a useful test to verify that the maximum likelihood estimation approach is properly working.

4.1.2. Twin experiments with linear noise

Increasing noise intensity is introduced in the forcing fields by linearly increasing values of α (see method). After the convergence of the optimization scheme towards its optimal solution, the error on the parameter estimation is measured with the Root Mean Square Error (RMSE) between the pseudo-observations and the new predicted biomass values.

When linear noise is added to velocity fields, the model has a quasi-linear response with respect to the perturbations (Figure 6). However, there are differences in the results according to the selected network of observations. PIRATA gives the best result and BAS the worst. Even for very high perturbations (up to 40%), the resulting error with PIRATA on the estimated biomass is only 60 mg WW m-2. It reaches already 100 mg WW m-2 for perturbations four times smaller (only 8%) when using the BAS network. The response is not so linear when the noise is added to the temperature fields (Figure 5). The range of errors in the predicted biomass starts to grow quickly and then slow down beyond a threshold value of about 0.05°C of the average in absolute errors. As for currents, PIRATA gives the best score and BAS the worst. With an average perturbation of 0.1°C, the error is already 6 times higher for the BAS (~30 mg WW m-2) than for PIRATA (5 mg WW m-2). Finally, for primary production the model has a linear response as observed for the currents but the error on the estimation is much lower.

The spread of all simulation error curves gives useful information on the sensitivity of the optimization with respect to its forcing fields. An adimensional measure of this spreading can be computed taking the ratio between the rates of increase of the steepest and flattest curves, i.e., here BAS and PIRATA respectively. A ratio close to one indicates a small spreading and no sensitivity to the considered forcing field. It takes the values 13.3, 11.4 and 2.1 for currents, temperature and primary production respectively, confirming the highest sensitivity of the model to current velocities and then temperature.

It is also very useful to note that combining all datasets may be detrimental to the accuracy of estimation due to the strong negative impact of the BAS sampling dataset that likely brings too noisy information. All experiments provide the same ranking between forcing variables and indicate that the PIRATA sampling network provides the best environment to estimate the model parameters. The optimality of the observation network seems more constrained by the environmental conditions associated to the oceanic region observed rather than by the error made on the forcing fields.

4.1.3. Twin experiments with white noise

Three different twin experiments with white noise of increasing amplitude of 10, 20 and 30% were performed. The absolute value of relative errors from these simulations are proportional to the intensity of the perturbation. For a white noise of amplitude 10%, they rarely get above 3% (except for MarEco and the BAS networks). With the amplitude 30% they are of the order of 10%. As for the linear noise experiments, PIRATA achieves the best score with averaged relative error of 1%.

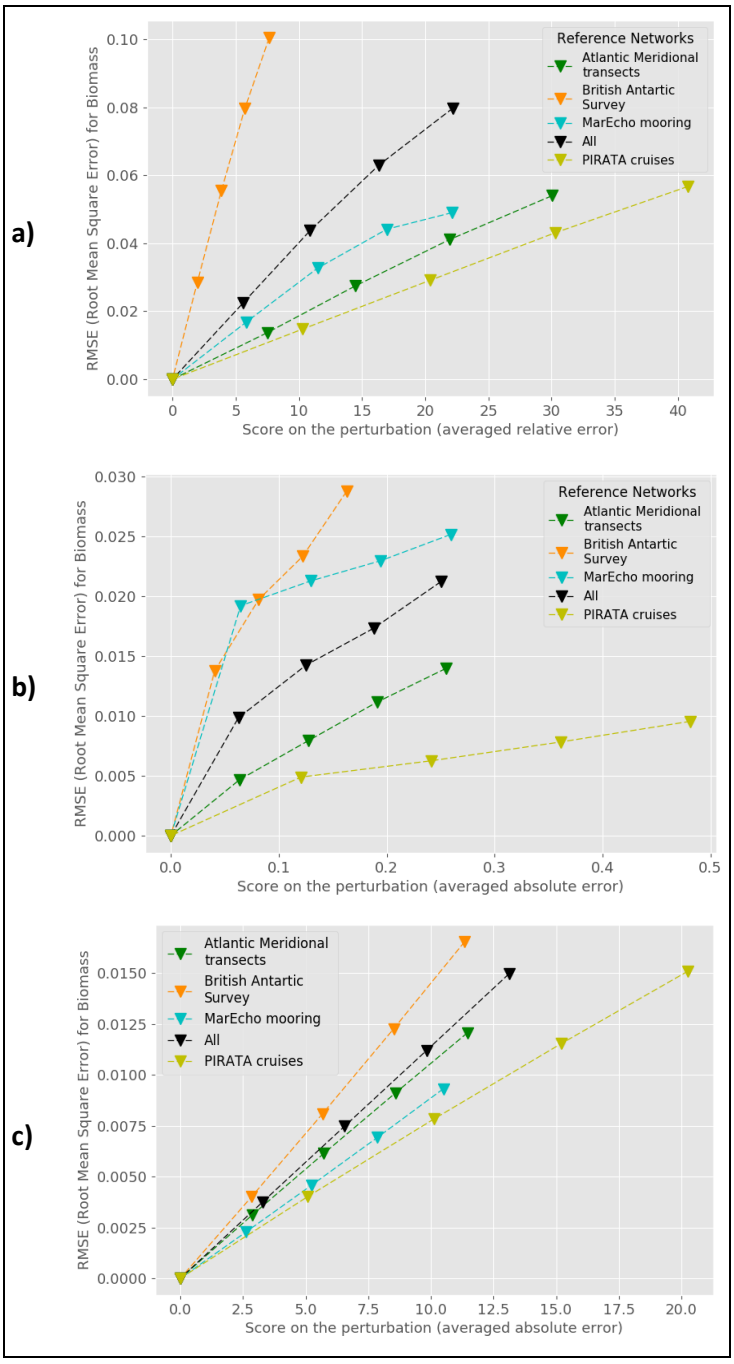

Figure 6: Impact of forcing field perturbations with linear increase in noise on the predicted biomass at the location of the observations. The root mean square error of the biomass is plotted against the local averaged relative error of a) the velocity field, b) the temperature and c) the primary production.

4.2. Optimisation based on eco-regions

To complement the first results above, a new series of twin experiments was conducted using pseudo-observation datasets generated in a series of ocean eco-regions characterized by well-known oceanographic conditions in terms of temperature, velocity and primary production (Figure 7). Data were randomly selected

inside 10 geographical boxes over the time series of the reference simulation. Thus, we focus on the characteristics of the sampling zone only without considering the design of the network. The regions shown on Figure 7 were selected following the biogeographic classification of the mesopelagic zone by Sutton et al. (2017), based on physical, biogeochemical and taxonomic variables (temperature, salinity, oxygen, species).

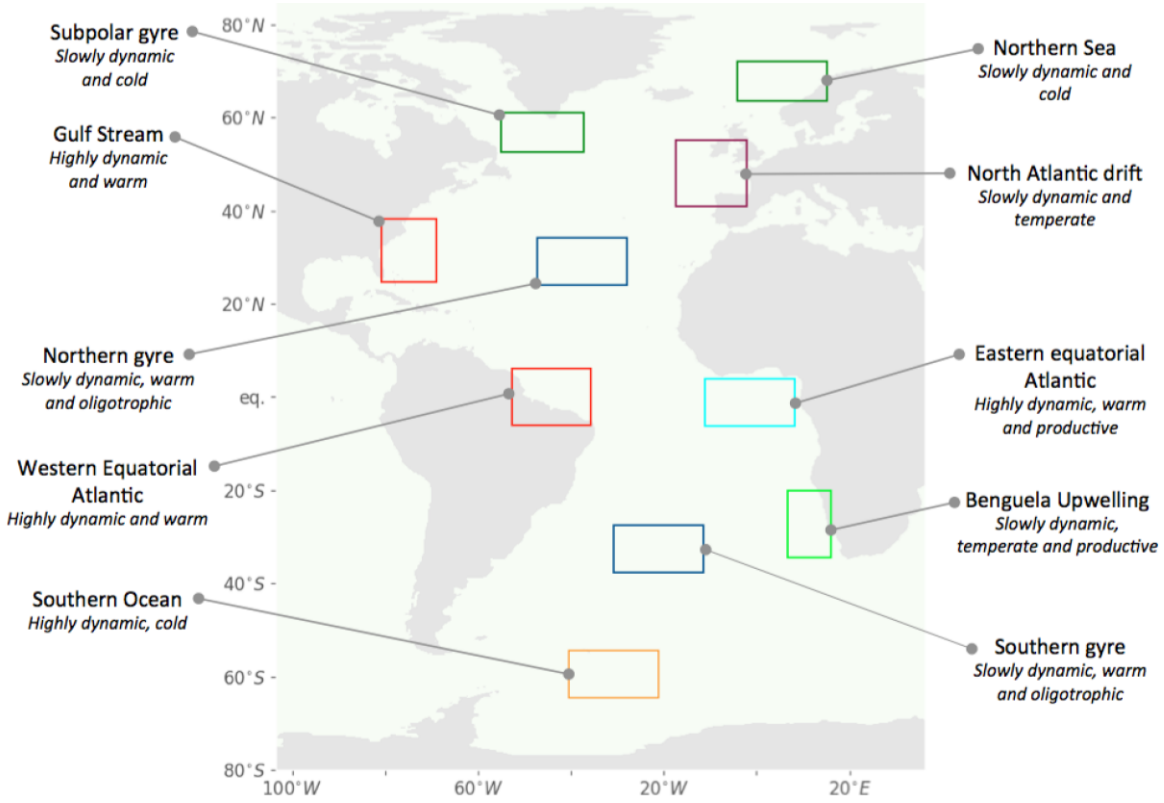

Figure 7: Sampled regions in the Atlantic Ocean and their characteristics.

For each region, the twin experiment is conducted with white noise added to currents and temperature, since they have been shown the most sensitive forcing variables for this model. The resulting error on the parameter estimates (averaged over the 6 coefficients) is shown on Figure 8 and key feature for each region summarized below:

- **Southern Ocean:** The currents in this cold region are strong, reaching occasionally values above 1 ms^{-1}. The optimization capability is poor in this region with an averaged error of 20% on the coefficients;
- **Gulf Stream**: In this region, the currents are also very strong, up to 2 ms^{-1}, but in a warm seasonal environment. The mean error in this region is also around 20%;
- **Northern and Southern gyres**: These two regions display very similar characteristics with weak currents, temperate water masses but low primary production. Both give an average error of 3%;
- **Subpolar gyre and Northern seas**: These two regions present similar environmental conditions with relatively low dynamics and cold waters (5 - 7°C). Both give an average error of 6%;
- **Benguela upwelling**: a highly productive system with moderate velocities and relatively warm temperatures. The averaged error is minimum close to 1%;
- **Western Equatorial**: Productive warm waters in the very dynamic systems of the north Brazil retroflexion current with strong mesoscale activity and eddies. The error is approaching 10%.
- **Eastern equatorial Atlantic**: The region experiences quite strong currents called equatorial jets. Very warm waters, up to 30°C locally and increased productivity in the eastern part. The averaged error is very low: 1%;
- **North Atlantic Drift:** Strong seasonality in productivity, low velocities and moderate temperatures. The averaged error is below 1%.

These results indicate that observation datasets generated in regions characterised by strong circulations (Gulf Stream, western equatorial and Southern Ocean) provide the less useful information for the model parameter estimation. When the circulation is moderate to weak, then the temperature becomes the predominant influential factor. In that case, cold waters (Subpolar gyre and Northern seas) make the estimate less accurate than warm waters. Therefore, despite that the eastern equatorial system is rather dynamic, the warm waters seem to compensate the difficulty to retrieve the good parameter values in strong currents. The Figure 8 illustrates this relationship between temperature, velocity and accuracy of estimate. These results confirm that the bad score achieved with the BAS network is associated to the combination of cold waters and dynamic circulation in the southern Austral Atlantic.

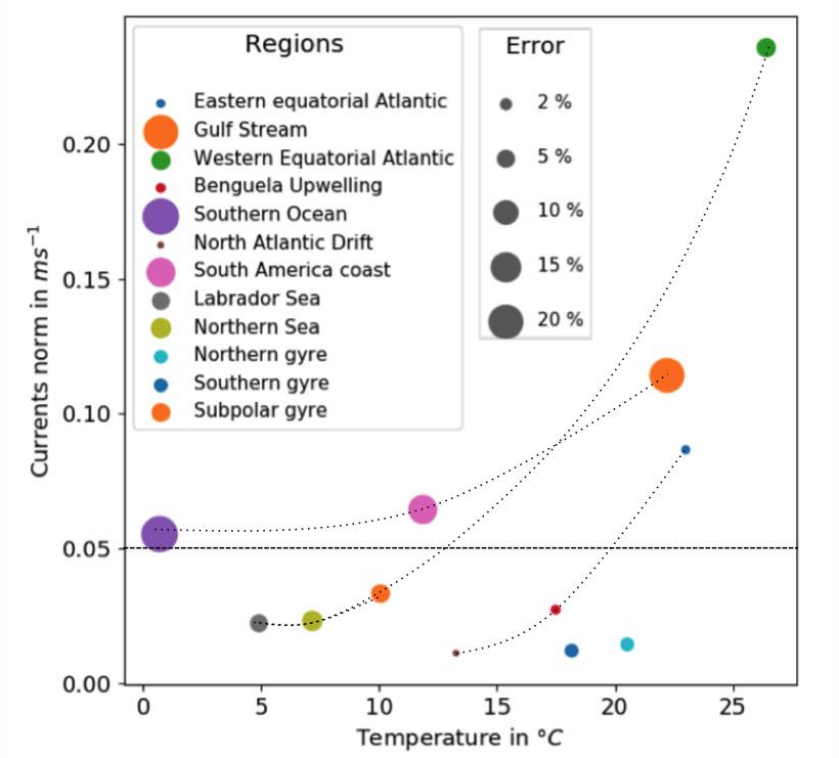

Figure 8: Relation between environmental conditions (temperature and currents norm in the first layer of the model) and averaged relative error between optimal and target coefficients. Each coloured dot represents one of the regions. The dots are positioned in the plane according to the temperature and current characteristics of the region. The size of the dots is proportional to the error made by optimizing the coefficients using observations localized in the region. Dotted lines connect the regions with same range of errors.

5. Discussion

This study allowed to characterize the optimal environmental conditions to collect observations of micronekton biomass for estimating energy transfer efficiency coefficients of the SEAPODYM micronekton model. The multiple simulation experiments conducted indicate that these conditions combine warm, slow to moderately dynamics and productive waters as for instance the PIRATA region in the eastern equatorial Atlantic Ocean. The results are less sensitive to errors in the primary production. This is potentially because here the approach of optimisation is focusing on the estimation of relative rather than absolute values of energy transfer between functional groups (Lehodey et al., 2015). In that context, it is quite logical that temperature controlling the time of development of micronekton and currents redistributing the biomass over time appear the most influential factors.

In cold waters, the slower time of development means a slower turnover and longer time to build up the biomass. Therefore, it can be accumulated and transported over longer distances. The model simulating the biomass in this environment will aggregate more noise and errors during this longer period of transport. This is all the more critical when the environment is characterized by strong dynamics and mesoscale activity making the biomass distribution very patchy, while generating more errors from the circulation models. In this type of environment, the link between primary production and micronekton biomass becomes certainly more and more noisy and difficult to estimate. A good example is the Austral Atlantic region of BAS that got the worst score in all experiments. Strong oceanic circulation remains a major constrain to estimate the model parameters even in warm waters as observed with the north Brazil current region.

Eco-regions with warm waters and intermediate to low dynamics are a better choice to collect micronekton biomass observations, since there is a short link between phytoplankton production and micronekton biomass, e.g. a few months. Nevertheless, there is still some difference in estimation errors between regions with both warm waters and intermediate to weak dynamics as the tropical gyres and the eastern equatorial Atlantic. The equatorial region gets the best scores. It seems possible to assume here that the higher productivity in this region compared to oligotrophic gyres brings a stronger “easier to detect” signal. A stronger seasonality in the coastal upwelling regimes may also be useful information to correlate peaks of productivity. Besides, this seasonal signal is likely the reason explaining a better score achieved in the temperate region of the north-east Atlantic rather than in the tropical gyre despite the difference in temperature.

A last but very useful result from this study is the lower score achieved by combining all datasets instead of the best of them. This is a key result to orientate the monitoring effort and avoid spending too much effort in areas where the data will have a limited interest, at least at the current level of model developments (both physical and micronekton). Finally, there are other sources of uncertainties that remain to explore, especially those linked to the acquisition and processing of acoustic data. This is without considering all the uncertainty associated to the estimation of micronekton biomass from acoustic signal, that needs to be accounted for through specific developments, especially acoustic observation models. Other, maybe more realistic perturbations of forcings could be tested as well, since the ocean circulation models have complex errors and biases that are subject to discussion (Lellouche et al., 2012).

The modelling of ocean ecosystem is a real challenge that requires appropriate datasets for parametrisation and evaluation. The mid-trophic level in the ocean is poorly observed despite its central role to support higher predators. It is essential to identify the best sampling strategy to propose networks of observation at realistic cost. The present analysis illustrates the interest of testing such strategies for one micronekton model that includes a maximum likelihood estimation approach to optimise its parametrisation. It suggests that a few but accurate sampling networks of micronekton biomass in selected areas would provide useful key observation at a minimum cost to optimise the model. Then validation can be conducted with observations in other regions, while taking into account the sensitivity of the model identified in relation to the physical characteristics of these regions.

6. References

Behrenfeld, M.J., Falkowski, P.G., 1997. A consumer's guide to phytoplankton primary productivity models. Limnol. Oceanogr. 42, 1479–1491.

Davison P.C., Checkley Jr. D.M., Koslow J.A., Barlow J. (2013). Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Progress in Oceanography*, 116, 14-30.

Davison, P. C., Koslow, J. A., and Kloser, R. J. 2015. Acoustic biomass estimation of mesopelagic fish: backscattering from individuals, populations, and communities. ICES Journal of Marine Science, 72: 1413–1424. http://icesjms.oxfordjournals.org/cgi/doi/10.1093/icesjms/fsv023.

Kaartvedt S, Staby A, Aksnes DL (2012) Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. Mar Ecol Prog Ser 456:1-6. https://doi.org/10.3354/meps09785

Lehodey, P., André, J.-M., Bertignac, M., Hampton, J., Stoens, A., Menkès, C., Mémery, L., and Grima, N. (1998). Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical biogeochemical model. Fisheries Oceanography, 7(3-4): 317-325.

Lehodey, P., Conchon, A., Senina, I., Domokos, R., Calmettes, B., Jouanno, J., Hernandez, O., and Kloser, R. (2015) Optimization of a micronekton model with acoustic data. – ICES Journal of Marine Science, 72(5): 1399-1412. doi: 10.1093/icesjms/fsu233

Lehodey, P., Murtugudde, R., and Senina, I. (2010). Bridging the gap from ocean models to population dynamics of large marine predators: A model of mid-trophic functional groups. Progress in Oceanography, 84: 69-84.

Lellouche, J.-M., Galloudec, O. L., Drévillon, M., Régnier, C., Greiner, E., Garric, G., and Ferry, N. (2013). Evaluation of real time and future global monitoring and forecasting systems at Mercator-Océan. Ocean Sci., 9, 57-81. https://doi.org/10.5194/os-9-57-2013

Proud, R., Handegard, N. O., Kloser, R. J., Cox, M. J., and Brierley, A. S. (2018). From siphonophores to deep scattering layers: uncertainty ranges for the estimation of global mesopelagic fish biomass. – ICES Journal of Marine Science. doi:10.1093/icesjms/fsy037

St John, M. A., Borja, A., Chust, G., Heath, M., Grigorov, I., Mariani, P., Martin, A. P., and Santos, R. S. (2016). A dark hole in our understanding of marine ecosystems and their services: perspectives from the mesopelagic community. Frontiers in Marine Science, 3: 31.

Sutton T.T., Clark M.R., Dunn D.C., Halpin P.N., Rogers A.D., Guinotte J., and 17 others (2017). A global biogeographic classification of the mesopelagic zone (2017). Deep-Sea Research Part I, 126: 85–102