Deliverable D4.2

Report on Summary V2 parameterisations

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About this document

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Contents

1. Key messages for the Ocean ICU stakeholders

- **Plankton shape the ocean's role in carbon storage**

  Microscopic ocean life—phytoplankton and zooplankton—play a crucial role in how effectively the ocean captures and stores carbon. Their composition, size, and behaviour influence the amount of carbon that can be sequestered in the deep ocean, setting natural limits on the ocean's capacity to mitigate climate change.

- **Whales boost ocean carbon and nutrient cycling**

  Large marine animals like whales play a vital role in recycling nutrients and exporting carbon via waste and carcasses. WP4 is quantifying these fluxes in the Nordic Seas to assess their impact on primary production and regional carbon budgets.

- **Sinking particles link surface productivity to deep-sea storage**

  When biological particles sink from the surface to the deep ocean, they carry carbon with them. How much is stored depends on the size and lability of the particles and their interaction with plankton communities. WP4 is compiling global data to understand these processes and how they vary by region, or at smaller scales, informing how their flux to the ocean interior and the production of inorganic carbon by microbes in the dark ocean, may affect deep-sea ecosystems and carbon storage.

- **Deep ocean respiration affects long-term carbon sequestration**

  Carbon storage in the ocean isn't only about what goes in—it's also about what comes out. Respiration in the deep sea determines how much carbon remains stored over the long term. WP4 is investigating how this varies globally and regionally to refine climate models and forecast low-oxygen zones that could disrupt marine ecosystems.

- **From science to policy: improving climate models**

  WP4 is translating field observations and biogeochemical processes into usable parameterizations for integration into global ocean and climate models (WP6). This will enable more accurate predictions of how ocean carbon storage will evolve under climate change, providing critical insights to guide mitigation strategies and sustainable ocean management.

2. Abstract

This report presents progress in fieldwork, data synthesis, and modeling experiments conducted within the framework of WP4. The results offer new insights into ecological processes operating in the upper ocean and the mesopelagic zone, particularly those influencing oceanic carbon uptake and storage. Novel field observations and integrated data analyses have been used to develop improved parameterizations for incorporation into global ocean models. These advancements contribute to enhancing the predictive capability of Earth system models with respect to future changes in ocean carbon storage under climate change scenarios.

3. Work carried out

Task 4.1 Controls over gravitational flux

4.1.1 Linking phytoplankton, particle size and POC flux: a global data synthesis

NOC continue to investigate the relationships between phytoplankton and particle size spectrum, and POC remineralisation depth. In order to mitigate the sparsity of field data, particularly for surface phytoplankton size distributions, we have included satellite-derived surface ocean particle size distribution (PSD) slopes from Kostadinov et al. (2023), and phytoplankton size class (PSC) and phytoplankton functional type (PFT) data, as well as Chlorophyll concentrations, from the Copernicus Glob-Colour product. Additionally, depth-resolved POC concentrations and POC flux estimates from the GLOBESINK product are being used to provide estimates of Martin's b and remineralization depth. We continue to use PSD slopes for particles in the 105µm - 5mm size range at different depth horizons calculated from the UVP database (Kiko et al., 2022).

An investigation into the correlations between different components of the surface ocean ecosystem (**Figure 1**) and PSD slopes at a range of depths has highlighted a number of features and yielded some preliminary parameterisations for PSD slopes and POC remineralisation depth. Proxies for micro- and nano-phytoplankton, based on both PFTs and PSCs, are consistently more highly correlated (0.4-0.51) with PSD slopes at depth than proxies for pico-phytoplankton (-0.04 – 0.2). Surface phytoplankton PSD slopes are also well correlated with PSD slopes at depth (0.3-0.4), with Chlorophyll concentrations equally well correlated (or better), suggesting that effective parameterizations for sub-surface PSD slopes can be based on Chlorophyll, rather than requiring more detailed surface ecosystem data.

A preliminary attempt to apply our data-derived parameterizations to output from the MIT Darwin ecosystem model had mixed results. The parameterisation based on surface phytoplankton PSD slopes appeared to perform badly compared to climatological observational data. This was largely due to a mismatch between the surface phytoplankton PSD slopes estimated from the model community composition as compared to observations, with the model consistently generating flatter slopes.

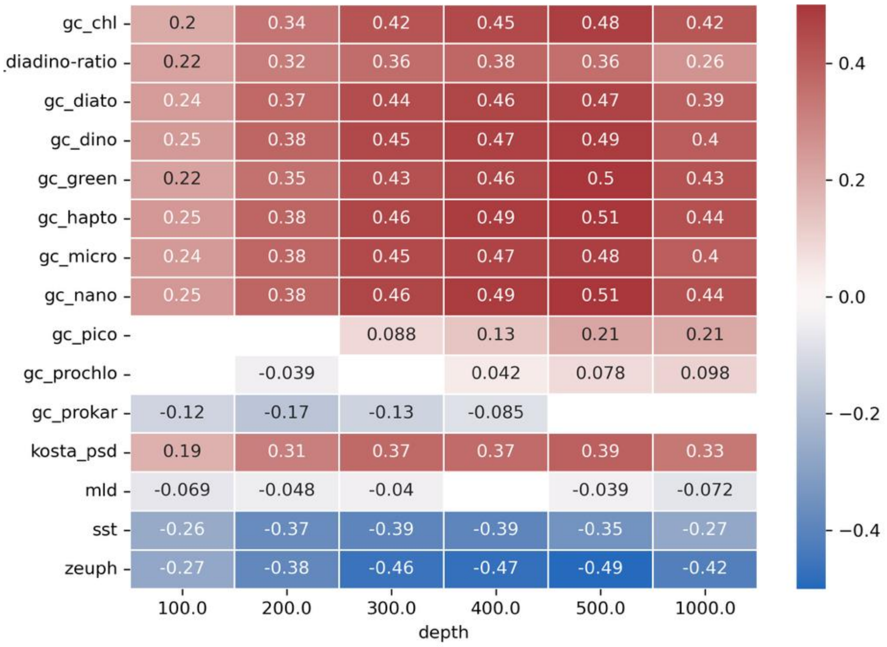


Figure 1. *An analysis of the correlation between surface ocean ecosystem proxies and the particle size distribution slope at a range of depths (x-axis). The Pearson r correlation coefficient is given for each combination of parameters.*

Task 4.2 Higher trophic level active fluxes

4.2.1 The role of zooplankton community structure in the production and consumption of sinking particles

DTU has continued to work on the effect of zooplankton community structure on the production and degradation of sinking particles, with the rationale that whereas large vertically migrating calanoids will enhance vertical flux through active carbon transport and production of large fast sinking fecal pellets, small non-calanoids will feed on sinking particles at the surface ocean thus contributing to their recycling. Our results from the North Atlantic spring bloom indicate that, at their peak abundance, aggregate-feeding copepods can clear the surface ocean from algal aggregates before they sink out of the euphotic zone, although fecal pellets that sink fast might still be exported. Also, it appears that seasonal changes in physiological rates of calanoid copepods have a large effect on both passive and active flux, with all physiological rates (pellet and egg production, respiration) increasing almost linearly with the advancing spring (Koski & Pankoke, submitted). Based on this work, we have 1) continued to collect data on zooplankton community composition (large calanoids vs. small aggregate-feeders) from a larger geographic area, 2) investigated the environmental control of their physiological rates and 3) sampled for day/night distribution to investigate diurnal vertical migration. Also, we have 4) included measurements on the vertical distribution of copepod carcasses, as these are a potentially significant source of exported carbon.

Environmental control of physiological rates: The environmental control of fecal pellet production was investigated onboard RV Sarmiento de Gamboa, during the OceanICU cruise from Walvis Bay to Las Palmas. For pellet production (**Figure 2a**), dominant copepods of different sizes were collected from the zooplankton net catches and incubated in water from the chl-*a* maximum. After 24 h, pellets were counted, measured and collected for later C:N analyses, and the copepods were collected for gut chl and C:N analyses. The production and stoichiometry of copepod fecal pellets was also investigated during a cruise to the Davis Strait in the Arctic, using similar methods. Preliminary results from the southern Atlantic show large variability in the pellet production between the stations (**Figure 2a**), as was also the case in Davis Strait (data not shown). Pellet production was likely related to food availability (phytoplankton concentration) and quality, although this remains to be verified. Once the samples for C:N ratios and gut chl have been analyzed, we will be able to relate the carbon and nitrogen in fecal pellets both to the environmental variables (C:N in phytoplankton, temperature, salinity) and to the feeding mode (herbivory) and stoichiometry of grazers, and use the data as input to the trait-based model of vertical flux (EXPORT).

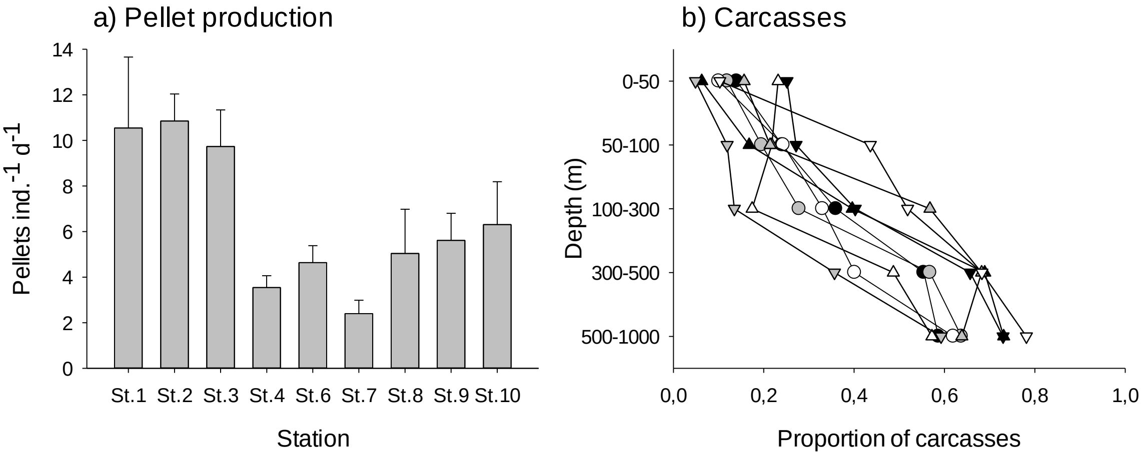


***Figure 2**. a) Fecal pellet production of dominant large and mid-sized copepods at the different stations of the cruise onboard RV Sarmiento de Gamboa (pellets ind.$^{-1}$ d^{-1}; mean ± SD) and b) vertical distribution of copepod carcasses at different stations during the same cruise (proportion). Different symbols in b) indicate different stations.*

The work related to the physiological rates of aggregate feeding copepods has focused on the effects of temperature on respiration and ingestion rates of the pelagic harpacticoid *Microsetella norvegica*. These experiments were conducted with *M. norvegica* collected from a sub-Arctic north Norwegian fjord. The experiments had two goals: 1) To obtain maximum feeding rates of *M. norvegica* that could be used to indicate aggregate degradation in trait-based models and 2) to investigate whether *M. norvegica* would profit from increasing temperature in the Arctic. *M. norvegica* clearance, ingestion and pellet production rates were doubled with a temperature increase between 6 and 8 °C (**Figure 3**), with maximum daily ingestion rates exceeding their body weight at 8 °C. At the temperatures ≤ 8 °C, the respiration rate increased modestly with increasing temperature, but at the higher temperatures the increase in respiration rate was many folds (**Figure 3**). *M. norvegica* could thus profit from a modest temperature increase, but become food limited at the higher temperatures when the carbon demand of respiration would exceed the maximum ingestion rate. As *M. norvegica* is efficient in feeding on aggregates and can build up extremely high biomasses, its response to temperature increase can have consequences for the vertical flux and its attenuation.

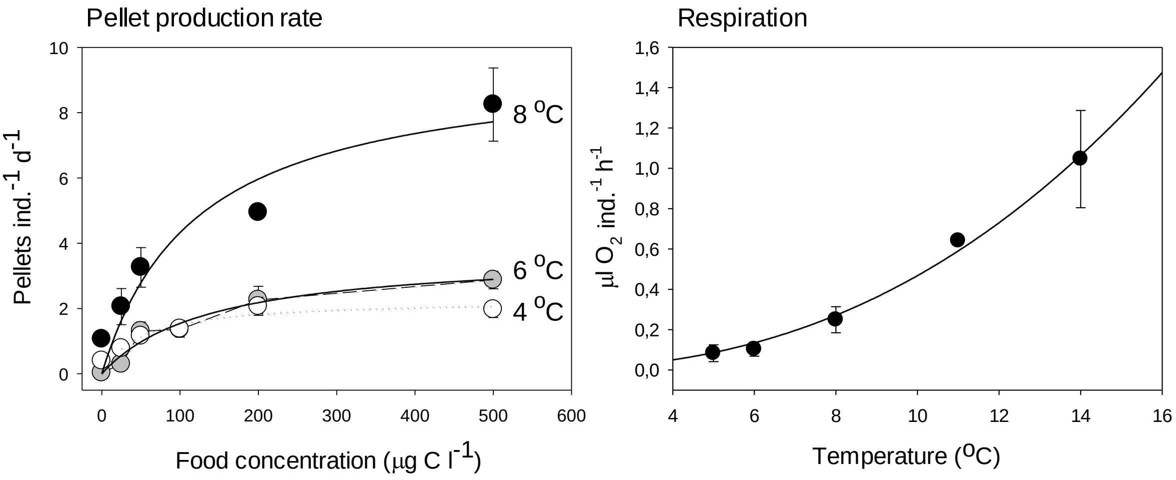
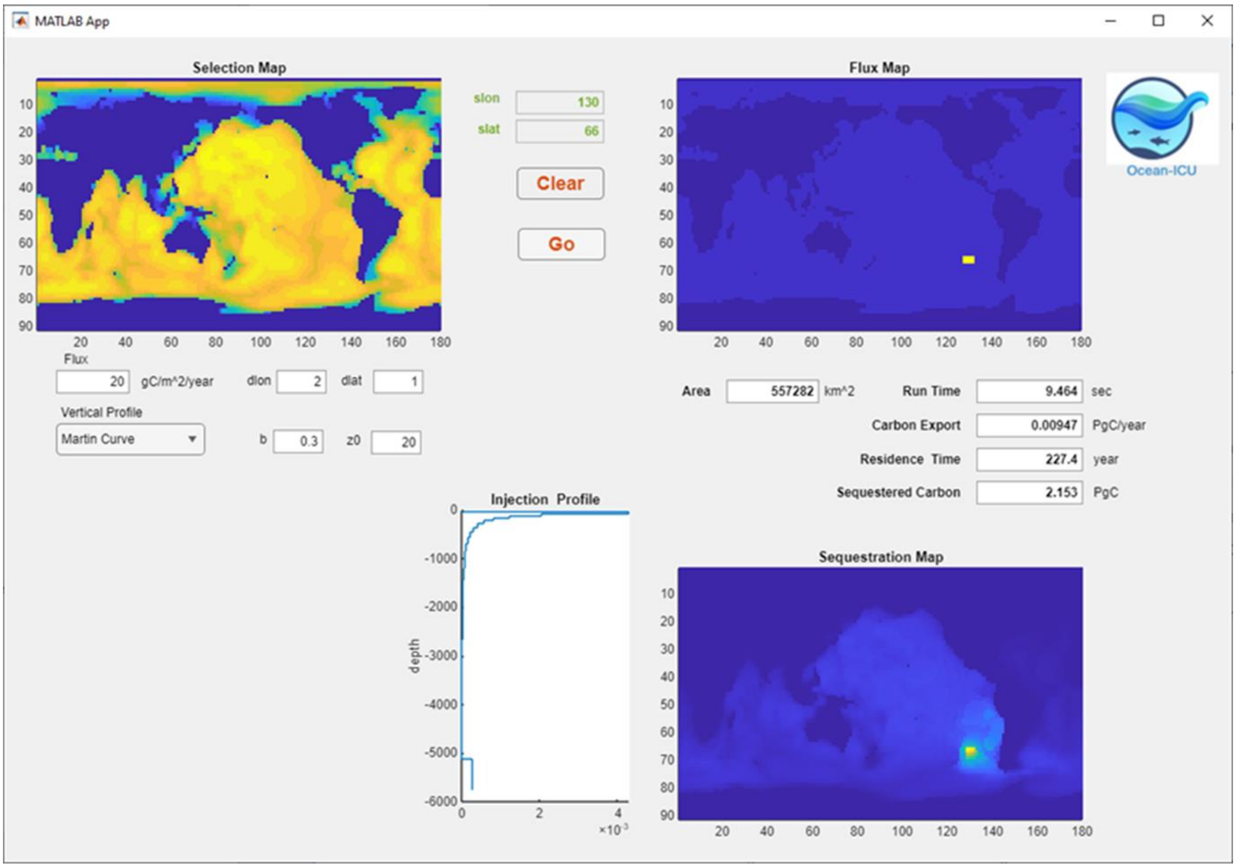


Figure 3. *Pellet production (pellets ind.$^{-1}$ d^{-1}) of Microsetella norvegica as a function of food concentration (µg C L^{-1}) at three different temperatures and respiration (µl O2 ind.$^{-1}$ h^{-1}) of M. norvegica as a function of temperature (mean ± SE). The lines represent the equation of hyperbola fitted to the data.*

Vertical distribution of copepods and carcasses: The vertical distribution of copepod carcasses in the southern Atlantic and in Davis Strait was estimated using Neutral Red staining method that colours the living organisms red but leaves the carcasses uncoloured. The staining was applied to a sub-sample of the vertical zooplankton samples collected using a Hydrobios Multinet with a 50 µm mesh size. After an incubation of ca. 20 min., excess stain was washed out, and the ratio of coloured to non-coloured copepods was counted. The proportion of carcasses ranged from 5-30% in the surface to 60-80% in the deepest samples, with a large variation between the stations, particularly at mid-depth where the oxygen minimum zone was located (**Figure 2b**). Although high, the proportions of carcasses were not much different from the few existing studies from tropical areas, that also observed that most of the zooplankton in deeper waters were dead. This suggests accumulation of carcasses in the mesopelagic, which would both imply relatively high non-consumptive mortality in copepods and low degradation of sinking carcasses.

Finally, samples for the vertical day / night distribution of larger mesozooplankton were collected at 10 stations during the Sarmiento de Gamboa cruise, using a Hydrobios multinet with a 330 µm mesh size. Once counted, these samples will be used to investigate the environmental factors that influence the vertical migration (or lack of it), and in combination with the pellet production, to test the influence of vertical migration on the residence time of carbon using trait-based models. Our results thus provide insights and data on the environmental dependency of physiological rates and behaviour of the key functional groups of copepods, which is needed to understand the role of zooplankton for the export flux and its attenuation.

DTU continues to work on quantifying the role of different taxa and pathways for maintaining the sequestered pool of respired carbon in the oceans. Having completed this for several zooplankton populations in terms of their seasonal migration (Pinti et al 2024) and krill fecal pellets (Cavan 2024), we are now focusing on mesopelagic fish, where we are assembling a large database of observations. This includes a database on the deep scattering layer. To help in this task, and to facilitate other partners in exploring similar questions, we have developed an app that calculates the sequestered carbon and residence time associated with the injection of dissolved inorganic carbon (DIC) for any user supplied geographical region and injection profile **(Figure 4**). The profile can for instance represent the remineralization of sinking particulate organic carbon (POC) by microbes, or the respiration of vertically migrating metazoans.



slon 130
slat 66
Flux 20 gC/m^2/year
dlon 2
dlat 1
Vertical Profile Martin Curve
b 0.3
z0 20
Area 557282 km^2
Run Time 9.464 sec
Carbon Export 0.00947 PgC/year
Residence Time 227.4 year
Sequestered Carbon 2.153 PgC

***Figure 4**. Screen shot of the Carbon Sequestration App developed for OceanICU. This app is available to partners and will become publicly available when it is translated from MATLAB to PYTHON. The interface allows users to select a geographic location (in the case shown; a 55,000 km^2 box in the South Pacific), an injection profile (in this case a Martin curve with b = 0.3 and z_0 = 20 m) and a total injection (export flux) of 20 gC/m^2. In this case, the mean residence time is about 230 years, and the net sequestered carbon from this export (when run to steady state) is 2.15 PgC. The lower right panel indicates the geographical spread (vertically integrated inventory) of this sequestered carbon. This allows a rapid evaluation of one of the key tasks of OceanICU, to evaluate the contribution of various processes to the overall carbon storage in the oceans.*

4.2.2 Lipid pump contributions to carbon storage

EXE: Mayor and Cook participated on the BIOPOLE II expedition to the Scotia and Weddell Seas, Southern Ocean (Feb-March 2025; Figure 5). Vertically resolved samples of lipid storing copepods were collected and frozen for subsequent ETS activity analysis. The associated laboratory work is expected to take place during 2025. The resulting data will contribute to parameterisations of copepod respiration rates during diapause (ST1, ST2, ST3).

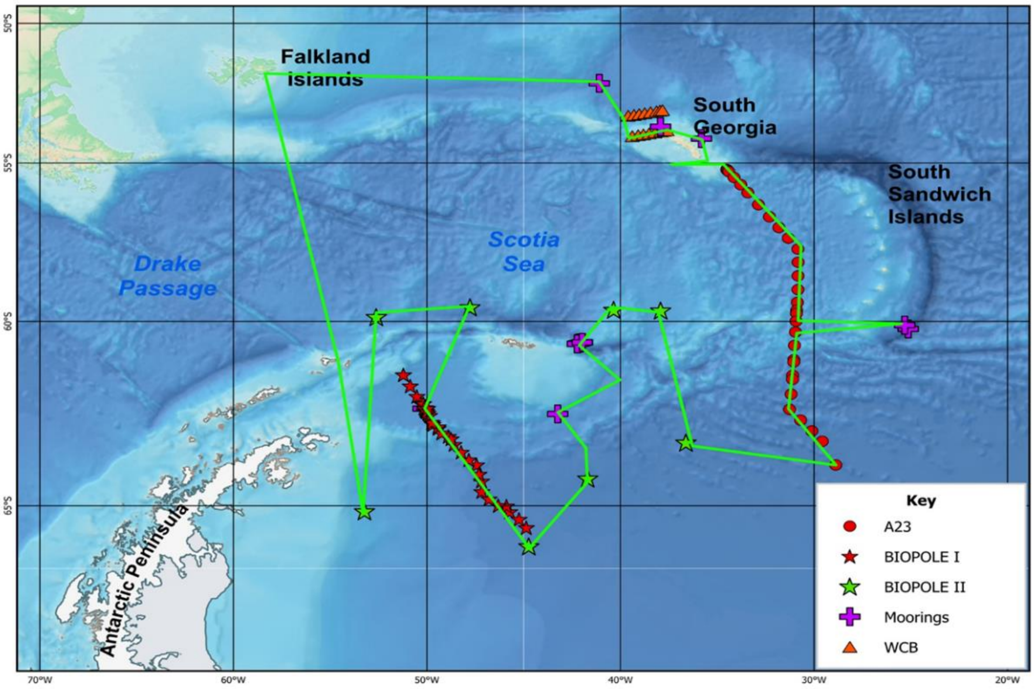


***Figure* 5**. *Cruise track of the completed BIOPOLE II expedition (05/02/25 to 28/3/25) to the Scotia and Weddell Seas, Southern Ocean.*

Trophic linkages between *Calanus* spp. and deep-sea benthos have been examined by undertaking lipid biomarker analysis and determining $\delta^{15}N$ signatures of *Calanus* spp. and selected benthic taxa collected from 1255 – 5414 m in the Fram Strait, Arctic Ocean.

Biomarker analysis indicates that *Calanus* spp. lipid profiles were dominated by C20:1 and C22:1 fatty acids and alcohols. Substantial quantities of these biomarkers were present in the lipids of all the benthic taxa examined: mean relative abundances ranged from 11.18 mol% in holothurians (trophic level = 1.73) to 29.27 mol% in mysids (trophic level = 2.85) (**Figure 6**). These results suggest an important trophic connection between *Calanus* spp. and deep-sea benthic Arctic ecosystems. They also suggest that *Calanus* spp. may act as a vector for transporting lipid-soluble anthropogenic contaminants into deep-sea ecosystems. This work provides insight into copepod mortality during diapause and their wider role in the ecology of deep-sea ecosystems (ST1, ST3). We presented this work as a poster at the OceanICU ASM and have submitted the associated manuscript for publication (Ford et al., 2025)

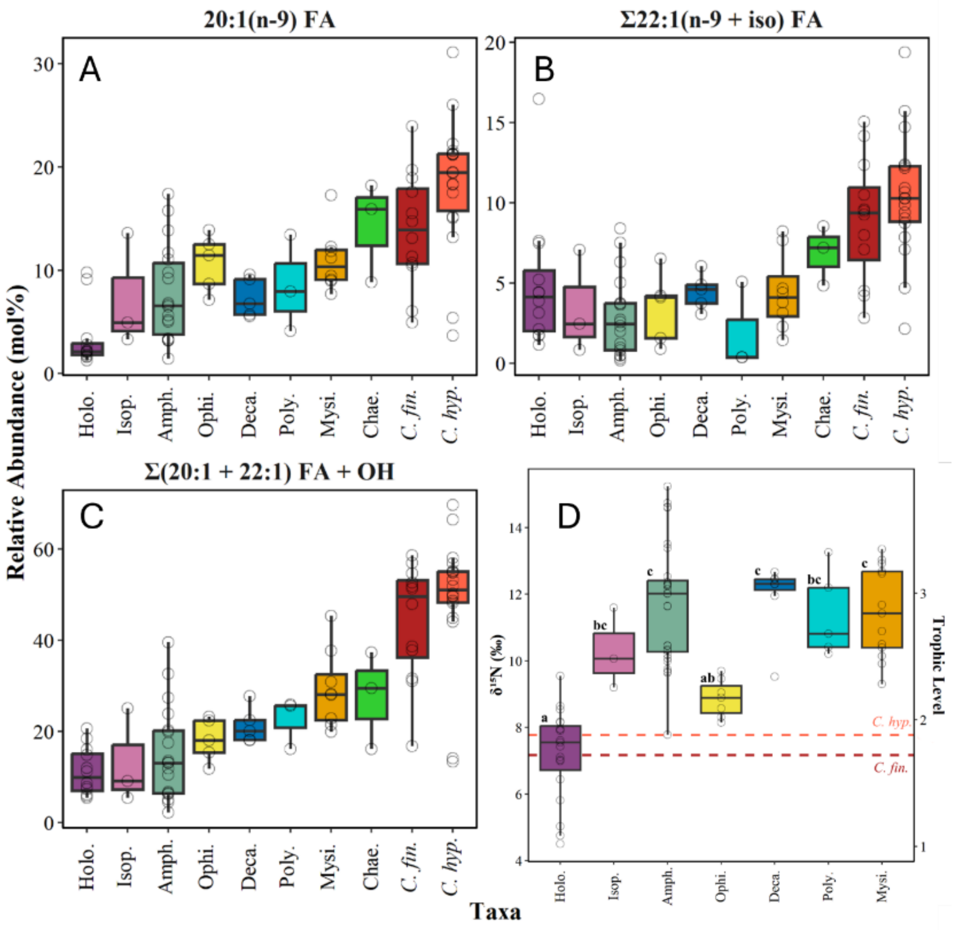


***Figure 6**. The relative abundances of key Calanus spp. biomarkers and $\delta^{15}N$ signatures in Calanus spp. and different benthic taxa. A) Relative abundances of the fatty acid 20:1(n-9), B) Relative abundances of the fatty acid 22:1(n-9), C) the sum of 22:1(n-9) + 22:1(n-9), D) $\delta^{15}N$ signatures and trophic levels, estimated using a $\delta^{15}N$ baseline value of 4.43 ‰ and a $\delta^{15}N$ enrichment factor of 3.80 ‰ per trophic level (Bergmann et al. 2009 and references therein). Horizontal lines reference the mean $\delta^{15}N$ signatures for C. finmarchicus (7.18 ± 0.65 ‰) and C. hyperboreus (7.78 ± 0.86 ‰) specimens collected from the Svalbard region in May, as reported by Søreide et al. (2008). ANOVA results demonstrated that bulk $\delta^{15}N$ signatures varied between taxa ($F_{6,75} = 22.27$, $p < 0.001$). The different letters above individual boxplots are used to indicate which taxa groups featured significantly different ($p < 0.05$) $\delta^{15}N$ signatures based on Tukey HSD post hoc analysis. Amph. = Amphipoda; Deca. = Decapoda; Isop. = Isopoda; Mysi. = Mysidacea; Holo. = Holothuroidea; Ophi. = Ophiuroidea; Chae. = Chaetognatha; C. fin. = Calanus finmarchicus; C. hyp. = Calanus hyperboreus.*

The role of zooplankton diel vertical migration (DVM) in the transport of carbon into the mesopelagic zone in the Iceland Basin has been quantified during spring and summer in 2024. Paired day and night bongo net samples (63µm, 200-0m hauls) of mesozooplankton have been analysed via FlowCam macro, and the resulting data are being used to generate estimates of the 'active flux' at each location.

Preliminary DVM data from the Iceland Basin during spring and summer in 2024 indicate that zooplankton diel vertical migration (DVM) behaviour was more intense during the summer months (August/September) (**Figure 7**), likely driven by reduced surface phytoplankton concentrations, extended periods of darkness at night, and heightened pressure for predator avoidance. Larger zooplankton taxa dominated migrations below 200m and are therefore responsible for the greatest proportion of active [respiratory] carbon flux (estimated using allometrically-scaled respiration rates) (**Figure 8**). In contrast, smaller taxa display limited vertical migrations, resulting in a comparatively reduced role in contributing to the active flux. This work contributes to ST1, ST2 and ST3.

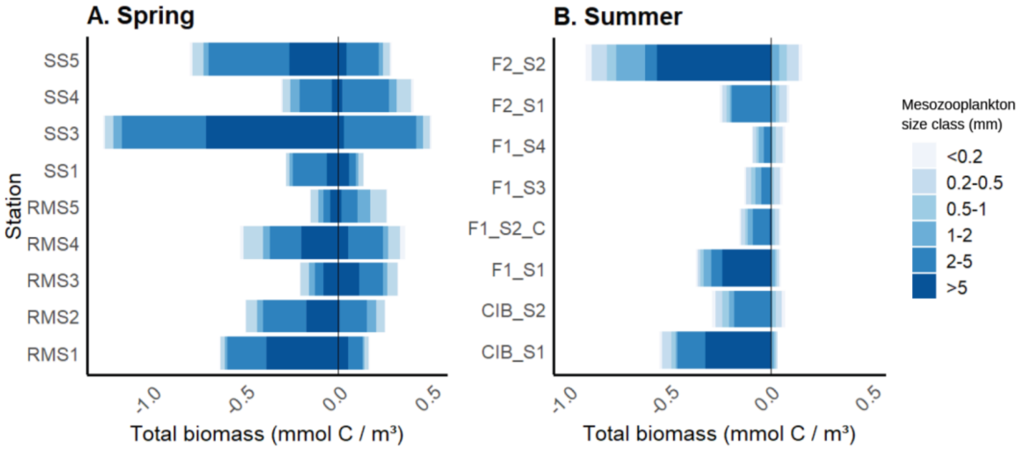


Figure 7. *Day and night zooplankton biomass in the upper 200m at each fixed station, compared seasonally in the North Atlantic. Proportionate biomass and size class calculated for each individual zooplankton. Night biomass is plotted as negative, day biomass as positive. A) Spring cruise, 9 paired deployments, classified zooplankton images (n=26,377). B) Summer cruise, 8 paired deployments, classified zooplankton images (n= 115,039).*

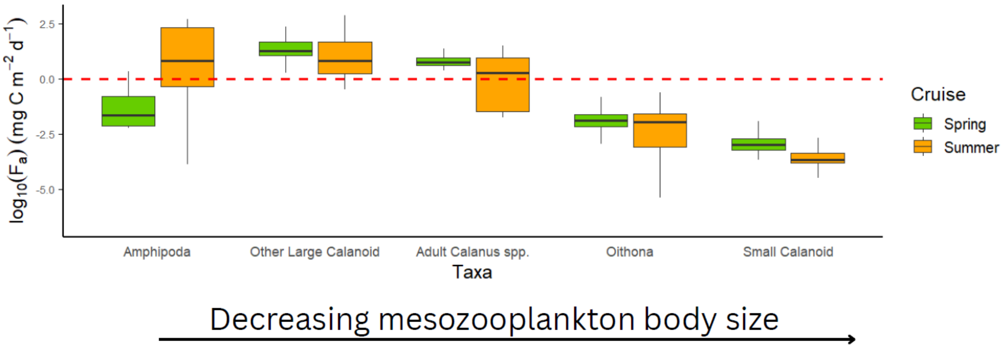


Figure 8. *Seasonal comparison of diel vertical migration (DVM)-mediated active flux for dominant mesozooplankton taxa in the Iceland Basin. Flux values have been log-transformed for each taxon during spring and summer and taxa plotted according to body size. Red line indicates active flux of zero, positive values represent net downward carbon transport below 200m, whilst negative values indicate carbon retention within the upper 200m.*

Modellers from PML (Powley and Millington) were hosted at EXE to discuss DVM and a range of other model parameterisations.

4.2.3 Carbon fluxes from whales

IMR is investigating the carbon fluxes associated with whales, specifically through the a) whale pump, b) deadfalls and c) faecal pellets.

Nutrient recycling and primary production enhancement from whales (whale pump)

Whales have long been suggested to enhance ocean productivity by recycling essential nutrients, a process known as the “whale pump”. However, the extent of their contribution to ocean primary production has remained unclear. Quantifying these effects is crucial for understanding the ecological role of whales in marine ecosystems and for informing ongoing debates about their influence on global carbon cycling.

As part of the OceanICU project, IMR is investigating the contribution of baleen whales to surface nutrient pools, based on multi-element analyses of whale faeces and urine. Additionally, satellite telemetry has been used to monitor whale diving behaviour to determine the depths at which nutrients are acquired and released. These data have been delivered to WP6 as part of Deliverable 4.1. By incorporating this information into an end–to–end ecosystem model (NORWECOM.E2E) we evaluated the impact of whale–released nutrients on primary production and eventual repercussions on zooplankton biomass.

Our findings show that the most important nutrients in minke and fin whale faeces are nitrogen (N), phosphorus (P), Zn (zinc), Fe (Iron), Mn (manganese) and copper (Cu) (Freitas et al. 2023; **Figure 9**). Elemental N is primarily excreted via urine, whereas P and trace elements are mainly released through faeces. Due to their abundance, minke and fin whales are the main contributors of nutrients among baleen whale species in the Nordic and Barents Seas. Ecosystem modelling indicates that baleen whales – including minke, fin, sei, humpback, blue and bowhead whales, support annual and seasonal net primary production, with varying impacts across space and time. While the annual effects are modest (<2%) in most areas, the greatest impacts (up to 10%) occur during summer stratification and in offshore areas far from other nutrient sources. These increases in primary production have cascading effects on the food web, driving rises in mesozooplankton biomass (Freitas et al. under review). This study highlights the ecological significance of nutrient cycling by whales and underscores the value of integrating whale nutrient data into ecosystem models to assess the broader impacts of whales on marine productivity.

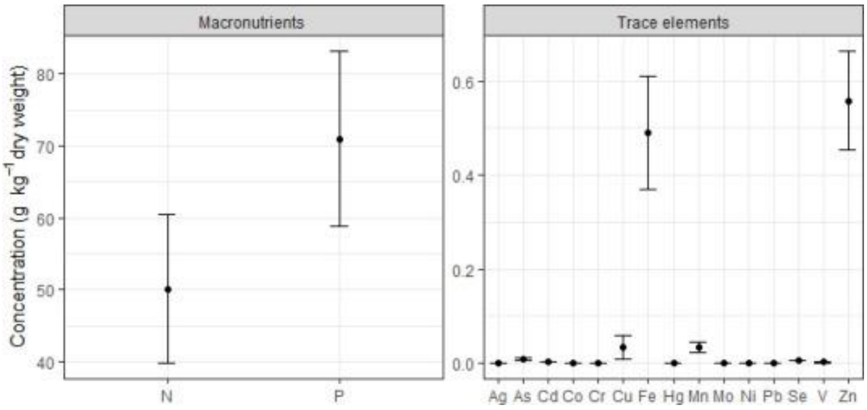


***Figure 9**. Concentration of macronutrients and trace elements in minke whale faeces (mean ± standard deviation). Data from Freitas et al. 2023.*

To investigate baleen whale diving behaviour, minke whales, fin and pilot whales were tagged with satellite tags in the study area (**Figure 10**). Tracked individuals dived both within and below the euphotic zone (Eide 2023), suggesting that these species contribute to both recycled and new nutrients in surface waters. However, whales spent most of their time within the euphotic zone, where most excretion (and therefore nutrient input) is likely to occur. These findings have been used to inform the ecosystem model described above, as well as used in a submitted publication (Eide et al. under review).

Figure 10*. Minke whale tagged with remotely deployed satellite tags (Wildlife Computers, Inc) in June 2023 in Northern Norway. Photo: Zoë Morange.*

Deadfalls

The oceanic biological pump transfers organic carbon from surface waters into the deep ocean, and marine mammal carcasses, called deadfalls, can store carbon on the seafloor for centuries. However, the significance of these contributions remains uncertain. IMR has estimated organic carbon export from marine mammal deadfalls in the Nordic and Barents Seas, covering the Icelandic shelf, Denmark Strait, Iceland Sea, Greenland Sea, Norwegian Sea, and Barents Sea. Using abundance, biomass, residency, mortality, and carbon content data for pinnipeds, toothed whales and baleen whales, we calculated a total annual organic carbon flux of approximately 2.68×10^{-5} Pg C yr^{-1} across all species (Dyrland 2024). Fin whales were the largest contributors (8,653 tonnes), followed by harp seals (5,072 tonnes) and minke whales (3,613 tonnes). Notably, over half of the total flux occurred in the Icelandic region (**Figure 11**). These data are ready to be delivered to WP6 for comparison with other fluxes of sinking organic carbon. While the overall contribution of marine mammal deadfalls is likely small relative to dissolved and particulate organic carbon fluxes, localised effects at individual carcass sites may be substantial. This study provides the first estimate of organic carbon export from a wide range of marine mammals in the Northeast Atlantic, emphasizing the importance of quantifying all components of the oceanic carbon cycle.

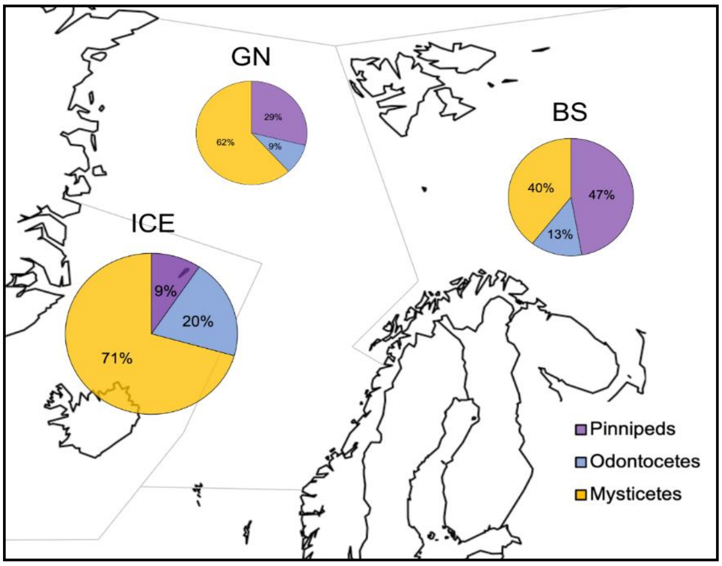


Figure 11. *Total contribution to organic carbon export through deadfalls by pinnipeds (seals and walruses), odontocetes (toothed whales)) and mysticetes (baleen whales) in the three study regions ICE (Iceland Sea), GN (Greenland and Norwegian Seas), and BS (Barents Sea). The size of the pie chart represents the total contribution percentage of each region, 51% for ICE, 21% for GN and 29% for BS. Figure from Dyrland (2024).*

Faecal pellets

Faecal pellets sinking out of the euphotic zone are also likely to result in some export of carbon to deep waters. Specific experiments were conducted using minke whale faecal matter, that was homogenized and added to a settling column. The faecal particles quickly divided into two fractions; a suspended phase that had very low settling rates over time; and a group of larger particles (81% of total carbon) with very high settling rates (**Figure 12**).

Our findings will be delivered to WP6 for a comparison with other carbon sinking flux estimates. This will help quantify the relative significance of this flux and assess its suitability for inclusion in regional and global ocean carbon cycles.

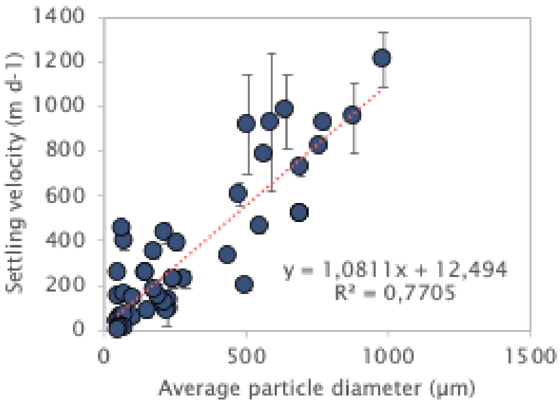


Figure 12. *Settling velocity of minke whale faecal particles plotted as a function of average particle diameter.*

Task 4.3 Carbon production and respiration in the interior ocean

4.3.1 Parameterizations of mesopelagic respiration derived from Biogeochemical-Argo data

OGS estimated mesopelagic respiration (R) from BGC-Argo oxygen data using an updated version of the code and of the raw BGC-Argo dataset. Overall, we obtained ~2400 estimates of R that, due to a limitation of the method, are spatially biased towards the Southern Ocean and North Atlantic. We also extracted the statistics of a set of environmental variables (pressure, T, salinity, oxygen, AOU, NO3, POC, DOC, semi-labile DOC) coincident with the water masses sampled by each float.

To derive a parameterisation for mesopelagic respiration (R), we initially analysed the relationships between R and single environmental variables and found no clear links. Specifically, R was not correlated with temperature (or oxygen) and nor was R normalized by POC or DOC. We therefore investigated non-linear multi-variate relationships between environmental variables and mesopelagic respiration using a Random Forest regression. Results show that the random forest regression can reproduce our estimates of mesopelagic respiration considerably better than the univariate approach (**Figure 13**) using four environmental variables selected to maximise the number of samples retained for training and validating the model. The selected environmental variables were pressure, temperature, salinity and oxygen concentration. It is important to understand that this relationship is not causal. The next step will be to test the extent to which this new parameterisation of R can be introduced into biogeochemical models and its effect on biogeochemical fields.

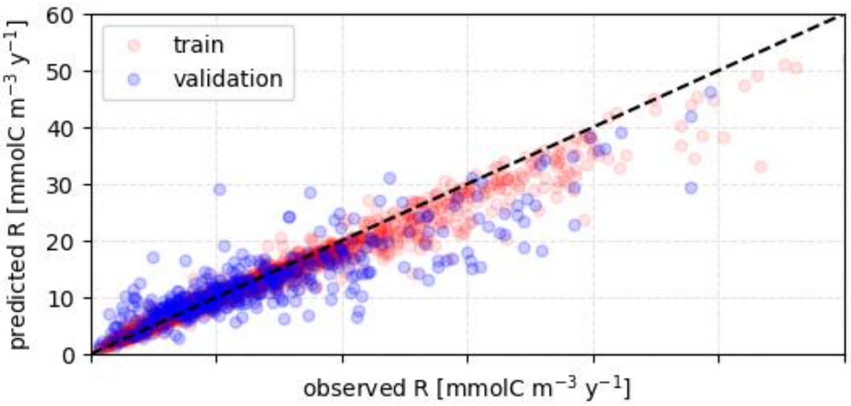


Figure 13. *Scatterplot of predicted vs. observed mesopelagic respiration (R) for the training and validation dataset.*

4.3.2 Regional parameterizations of respiration by respiratory ETS activity

ULPGC has been conducting ongoing investigations into the vertical variability of ocean respiration and the depth of organic matter remineralization. We have examined the relationships between respiration and temperature, dissolved organic matter (DOM), and suspended (slow sinking) particulate organic matter (POMsus). Since the previous deliverable (D4.1), the dataset has been expanded from approximately 3,000 ETS-based respiratory rates and associated environmental data to 5,000 data points, covering the epipelagic, mesopelagic, and bathypelagic layers. To facilitate the analysis of regional differences, the dataset has been grouped into six distinct zones: Boundary Currents (BC), Mediterranean Sea (MS), North Atlantic Subtropical Gyre (NSG), Equator (EQ), North Atlantic Region (NAR), and South Atlantic Subtropical Gyre (SSG).

Table 1. *Stepwise multiple linear regression statistics between ETS-derived respiration (R) and suspended particulate organic nitrogen (PON$_{sus}$), suspended particulate organic carbon (POC$_{sus}$), and dissolved organic carbon (DOC) for each region and water column layer. Only statistically significant relationships are shown in the Relative Importance (RI) column.*

		Epipelagic				**Mesopelagic**				**Bathypelagic**			
		R^2	**p-value**	**f-sta**	**RI(%)**	**R^2**	**p-value**	**f-sta**	**RI(%)**	**R^2**	**p-value**	**f-sta**	**RI(%)**
BC	PONsus	0.5	<0.001	28.7	44.1	0.4	<0.001	17.9	56.3				
	POCsus				-				43.7				
	DOC				55.9				-				
EQ	PONsus	0.0	0.9	0.1	-	0.1	0.8	0.3	-	0.6	<0.001	57.2	100.0
	POCsus				-				-				-
	DOC				-				-				-
MS	PONsus	0.3	<0.001	25.8	68.1	0.3	<0.001	29.3	-	0.0	0.6	0.7	-
	POCsus				-				-				-
	DOC				31.9				100.0				-
NSG	PONsus	0.3	<0.001	93.4	79.5	0.5	<0.001	137.6	21.3	0.2	<0.001	31.8	-
	POCsus				-				72.8				100.0
	DOC				20.5				6.0				-
SSG	PONsus	0.3	0.5	0.8	-	0.0	0.9	0.1	-	0.1	0.8	0.3	-
	POCsus				-				-				-
	DOC				*				*				-
NAR	PONsus	0.7	0.0	5.6	42.6	0.1	0.0	10.0	-	0.0	1.0	0.0	-
	POCsus				51.0				100.0				-
	DOC				6.4				-				-

Stepwise multiple linear regressions were performed for each region and water column layer to examine the relationship between respiration and organic matter (Table 1). Overall, organic matter accounts for approximately 30–50% of the variability in respiration, although in some cases it can explain up to 70%. Instances where correlations were not statistically significant were generally due to limited data availability. Regional differences were also observed. In the epipelagic layer, respiration variability is primarily explained by more labile substrates, such as suspended particulate organic nitrogen (PONsus) and dissolved organic carbon (DOC). In the mesopelagic and bathypelagic layers, suspended particulate organic carbon (POCsus) is the main factor explaining variability in respiration, likely because most labile compounds have already been remineralized at these depths.

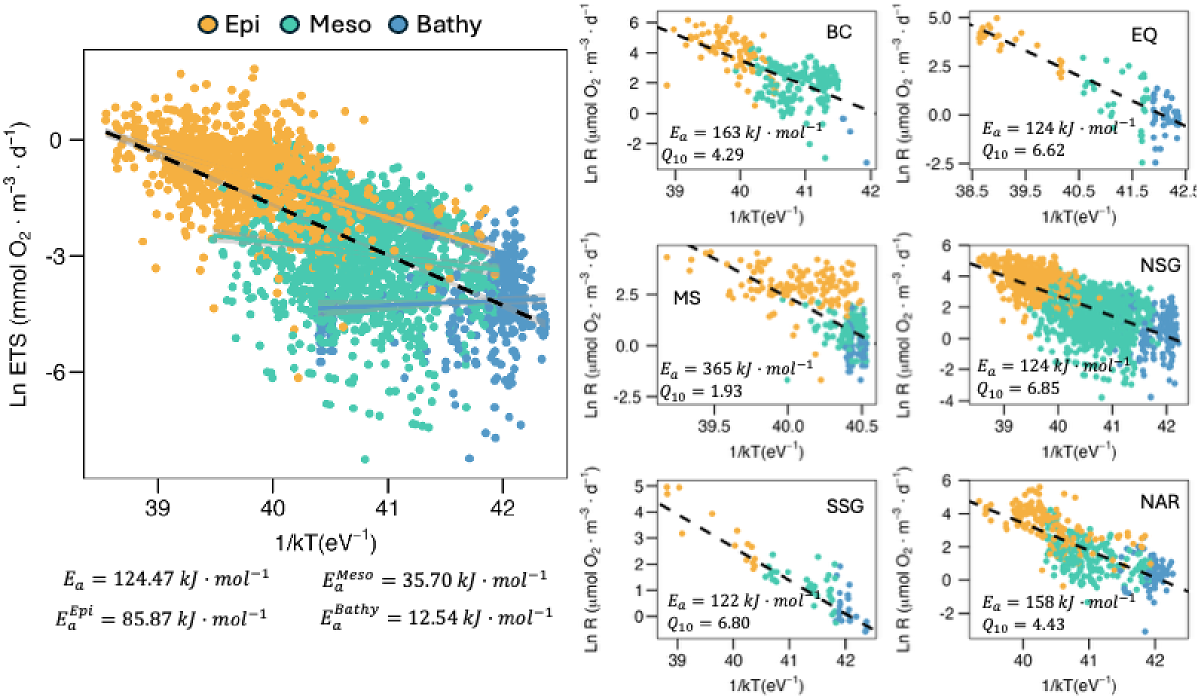


Figure 14. *Arrhenius plots of ETS-derived respiration versus temperature in the epipelagic, mesopelagic, and bathypelagic zones. Activation energies (Ea) and Q_{10} values for each geographical region are also shown.*

The dependence of respiration (R) on temperature (**Figure 14**) was assessed under the assumption that metabolic processes at the community or ecosystem level are influenced by ambient temperature (Robinson, 2019). Activation energies (Ea) ranged from 122 to 163 kJ·mol⁻¹ across most regions, except for the Mediterranean Sea (MS), which exhibited a notably higher Ea of 365 kJ·mol⁻¹. Similarly, Q_{10} values varied between regions, with the lowest observed in the Boundary Currents (BC) region (4.29) and the highest in the North Atlantic Subtropical Gyre (NSG) (6.85). Again, the MS stood out with a Q_{10} of 1.93.

We also observed depth-dependent differences in Ea values, which decreased with increasing depth: 85.87 kJ·mol⁻¹ in the epipelagic layer, 35.70 kJ·mol⁻¹ in the mesopelagic layer, and 12.54 kJ·mol⁻¹ in the bathypelagic layer. While Ea and Q_{10} values within these ranges have been reported in previous studies, they are considered elevated. Moreover, our mesopelagic and bathypelagic values exceed those obtained from oxygen utilization rates (OURs; see section below).

The next steps in this research will involve completing the organic matter database. For dissolved organic carbon (DOC), we will use the database developed by Hansell et al. (2021), which is also employed by WP researchers Markel Gómez-Letona and Xosé Álvarez-Salgado (see section below). For particulate organic carbon (POC), we will utilize the database compiled by Sauzede et al. (2016), currently in use by Giorgio Dall’Olmo within this WP (see section above). Following this, we will aim to assess the influence of water mass mixing on the relationship between organic matter and respiration (OM–R), as done in the case of OUR (see section below).

4.3.3 Parameterizations of mesopelagic respiration derived from OURs in the global ocean

IIM-CSIC has worked on estimating respiration rates in the global mesopelagic ocean, a process that determines the fate of the carbon exported from the surface layer, exerting control over the gradients of dissolved inorganic carbon, the residence times of carbon, and the organic matter input to deep microbial communities. Respiration rates have been calculated for 34 water masses (covering the Atlantic, Indian and Pacific oceans) as spatially resolved (10˚ × 10˚) oxygen utilisation rates (OUR), using dissolved oxygen concentrations (O_2) and transient tracer age estimates ($\text{Age}_{\text{CFC-11}}$, $\text{Age}_{\text{CFC-12}}$, Age_{SF6}). This work is currently submitted to a scientific journal for publication.

The estimated rates lay the groundwork to help validate respiration in global biogeochemical models, as well as to derive useful parameterisations in terms of—chiefly, but not limited to—temperature, organic matter concentrations and vertical input of carbon. Relationships with temperature have been evaluated in thermodynamic terms, as respiration is a metabolic process that is predicted to display a temperature dependence (Brewer and Peltzer, 2017). Activation energies (E_a) have been estimated separately for the OURs of each of the different 1) oceans and 2) tracer ages (Figure 12). E_a values ranged between 81.1 – 95.3 kJ mol^{-1} and corresponding Q_{10} values (for 5 – 15 ˚C) between 3.38 – 4.18 (**Figure 15**)

The dispersion of data in the temperature regressions, however, points to a variability in which other factors play a significant role, chiefly the vertical flux of organic matter. For central water masses (approximately, 150 – 500 dbar), relationships with surface productivity and particle flux proxies have been evaluated, obtaining significant positive relationships in all cases (**Figure 16**). Notably, different slopes have been obtained for different oceans, suggesting a stronger influence of the vertical flux of carbon on respiration within the central water masses of the Pacific Ocean.

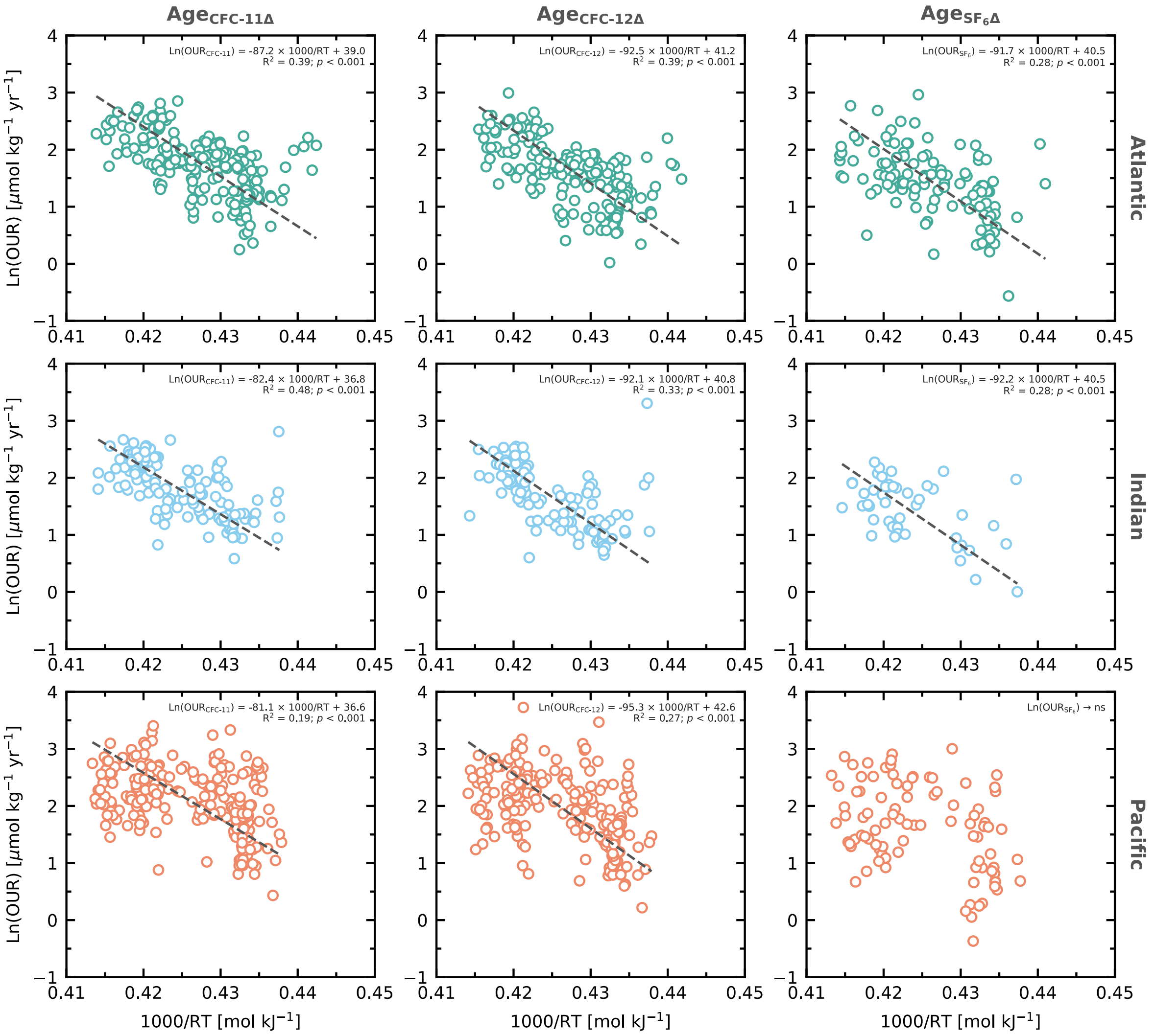


***Figure 15**. OUR estimates and their relationship with temperature, as Arrhenius plots. Columns correspond to regressions for OUR based on different age estimates ($Age_{CFC\text{-}11}$, $Age_{CFC\text{-}12}$, Age_{SF6}), and rows to regressions for different oceans (Atlantic, Indian and Pacific). Slopes correspond to activation energies.*

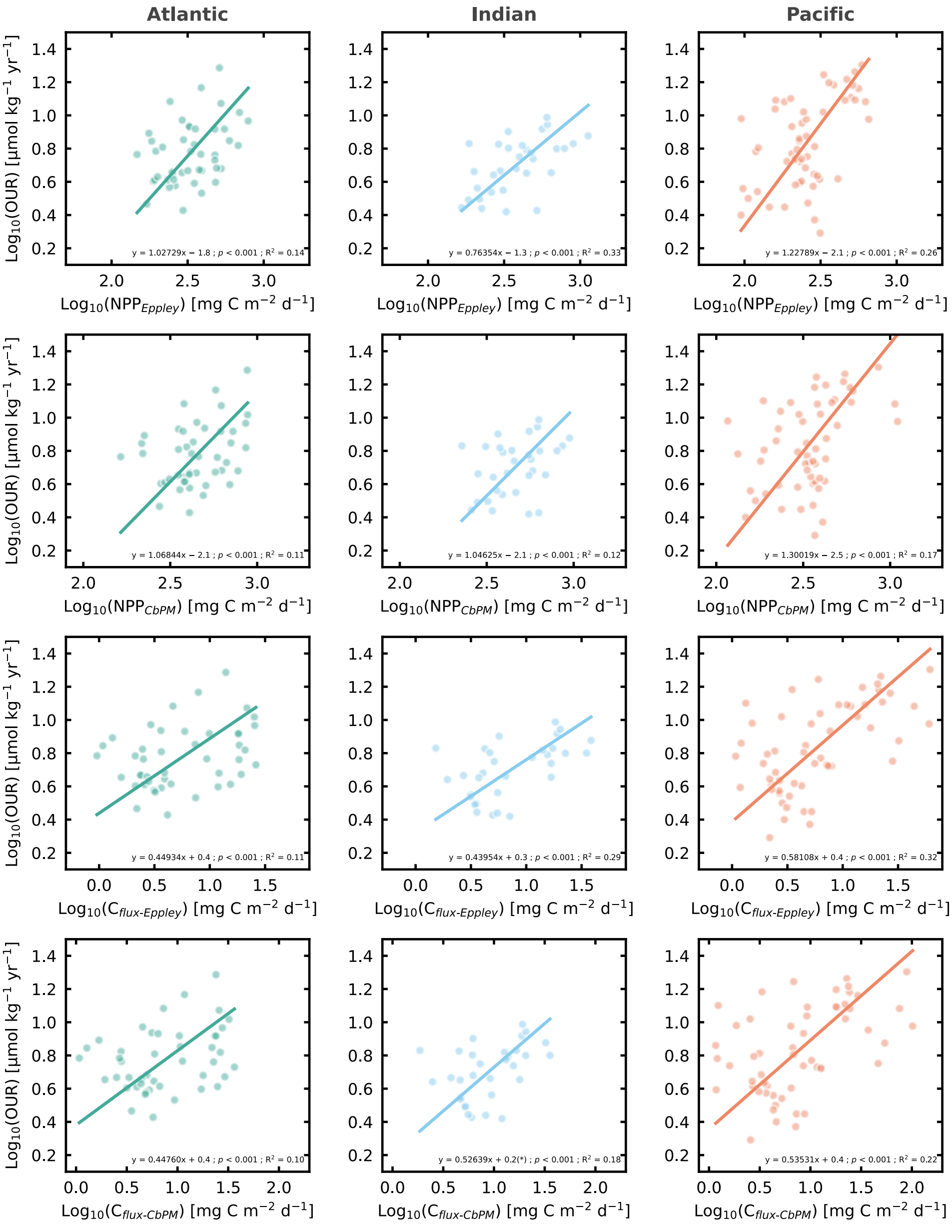


Figure 16. *OUR estimates and their relationship with proxies of vertical carbon flux. NPP corresponds to net primary production, and* C_{flux} *to carbon flux at the water mass depth, estimated with the power law function* $C_{(flux,z)}=C_{(flux,0)} \times (z/z_0)^{-b}$, *based on Martin et al. (1987), b being computed from the equation by Marsay et al. (2015). Results from this figure correspond to OURs based on* Age_{SF6}. *Analogous regressions were performed for* $Age_{CFC\text{-}11}$, $Age_{CFC\text{-}12}$.

Alongside other members of WP4 and WP6, specific guidelines have been set on how to 1) normalise rates and 2) approach the parameterisations. This was done in-person during the annual science meeting in Sopot and afterwards in an online meeting. Work in the immediate future will focus on proceeding with these matters, emphasising the information exchange with WP6.

4.3.4 Effects of mesoscale features on mesopelagic prokaryotic dark carbon fixation, heterotrophic production and carbon budgets

AMU-CNRS-MIO have focused on the vertical distribution of inorganic carbon fixation in the dark ocean (DCF) compared with prokaryotic heterotrophic production (PHP), in “suspended” (free-living prokaryotes and those attached to suspended particles) and prokaryotes attached to suspended particles, vs prokaryotes attached to gravitationally sinking particles.

The APERO cruise (Assessing marine biogenic matter Production, Export and Remineralisation: from the surface to the dark Ocean) was conducted in the NE Atlantic Ocean in June - July 2023, during a post-peak bloom phase (**Figure 17**). The mesopelagic zone (100-1000m) plays a crucial role in the global carbon cycle by transforming and transporting carbon to the deep ocean. Mesoscale oceanographic features, such as eddies and fronts, are known to influence surface productivity and carbon export, but their effects on microbial processes within the ocean remain poorly understood.

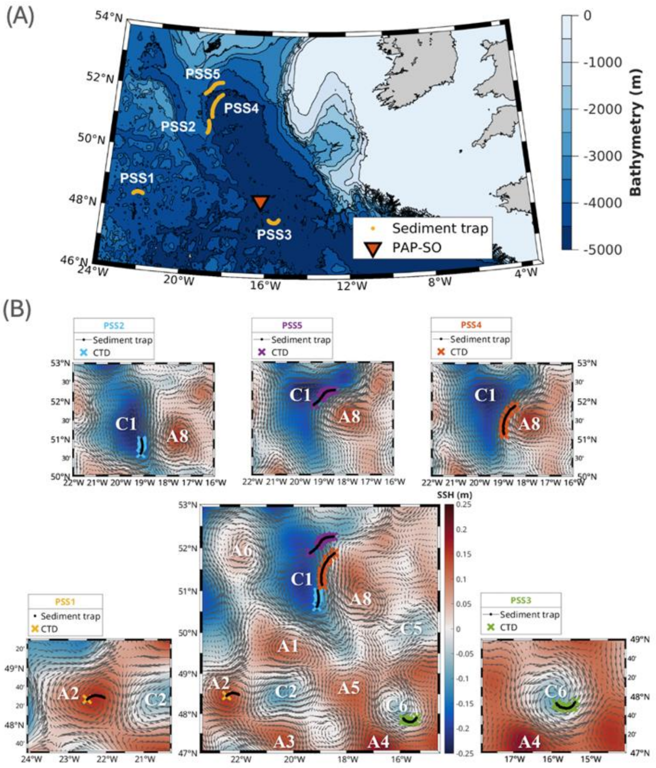


__Figure 17__- Overview of sampling sites during the APERO cruise. (A) Lagrangian drifts of the 0-1000 m mooring line deployed during the APERO cruise (June 3 to July 10, 2023) illustrating the localization of the Process Study Stations (PSS); the red inverted triangle locates the Porcupine Abyssal Plain site (PAP); bathymetry data are from the GEBCO 2023 grid at 15 arc-second resolution (GEBCO Compilation Group, 2023, https://doi.org/10.5285/f98b053b-0cbc-6c23-e053-6c86abc0af7b). (B) Sea level context and detailed localization of the drifting mooring line and associated CTD casts for each PSS; sea level data are European Seas Gridded L4 Sea Surface Heights And Derived Variables Reprocessed (1/8° resolution) from the European Copernicus Marine Environmental Monitoring Service (CMEMS) centered with reference to the mean (14-24°W/46-53°N) to highlight eddies’ structures (from Le Coq et al. Nature Geoscience, in revision).

A key originality of our work, presently in revision to Nature Geoscience (Le Coq et al., in revision) is the simultaneous quantification of DCF and heterotrophic activity of prokaryotes living in suspension in seawater and those attached to gravitational settling particles. We show the importance and relative contribution of dark carbon fixation (DCF)—the conversion of inorganic carbon into organic carbon by prokaryotes—across five contrasting hydrological features in the North Atlantic Ocean, using isotopic tracers and quantification of chemoautotrophy genes. We also identified distinct carbon fixation pathways linked to microbial lifestyle. Our results reveal that mesoscale variability strongly modulates microbial carbon cycling, highlighting the key role of the influence of eddy fronts in carbon sequestration. Heterotrophic prokaryotes attached to sinking particles contribute up to 21% of the total carbon demand, whereas DCF by suspended prokaryotes can contribute up to half of the total carbon input to the mesopelagic zone (**Figure 18**).

Our results complement previous work by showing that prokaryotes attached to gravitationally-sinking particles play an active role in particle degradation and respond dynamically to mesoscale physical variability. We also highlight that DCF by suspended prokaryotic communities represents a significant in situ carbon source, comparable to inputs from gravitational OC fluxes, helping to reconcile long-standing discrepancies in carbon flux estimates. Integrating these microbial processes into ocean ecosystem models, alongside a better understanding of their coupling with mesoscale physical dynamics, is essential to improve predictions of the biological carbon pump efficiency and refine global estimates of CO_2 sequestration. Integrating these microbial processes into ocean ecosystem models and their coupling with mesoscale physical dynamics is essential to improve predictions of the biological carbon pump efficiency and refine global estimates of CO_2 sequestration.

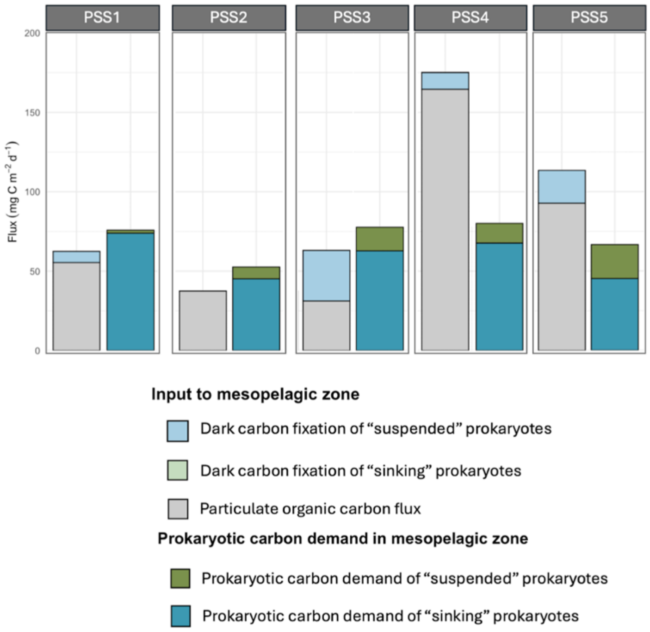


Figure 18. *Mesopelagic carbon budgets of the five stations (PSSs) of the APERO cruise. The fluxes were integrated between depths of 100 and 1000 m depths. We applied a* $PGE_{sinking}$ *of 0.026 and* $PGE_{Suspended}$ *of 0.087 as in Baumas et al. (2013). At PSS2 the lack of* $DCF_{Suspended}$ *values prevented integration.* $DCF_{sinking}$ *is <1% and therefore not visible (from Le Coq et al. Nature Geoscience, in revision).*

4. Main results achieved

- Empirical parameterisations have been developed to link surface phytoplankton size distribution (or chlorophyll concentration) with the slope of the particle size distribution and remineralisation depth. Initial testing of these relationships is currently underway using a size-structured ecosystem model.
- An 'Observations into Models' workshop, held jointly by EXE and PML, focused on translating empirical data and knowledge into model frameworks. This collaboration is expected to contribute to the development of improved parameterisations of diel vertical migration (DVM).
- Establishing a methodology to quantify the contribution of specific taxa and pathways to the biological carbon pump. Examples include contributions via the lipid pump from 5 populations of diapausing copepods, and the sinking of krill fecal pellets in the Sothern Ocean.
- Inputs of nitrogen and phosphorus from whale faeces and urine have been shown to support both annual and seasonal net primary production in the Nordic and Barents Seas. The impact varies in space and time, with the most significant effects (up to 10% increases in primary production) predicted during summer stratification and in offshore regions distant from other nutrient sources. These nutrient-driven productivity increases have cascading effects on the food web, including elevated mesozooplankton biomass.
- Parametrisation of respiratory activity based on temperature and organic matter, using various methodological approaches, enables integration into ocean biogeochemical models across temporal and spatial scales, from regional to global.
- Measurements of dark ocean respiration facilitate estimates of the amount of exported carbon that is remineralised in the deep ocean, as well as the depth at which this remineralisation occurs.
- Measurements of dark dissolved inorganic carbon fixation (the conversion of inorganic carbon into organic carbon by prokaryotes) reveal a relative contribution with a slight increase with depth for the fraction associated with the gravitationally sinking particles, with a strong contribution for the fraction associated with suspended particles or free-living prokaryotes. This latter input serves as a new carbon source for the mesopelagic zone, complementing POC input to varying degrees.

5. Contribution to the overall objectives and relevant (KPIs)

NOC is contributing to ST1 and ST2 by developing new understanding of how plankton and particle size are inter-related and associated with variability in remineralisation depth. These insights will be developed into parameterisation(s) suitable for inclusion in either size-resolving ocean models or global biogeochemical models, contributing to KPI2.

The work at **IMR** is increasing our understanding of the impact of whales on primary production and carbon cycling, thus contributing to ST1. Whale carbon fluxes will be integrated in ecosystem and carbon models, to quantify their importance on regional carbon cycles, thus contributing to ST3 as well.

EXE contributes to: KPI1 by describing respiration rates in overwintering copepods and active carbon flux into the mesopelagic by daily vertical migration (DVM) of mesozooplankton; KPI2 by liaising with PML modellers to provide insight into how to better parameterise mesozooplankton diel vertical migration in numerical models; KPI3 by submitting a manuscript (Ford et al., Submitted) that describes the role of seasonally migrating copepods in transporting food into deep sea ecosystems.

DTU contributes to ST1 and ST2 quantifying the contribution of various pathways and taxa to the biological carbon pump, and in assembling databases on copepod lipid content, aggregate sinking speeds and zooplankton respiration, and has contributed to KPI3 (Pinti et al 2023, Cavan et al 2024).

ULPGC contributes to ST1 by using respiratory ETS activity to quantify microbial respiration in the dark ocean, assess its regional variability, and evaluate its role in determining the remineralization depth. A parametrization of microbial respiration is currently being developed, based on dissolved and particulate organic matter, as well as temperature (KPI2 and KPI8). In addition, we have developed equations to facilitate the comparison of different techniques for measuring in situ primary production. This work has resulted in the publication of a scientific paper (Hernández-Hernández et al., 2025), contributing to KPI3.The resulting parametrization will be shared with WP6 researchers for integration into global biogeochemical models, thereby supporting ST2, KPI 2, and KPI 8. ULPGC has also served as the lead institution for the OceanICU research cruise, which took place from March to April 2025.

IIM-CSIC is contributing to ST1 by quantifying respiration rates in the water masses of the global mesopelagic ocean. To achieve this IIM-CSIC has worked with already existing databases (chiefly, GLODAPv2.2023) to compute new respiration rates based on dissolved oxygen and transient tracer age estimates. As set out in Deliverable 4.1, this work has resulted in a paper that has been submitted to a scientific journal for publication (KPI3). Parameterisations of respiration based on temperature and organic substrates are being derived from these new respiration rates (contribution to KPI2 and KPI8). Moreover, IIM-CSIC has participated in the oceanographic research cruise organised within WP4 that will contribute to the generation of new data for OceanICU.

AMU-CNRS-MIO has served as one of the lead institutions for the APERO research cruise, which took place from June to July 2023. AMU-CNRS-MIO contributes to ST1 by quantifying respiration rates in the water column and on sinking particles by prokaryotic heterotrophic production at the mesoscale. AMU-CNRS-MIO also contributes to ST1 by quantifying dark dissolved inorganic carbon fixation rates in the water column and on sinking particles. Discussion about parametrization has begun but understanding the key players or the energy sources supporting such dark carbon fixation is still under investigation. AMU-CNRS-MIO also contributes to O2 in support of science-based management of human activities to protect and increase the role of the ocean in Carbon sequestration by youtube videos (in French but subtitles available) based on the APERO cruise.

6. Impact and progress beyond state of the art

The role of particle size has long been recognised as likely to be important in determining organic carbon remineralisation depth, however the large-scale datasets to test this have been unavailable until recently. Research in WP4 will lead to the potential to include size effects on carbon fluxes in biogeochemical models.

Research on the role of whales in nutrient and carbon cycling is being advanced beyond the current state of the art. WP4 has conducted the first comprehensive screening of macronutrients and trace elements in whale faeces and urine before their dissolution in seawater (Freitas et al., 2023, Freitas et al. under review). The novel dataset has been integrated into ecosystem models enabling, for the first time, to assess the impact of whale-derived nutrients on primary production and zooplankton biomass across space and time. Ongoing faecal pellets experiments will provide the first empirical estimates of carbon dissolution versus sinking rates from whale faeces. Collectively, these advances will allow us to elucidate the significance of whales in regional and global carbon cycling.

The occurrence of exceptionally low respiratory rates in the dark ocean presents a methodological challenge for the most commonly-used techniques, due to the limited detection capabilities of oxygen measurement methods and sensors. As a result, mesopelagic respiration has often been estimated indirectly using vertical fluxes of particulate and dissolved organic carbon (POC and DOC, respectively) or inferred from oxygen utilization rates (OUR). The ETS activity dataset compiled here represents, to our knowledge, the most extensive collection of direct respiration measurements in the dark ocean. Leveraging this dataset will provide new insights into the magnitude and regional variability of dark ocean respiration. This improved understanding will be essential for refining and enhancing the accuracy of global biogeochemical models.

Spatially resolved estimates of OURs for the water masses of the global mesopelagic ocean will contribute to an improved assessment of respiration (and its impact on the carbon cycle) in the marine environment. As far as we know this is the first study tackling this issue with our scale and approach, complementing previous observational studies focusing on specific regions or those with global scope but very low spatial resolution. Our focus on water masses aims to help us to better understand, through the lens of oceanographic processes, the factors that shape respiration in the interior of the ocean. The respiration rate estimates that we have generated are intended to help validate global biogeochemical models.

7. Lessons learnt and links built

NOC have established a collaboration with researchers at LOV (France), NOAA (USA) and MIT (USA) to use their datasets of plankton and particle size, and size-resolved model.

IMR has established a collaboration with the Icelandic Marine and Freshwater Research Institute to obtain biological samples from fin whales, and with the UiT The Arctic University of Norway in the context of whale tagging.

EXE. ‘Observations into Models’ workshop helped grow collaborative links between EXE and PML.

DTU has established collaborative links with University of Bristol and the Alfred Wegner Institute with regards to aggregation processes, with Imperial College and NIWA (New Zealand) with regards to Southern Ocean processes, and with GEOMAR and UC Santa Barbara concerning ocean carbon uptake. We have also been active in promoting the concept of Ocean Carbon and fisheries through ICES workshops

ULPGC has established active collaborations with Markel Gómez-Letona and Xosé Álvarez-Salgado (WP4) within the framework of the OceanICU cruise. Together, we are working to estimate respiration rates using various methodologies that enable investigation across a wide range of temporal and spatial scales. Giorgio Dall’Olmo (OGS) is also contributing to this effort. In addition, we have initiated a collaboration with Iris Kriest from GEOMAR (WP6) to integrate the developed parameterization into biogeochemical models. The OceanICU cruise also facilitated collaborations with Marja Koski (DTU, WP4) and Alex Poulton (Heriot-Watt University, WP3) searching for ecosystem controls on carbon sequestration.

IIM-CSIC. Within WP4, researchers Nauzet Hernández-Hernández and Javier Arístegui from ULPGC, and Giorgio Dall'Olmo from OGS are estimating respiration estimates evaluated through different approaches, applied to different temporal and spatial scales. As this work on respiration is getting close to being completed, we will jointly carry out an intercomparison of the estimated rates. Moreover, as respiration rate estimates are close to their final form, we are engaging in an active information exchange with WP6 regarding validation and parameterisation of respiration in models, a process which is being mediated by Iris Kriest. By participating in the oceanographic research cruise organised by WP4, IIM-CSIC also closely collaborated with a number of researchers both from WP4 and WP3.

AMU-CNRS-MIO / EXETER. Within WP4, Christian Tamburini (AMU-CNRS-MIO) and Daniel Mayor (Exeter, UK) are co-supervising a PhD student (Elodie Jacob) in the framework of OceanICU. The PhD subject is on the impact of hydrostatic pressure on multi-cellular organisms to estimate oxygen consumption and motion of organisms that both do, and do not, undertake vertical migration. Data are obtained through laboratory experiments and fieldwork (BIOPOLE II in Scotia Sea and Weddel Sea – March / February 2025, BiolumOBS in Mediterranean Sea, August 2025).

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