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Organic carbon export and loss rates in the Red Sea

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Abstract

The export and fate of organic carbon in the mesopelagic zone are still poorly understood and quantified due to lack of observations. We exploited data from a BGC-Argo float that was deployed in the Red Sea to study how a warm and hypoxic environment can affect the fate of the organic carbon in the ocean's interior. We observed that only 10% of the particulate organic carbon (POC) exported survived at depth due to remineralization processes in the upper mesopelagic zone. We also found that POC exported was rapidly degraded in a first stage and slowly in a second one, which may be dependent on the palatability of the organic matter. We observed that AOU-based loss rates (a proxy of the remineralization of total organic matter) were significantly higher than the POC-based loss rates, likely because changes in AOU are mainly attributed to changes in dissolved organic carbon. Finally, we showed that POC- and AOU-based loss rates could be expressed as a function of temperature and oxygen concentration. These findings advance our understanding of the biological carbon pump and mesopelagic ecosystem.

Introduction

The ocean carbon cycle is regulated by physico-chemical and biogeochemical processes collectively called carbon pumps (Boyd et al., 2019). Among these, the biological carbon pump (BCP) exports organic matter in particulate and dissolved form to the deep ocean (Boyd et al., 2019). The export of particulate organic carbon (POC) is attributed to particles sinking to depth (Buesseler et al., 2007, 2020; Boyd et al., 2019). The BCP is driven by phytoplankton cells in the euphotic layer that uptake CO_2 to produce organic carbon, which is then transported downward to the mesopelagic zone (100 to 1000 m) through a wide range of processes (i.e., biological gravitational pump, mixed layer pump, eddy subduction pump and vertical migration pump) (Boyd et al., 2019; Buesseler et al., 2020). The BCP is mostly responsible for the annual export of surface POC that occurs during episodic events, such as seasonal phytoplankton blooms (Lutz et al., 2007; Honjo, 2014). The efficiency of the BCP is usually quantified based on two main metrics: (1) the attenuation of the export flux, which is typically estimated from the exponent of a “Martin’s curve fit” to the flux profile (i.e., a power-law fit, Martin et al., 1987), (2) the transfer efficiency corresponding to the fraction of POC exported in the mesopelagic zone with respect to that at the base of the euphotic zone (Llort et al., 2018, Buesseler et al., 2020).

In general, most of the organic carbon exported into the mesopelagic zone is lost due to heterotrophic remineralization processes (Giering et al., 2014; Cavan et al., 2017). Many studies revealed that remineralization of sinking organic particles is affected by local environmental conditions by either affecting particle size (fragmentation of particles) or the rate of remineralization (López-Urrutia et al., 2006; Martinez-Garcia et al., 2014; Marsay et al., 2015). Under lower oxygen concentration a larger fraction of organic carbon is thought to be unyielding to remineralization (Weber et al., 2016; Robinson, 2019). Temperature is also known to influence remineralization rates, as the heterotrophic processes responsible of the

organic carbon remineralization are temperature dependent (Marsay et al., 2015; Robinson, 2019).

However, most of these studies were not performed *in situ* which means that changes in oxygen or temperature could have been masking other drivers. Therefore, the roles of oxygen concentration and temperature on heterotrophic remineralization remain unclear (Laufkötter et al., 2016). A warm and/or oxygen-depleted ocean may affect the behavior of heterotrophs and thus the attenuation of organic carbon flux. Since the exported organic carbon is remineralized by heterotrophs back into inorganic carbon, oxygen and temperature changes may also impact the ocean's capacity to control the concentration of atmospheric CO₂ (Kwon et al., 2009, Briggs et al., 2020). Under a warm environment, most remineralization may occur in the upper layer of the mesopelagic zone (100 – 300 m) modifying how carbon and nutrients are fixed and recycled into the ocean's interior (Kwon et al., 2009). Thus, a better understanding of the processes controlling biological carbon fluxes is fundamental to predict the ocean's capacity in regulating climate change (Boyd et al., 2019; Briggs et al., 2020).

The attenuation of the flux of particles should be balanced by community processes responsible for the loss of organic carbon in the mesopelagic layer (Giering et al., 2014, Boyd et al., 2019). Several previous studies have shown that the carbon budget in the mesopelagic zone remains unbalanced (Baltar et al., 2009; Burd et al., 2010), with the notable exception of Giering et al (2014) who were able to balance the attenuation of POC flux with the community metabolism (heterotrophic respiration). Recent studies identified additional mechanisms, such as fragmentation of particles by zooplankton, which may contribute to balancing the carbon budget in the mesopelagic zone (Briggs et al., 2020). Overall, we only have a limited knowledge of the role of the heterotrophic community in the turnover of organic matter and its responses to changes in environmental conditions (i.e., oxygen and temperature sensitivity), which compromises our predictions of carbon storage in the global ocean (Burd et al., 2010).

In the past decade, several studies demonstrated the potential of using autonomous platforms equipped with optical sensors to estimate export flux by providing particle measurements over sustained periods of time in diverse areas of the global ocean (e.g., Dall'Olmo and Mork, 2014; Estapa et al., 2017, 2019, Briggs et al., 2020). For instance, using BioGeochemical-Argo (BGC-Argo) floats, estimates of carbon sequestration were improved as these provide information to track particle accumulation rates in the water column (Briggs et al., 2020).

While the Red Sea is known as a warm environment and characterized by highly stratified waters in the upper layers, its northern part behaves as a temperate ecosystem with deepening of the mixed layer depth during winter and highly stratified waters during summer (Gittings et al., 2018, 2019). The Red Sea, is the northernmost tropical sea of the global ocean and displays a strong latitudinal gradient of decreasing temperature from south (26-32°C) to north (21-28°C) (Chaidez et al., 2017; Kheireddine et al., 2018). The Red Sea has been recently identified as a fast-warming oceanic region of the global ocean, especially in its northern part (Chaidez et al., 2017). The Red Sea is also experiencing warming-related decreases in oxygen levels and hypoxic conditions in some areas of the basin (Stramma et al., 2010; Breitburg et al., 2018).

Such conditions may impact the entire Red Sea ecosystem (i.e., phytoplankton community structure, primary production, nutrient availability, temperature and oxygen concentration), which in turn would affect the organic carbon export flux by influencing the remineralization rates of sinking particles and dissolved organic carbon (Guidi et al., 2015; Marsay et al., 2015; Cavan et al., 2017; Puigcorbé et al., 2017). Marsay et al. (2015) demonstrated a strong correlation between the Martin's exponent and the median upper 500 m water temperature for various regions of the global ocean, suggesting a strong temperature dependence of the rate of attenuation of the export flux of particulate organic carbon (POC).

In this study we examined the effect of temperature and oxygen on the remineralization of total and particulate organic carbon using measurements collected by a BGC-Argo float in the northern Red Sea. Our results suggest that remineralization processes mainly occurred within the upper layer of the mesopelagic zone and that both temperature and oxygen may control the heterotrophic respiration of the organic carbon entering the mesopelagic zone.

Materials and Methods

Deployment, sampling strategy and measurements --- In September 2015, a biogeochemical profiling float was deployed in the northern Red Sea at 34.73°N and 27.66°E where the bathymetry is variable and shallow (<1000 m depth) (Fig. 1A). This float, identified from its World Meteorological Organization number 6901573 (<http://argo.jcommops.org>), acquired vertical profiles of bio-optical and biogeochemical variables as well as temperature and salinity measurements. The mission parameters and equipment of the float are summarized in Table 1 and its trajectory is displayed in Figure 1A. The maximum parking depth was set to 1000 m. The float was programmed to surface at noon every 2, 5 or 10 days depending on the season. Data acquisition was nominally at 10-m resolution between 250 and 1000 m of depth, 1-m resolution between 10 and 250 m, and increased to 0.20-m resolution between 10 m and the surface (Organelli et al., 2016). Float data were downloaded from the global Argo database (<ftp://ftp.ifremer.fr/ifremer/argo/>).

Vertical profiles of chlorophyll-a fluorescence (chl_a) and the volume scattering function (measured at 124° and at 700 nm) were obtained using a Wet Labs ECO sensor. The Photosynthetically Available Radiation (PAR, see acronym definitions in Table 2) was measured with a Satlantic OCR radiometer. Raw counts for each parameter were transformed into geophysical quantities by applying the manufacturer-provided scaling factor and dark count. Then, as recommended by the Argo data management procedures (Wong et al., 2015), each profile was quality controlled by applying methods that have been specifically developed

for each variable (Thierry et al., 2018a, b; Organelli et al., 2017 and references therein). Dissolved oxygen concentrations (O_2) were determined using an Aanderaa optode sensor (model 4330).

Following Schmechtig et al. (2015), vertical profiles of chl *a* concentration ($mg\ m^{-3}$) were adjusted for non-zero deep values, and corrected for non-photochemical quenching according to Xing et al., (2018). The chl *a* values were further divided by a factor of 2 to correct for the overestimation observed by standard WetLabs fluorometers as described in Roesler et al. (2017). The particulate backscattering coefficient at 700 nm ($b_{bp}(700)$ in m^{-1}) was calculated as described in Schmechtig et al. (2016). First, the particulate volume scattering function was calculated by removing the contribution of pure seawater that depends on both temperature and salinity (Zhang et al., 2009). Then, the particulate volume scattering function was converted into b_{bp} as recommended in Boss and Pegau (2001) and Sullivan et al. (2013). Spikes were removed from the chl *a* and b_{bp} measurements as described in Briggs et al. (2011). The PAR vertical profiles acquired during unstable sky and sea conditions, as well as during sporadic atmospheric clouds were discarded following Organelli et al. (2016b). Then, the remaining PAR profiles with nonzero dark measurements at depth and wave focusing in the upper part of the profiles were removed (Zaneveld et al., 2001). O_2 measurements were processed by applying a locally-derived factor (~ 1.06) to each profile based on the comparison between the float's percent oxygen saturation (O_{2sat}) values and those from the monthly World Ocean Atlas climatology (WOA09) (Fig. S1), as described by Takeshita et al. (2013). Finally, quality-controlled vertical profiles of chl *a*, b_{bp} , PAR and O_2 were binned in 1-m intervals and used for the analyses in this study.

Apparent oxygen utilization (AOU) was computed as the difference between O_2 and the oxygen concentration at saturation (O_{2sat}) following the method of Garcia and Gordon (1992). Then

positive changes in AOU were converted to changes in total organic carbon (TOC) using the molar ratio $\Delta\text{C}:\Delta\text{O}_2 = 0.688$ (Anderson & Sarmiento, 1994).

The mixed layer depth (MLD) was calculated as the depth at which density exceeded the density at 10 m by 0.03 kg m^{-3} (de Boyer Montégut et al., 2004). The euphotic depth was calculated as the depth at which PAR was 1% of its surface value (Morel & Berthon, 1989) which corresponded to the depth below which less than 5% of chlorophyll-containing particles were detected. Finally, the bottom of the productive layer (z_p), defined as the region where particles can be produced by photosynthesis, was computed as the maximum between the euphotic depth and the MLD.

From b_{bp} and AOU to organic carbon stocks and fluxes --- Particle backscattering is sensitive to the presence of particles in the size range $0.2\text{-}20 \mu\text{m}$ in general (Stramski et al., 2004) and more specifically between $1\text{-}10 \mu\text{m}$ within the surface of oligotrophic waters (Organelli et al., 2018). In this study, b_{bp} was used to estimate the concentration of particulate organic carbon (POC) using an empirical relationship ($[\text{POC}] = 40233 b_{bp} - 11$) established for Red-Sea waters based on in-situ measurements collected during different cruises performed between 2014 and 2016. The slope of this relationships was within the range of those reported in previous studies (Stramski et al., 2008; Cetinic et al., 2012; Rasse et al., 2017). Details about the POC vs. b_{bp} (700) relationship are provided in supplementary material.

To compute stocks and net rates of POC accumulation within homogeneous water masses, density measurements were used to define different layers within the mesopelagic zone. To verify the homogeneity of these layers along the trajectory of the float, the spiciness metric was calculated according to Flament (2002). This variable allowed us to identify changes in water masses with distinct thermohaline properties but having similar density, and thus to ensure spatial and temporal homogeneity within the chosen isopycnal layers. The float remained in nearly homogeneous water masses only during the year 2016 (see supplementary information)

and thus only data from this year are further considered in this study. Because the float moved significantly over the period of the analysis (Fig. 1A), Lagrangian particle tracking, based on previously validated model results, was used to further test the extent to which the float sampled homogeneous water masses during the analysis period. Essential information regarding the modelling study is described in the supplementary material. Briefly, the general (1 km) circulation in the Red Sea was simulated based on a three-dimensional high-resolution MIT general circulation model (MITgcm) (Marshall et al., 1997) configured for the Red Sea (Yao et al., 2014a, b). The trajectories of numerous passive particles from a point-source region corresponding to the float location were then simulated and tracked using the Connectivity Modeling System (CMS) (Paris et al., 2013).

POC values were integrated over the productive layer and over different isopycnal depths (28.30 to 28.57 kg m⁻³) below the productive zone (Dall’Olmo & Mork, 2014): (1) from the surface (z_0) to isopycnal depth 28.57 kg m⁻³ ($z_{28.57}$) ($z_0 - z_{28.57}$, $iPOC_0^{28.57}$) corresponding to the whole water column (excluding bottom effects), (2) within the productive layer ($z_0 - z_p$, $iPOC_0^{z_p}$), (3) within the entire mesopelagic layer defined as the isopycnal layer 28.30–28.57 kg m⁻³ ($z_{28.30} - z_{28.57}$, $iPOC_{28.30}^{28.57}$), and (4) over gradually deeper isopycnal layers of the mesopelagic zone ($iPOC_{28.30+z_i}^{28.57}$, with $z_i = 0.1, 0.22, 0.25, 0.27$ kg m⁻³ isopycnals). The different isopycnal layers were chosen based on their physical properties and the vertical resolution of the float in order to have enough data points to integrate POC values over gradually deeper layers of the mesopelagic zone. We paid particular attention to exclude sediment re-suspended from the bottom from the analysis to avoid interpreting these resuspensions as POC fluxes.

The net POC flux (E) within the isopycnal layers 28.30 + z_i was then estimated from the rate at which POC stocks in the different layers of the mesopelagic ($iPOC_{28.30+z_i}^{28.57}$) varied as a function of time, and E_{z_p} represents the net POC flux just below the productive layer (Dall’Olmo & Mork, 2014). As the float did not sample at high vertical and temporal resolution,

it was not possible to extract information about sinking of large particles in the mesopelagic layer (Briggs et al., 2020). Thus, the potential export of large particles/aggregates was not considered in this study. Our estimates of POC fluxes are mainly attributed to small slowly-sinking particles, given that de-spiked b_{bp} measurements are not expected to be sensitive to large particles (Briggs et al., 2011).

The vertical variation of E was then used to estimate the so-called Martin's exponent, b , using the power-law function, $E_z = E_{z_p} (z/z_p)^b$ (Martin et al., 1987). While this model remains debated (Guidi et al., 2015, Marsay et al., 2015), estimates of the b exponent allow us to compare the results from our study with other previously studied regions of the global ocean. The fraction of surface POC flux exported to the different layers of the mesopelagic zone, T_{z_i} (transfer efficiency) was computed as the ratio E_{z_i}/E_{z_p} (Buesseler & Boyd, 2009).

The seasonal net export rate in the mesopelagic layers (E_{z_i}) was also estimated by fitting a linear least-squared model from the time when $iPOC_{28.3}^{28.57}$ was minimal (late January) to the time when $iPOC_{28.3}^{28.57}$ reached its maximum value (late February). The fast maximum (instantaneous) net carbon export, $E_{z_{iF}}$, within the mesopelagic zone was determined from the slope of the straight line fitted by a linear least-squared model over the time period of fast POC export (late February, about 6 days).

Removal of POC occurred in two stages. The first stage was observed during a short period of time qualified as “fast removal” and the second was observed over a longer period of time qualified as “slow removal”. Thus, carbon fast and slow net loss rates, $L_{z_{iF}}$ and $L_{z_{iS}}$ respectively, were estimated as the time rate of change of POC stocks (linear fit), when POC stocks within a given layer of the water column were observed to decline for each stage. Fast losses occurred in early March (for about 6 days), while slow ones occurring from March to September (about 205 days). Fast and slow carbon-specific loss rates, $L_{z_{iF}}^*$ and $L_{z_{iS}}^*$ respectively, were computed by dividing $L_{z_{iF}}$ or $L_{z_{iS}}$ by the average POC stocks during the period of removal. Finally, the

loss rates in TOC (derived from AOU), L_{zi}^{AOU} , were estimated as the time rate of change of AOU (linear least-square fit) from early March (minimum of the average of AOU) to early June (maximum of the average of AOU) within a given layer of the water column.

Results

Physical characteristics along the float trajectory --- All particles released in the model at the location of the float on the 1st January 2016 (34.27°N and 27.20°E) within the productive layer and the four gradually deeper isopycnal layers of the mesopelagic zone followed the western boundary currents along the African coast up to a latitude of 24°N. Their average trajectories within each layer are presented in Figure 1B, C, D, E and F, respectively, and agree reasonably well with the float's trajectory. They generally exhibited low dispersion in their pathway. The mean transport velocities and the related drift times were related to the initial release depth. Specifically, particles in the productive layer (145 ± 37 m) needed 53 ± 26 days to reach the position of the float at the end of the period considered in the analysis (Fig. 1B), whereas this time increased to 113 ± 18 days at 180 ± 43 m depth (Fig. 1C), and to 334 ± 7 days for those released deeper (300-485 m) (Fig. 1F). Even if the surface particles travelled faster than the float, this is not a major problem for our study because particles were injected into the mesopelagic from the surface layer only during a localized event (late February 2016). Furthermore, the rest of the dynamics we analyzed occurred in the mesopelagic zone, where the float followed water masses in a quasi-Lagrangian fashion.

Temperature-salinity diagrams produced from the CTD measurements collected along the float trajectory, as well as a compilation of historical stations (see supplementary material) collected in the Red Sea are presented in Figure S4. Different water masses were identified with distinct physical and chemical characteristics: the Red Sea Surface Water (RSSW), the Red Sea Outflow Water (RSOW) and the Red Sea Deep Water (RSDW; Sofianos & Johns, 2007). The RSSW mass corresponds to the surface waters and are characterized by relatively high

variability in salinity. On the other hand, the RSOW and the RSDW are deeper water masses characterized by constant temperature and salinity.

Each of the four mesopelagic layers studied were characterized by temperatures and salinities that corresponded to the RSOW and RSDW masses (Fig. S4 and S5). During 2016, the four isopycnal layers sampled in mesopelagic zone exhibited fairly stable temperatures ($22.15^{\circ}\text{C} \pm 0.10^{\circ}\text{C}$; $21.85^{\circ}\text{C} \pm 0.09^{\circ}\text{C}$; $21.68^{\circ}\text{C} \pm 0.05^{\circ}\text{C}$ and $21.63^{\circ}\text{C} \pm 0.04^{\circ}\text{C}$, respectively) and salinities (40.47 ± 0.05 ; 40.52 ± 0.03 ; 40.53 ± 0.01 and 40.53 ± 0.01 , respectively) along the float trajectory (Fig. S5). In addition, the spiciness metric was used to reveal the underlying isopycnal mixing that could alter the variability of biogeochemical properties on the same isopycnal layers (Fig. S6). We found that each of the four mesopelagic layers was also characterized by low spiciness variability (Table 3), whereas high spiciness variability was observed in response to unstable vertical salinity and temperature gradient immediately near the surface layer (Fig. S6).

Temporal evolution of chl_a and b_{bp} vertical distribution --- The seasonal dynamics of chl_a and b_{bp} are displayed in Figure 2. In the upper productive layer, chl_a and b_{bp} exhibited a similar seasonal pattern with highest values during winter and lower values during the rest of the year. These concomitant high chl_a and b_{bp} values within the surface layer were associated with an increase of phytoplankton biomass following the deepening of the MLD (Fig. 2). In the summer stratified period, chl_a showed a pronounced deep chlorophyll maximum (DCM) (Fig. 2A).

Export fluxes and transfer efficiency --- After the phytoplankton biomass increased in the productive layer, the POC stock in the mesopelagic zone ($iPOC_{28.57}^{28.57}$) increased to its maximum value ($\sim 333 \text{ mmol POC m}^{-2}$, Fig. 3). About seven days later, this POC stock decreased by about $166 \text{ mmol POC m}^{-2}$. Then, over the spring-summer seasons, a slow decline of the stock was observed that amounted to around $83 \text{ mmol POC m}^{-2}$.

The seasonal net carbon export flux below the productive layer, E_{zp} , was 233 ± 46 mmol POC $m^{-2} y^{-1}$ and was mainly associated with a fast export event (25.8 ± 5.2 mmol POC $m^{-2} d^{-1}$) that occurred just after the summer stratification was established (Fig. 3). Vertically-resolved seasonal and fast values of carbon export below the productive layer, E_{zi} and E_{zif} , respectively, decreased exponentially as a function of depth (Fig. 4A, B). Most of the POC was degraded in the upper part of the mesopelagic layer (about 72% between 72 m and 157 m depth), while less than 10% of the POC reached the bottom of the mesopelagic zone (Fig. 4C).

The seasonal estimates of POC flux were fitted to the equation of Martin et al. (1987) to determine the exponent of the attenuation flux, b , which had a mean (\pm standard deviation) value of 1.53 ± 0.16 .

Oxygen-based respiration rates --- The AOU inventory exhibited a ventilation-respiration cycle (Fig. 5). When the mixed layer reached its maximum depth in Jan- Feb, the AOU inventory was ventilated. During this mixing period, ephemeral re-stratifications were observed that caused an anomalous rise in the average AOU values, but these were excluded from the rest of the analysis. During the period of stratification, the AOU inventory increased by 7 to 55% throughout the winter spring until the end of spring (early-June). Then, over the summer, the inventory in AOU remained relatively stable and increased again from October.

Organic carbon losses --- In early March, the POC stock just below the productive layer decreased approximately from 333 to 166 mmol POC m^{-2} in about 7 days (Fig. 3), corresponding to a fast POC-loss rate L_{zpf} of 24 ± 6 mmol POC $m^{-2} d^{-1}$. POC stocks decreased further by around a factor of 2 over the spring-summer (~205 days), corresponding to a slow loss rate L_{zps} of 0.41 ± 0.16 mmol POC $m^{-2} d^{-1}$ (Fig. 3). As observed for E_{zi} and E_{zif} , L_{zif} and L_{zis} also decreased exponentially as a function of depth (Fig. 6A, B, Table 4). Average AOU just below the productive layer increased from ~44 to ~66 $\mu mol kg^{-1}$ until the end of the spring season (~92 days), corresponding to a loss of TOC at a rate, L_{zp}^{AOU} , of 1 ± 0.25 mol C $m^{-2} y^{-1}$.

(10.8 ± 2.7 mmol C m⁻² d⁻¹). $L_{z_i}^{AOU}$ also decreased exponentially as a function of depth (Table 4).

Discussion

Assumption of spatial homogeneity --- The model-based Lagrangian particle tracking suggested that deep mesopelagic waters moved approximately at the same speed as the float, while surface waters moved faster than the float (Fig. 1). This suggests that the float followed in a quasi-Lagrangian manner the same mesopelagic water masses during the analysis period. This conclusion is further supported by the spatio-temporally coherent physical characteristics (temperature, salinity and spiciness) that we observed within each layer of the mesopelagic zone. Overall, these results support our use of the float data as a time series.

Small-particle dynamics --- Large post-bloom sinking organic aggregates were likely fragmented by biological and/or physical mechanisms (Burd & Jackson, 2009) and generated the small particles we observed in this study. These small slowly-sinking particles are expected to be mostly remineralized by heterotrophic bacteria in the mesopelagic zone (Goutx et al., 2007; Herndl & Reinthaler, 2013), because only low concentrations of zooplankton can be found in the Red Sea mesopelagic waters (Dypvik & Kaartvedt, 2013). In addition, bacterial activities, including remineralization rates, are enhanced by warm environments as the Red Sea (Lopez-Urrutia et al., 2006, Sarmiento et al., 2010).

POC fluxes and transfer efficiency --- We observed that about only 10% of the material exported reached depths greater than 220 m (Fig. 4C). This suggests that most of the particulate matter was relatively labile and was remineralized in the upper mesopelagic zone, which is consistent with the relatively high value of Martin's b exponent we estimated. Marsay et al. (2015) found a b value of 1.59 in the North Atlantic Subtropical gyre and hypothesized that a strong attenuation of the flux may occur in the upper mesopelagic in warm waters due to strong recycling of organic material by heterotrophic respiration. In our study, the high value of 1.53

± 0.16 suggests that strong remineralization processes occurred in the upper layer of the mesopelagic zone, possibly as a response to the high temperature of the Red Sea.

Organic carbon losses --- To the best of our knowledge, this study presents the first seasonal estimates of fast and slow net POC loss rates from small slowly-sinking particles in the mesopelagic zone. Losses of POC through the mesopelagic zone are mainly attributed to remineralization by bacteria (Robinson et al., 2010; Herndl & Reinthaler, 2013). However, the temporal and spatial variability of bacterial remineralization rates in the mesopelagic zone still need to be quantified accurately and leads to uncertainties in the mesopelagic carbon budget (Giering et al 2014). The contribution of small slowly-sinking particles could be a potential supplementary carbon source capable of balancing carbon budgets in the mesopelagic zone (Giering et al., 2014; Boyd et al., 2019). Thus, our estimates of net POC loss rates from small particles could be used to further constrain the mesopelagic carbon budget as well as to parameterize biogeochemical models.

Our AOU-based remineralization rates ($1.00 \pm 0.25 \text{ mol C m}^{-2} \text{ y}^{-1}$) are within the range of values of organic carbon remineralization rates previously reported in the Red Sea ($1.25 \pm 0.70 \text{ mol C m}^{-2} \text{ y}^{-1}$; Calleja et al., 2019) and in other oceanic regions (0.7 to $3.6 \text{ mol C m}^{-2} \text{ y}^{-1}$) using similar or different techniques (AOU, oxygen, leucine incorporation, DOC measurements) (Feely et al., 2004; Giering et al., 2014; Devries & Weber, 2017; Robinson, 2019 and references therein).

Our oxygen-based remineralization rates are significantly higher (25 fold) than our POC-based loss rates. These differences likely arise because changes in AOU integrate processes and carbon stocks that we cannot detect with b_{bp} . Also, they could be due to differences observed in the timing between POC and AOU losses which may be due to variability and sensitivity of the carbon pool (type and stoichiometry). Among these additional carbon stocks detected by AOU, but not b_{bp} , the most important is the pool of dissolved organic carbon that is known to

support most (50-90%) of the remineralization (Abell et al., 2000;; Hansell & Carlson, 2001). In agreement with these previous studies, we found that slow-sinking POC could account for less than 10% of the overall organic matter remineralization recorded by losses in oxygen. Recently, Torftein et al. (2020) observed high POC fluxes values (1.7 to 4.6 mol C m⁻² y⁻¹) within the mesopelagic layer in the Gulf of Aqaba in the Red Sea which suggest that a large fraction of POC flux attributed to large fast-sinking particles (> 10 µm) might not be detected here. The remaining part of these losses should thus assigned to the consumption of DOC and larger particles (>10 µm).

Drivers of organic carbon loss --- Our estimated POC and AOU-based loss rates decreased with depth, which could be due to multiple factors that also decrease as a function of depth. These depth-dependent factors include: 1) the concentration of POC and DOC that are the substrates for remineralization; 2) the lability of carbon (e.g., their composition, Roder et al., 2013); 3) temperature and oxygen concentration (Robinson, 2019 and references therein) that affect microbial rates. To attempt to explain the variability of our loss rates with depth (~65% of variation), we computed POC-specific loss rates (rates per unit POC stock). Unfortunately, we do not have in situ measurements of TOC, so we could not normalize the AOU-based loss rates. The POC-specific loss rates still varied over a significant range (~40% of variation) suggesting that the POC variability with depth could not explain all the observed variations in the organic carbon loss rates. In other words, the variability in loss rates with depths could not be explained entirely by a decrease in the available substrates.

We then investigated the variability of POC-specific and AOU-based loss rates as function of temperature (Brewer & Peltzer, 2017; Fig. 7 and 8). POC-specific loss rates and AOU-based loss rates were significantly correlated with temperature, despite the relatively narrow range of temperatures observed ($[L_{ziF}^* = 1.47T - 31.5]$, $R^2 = 0.94$, Fig. 7A; $[L_{ziS}^* = 0.74T - 15.7]$, $R^2 = 0.98$, Fig. 7C; $[L_{zi}^{AOU} = 17.5T - 373]$, $R^2 = 0.88$; Fig. 8A; N=4, p<0.01).

Using the Arrhenius law (Arrhenius, 1889), we estimated the activation energy (E_a) from the slope of a plot of the natural logarithm of the change in the AOU or POC averaged at each time step within a given isopycnal layer of the mesopelagic zone versus the inverse absolute temperature in Kelvin ($1/T$) (Fig. 9, Brewer & Peltzer, 2017). The activation energy is expected to be inversely related to the lability of the substrate of a chemical reaction (in this case, the remineralisation of organic matter): the more a compound is recalcitrant, the higher is E_a . Furthermore, E_a can vary as a function of the organisms degrading the organic matter (Davidson et al., 2000; Davidson & Janssens, 2006). No significant differences between E_a reported for POC and TOC loss rates were found (Fig. 9).

However, we found higher E_a values ($> 1760 \text{ kJ mol}^{-1}$) compared to those reported for other regions of the global ocean ($60.8 - 758.1 \text{ kJ mol}^{-1}$) as well as the Red Sea ($392.5 \text{ kJ mol}^{-1}$), even though our carbon loss rates are within the same range than those reported for the Red Sea by Brewer and Peltzer (2017) (Fig. S7).

Our estimates of E_a are, however, similar to those reported for the eastern part of the Mediterranean Sea (1663 kJ mol^{-1} , Brewer & Peltzer, 2017). These authors suggested that their Mediterranean site had experienced a full column overturn and thus suspected that their data set was not in a steady-state condition due to a deep mixing event, which could explain the high E_a value obtained. Our analyses of the stability of the water column (Fig. S6 and Table 3) indicate that this was not the case for our study. Thus, our relatively high E_a values are consistent with slow remineralization of relatively recalcitrant organic matter and/or might be an artifact of the very narrow range in temperature observed in our study. Alternative explanations for the differences in E_a observed between our study and that of Brewer & Peltzer (2017) could be that our loss rates were (1) estimated using different techniques and (2) estimated within the northern Red Sea compared to the whole basin in Brewer & Peltzer (2017). Indeed, the data used for the Red Sea in Brewer & Peltzer (2017) are based on AOU

measurements, which were collected during spring and fall seasons along the central axis from south to north. Further investigations are needed to explain these differences in activation energies.

Although it is tempting to interpret the strong correlations between loss rates and temperature presented in Figures 7 and 8 as causal links, the real driving factors of the variability in L_{zi}^* and L_{zi}^{AOU} could co-vary with, and thus be confounded by oxygen. Indeed, POC-specific loss rates were also strongly correlated with oxygen, which varied over a wider range than temperature ($[L_{ziF}^* = 0.008O_2 - 0.06]$, $R^2 = 0.91$, Fig. 7B; $[L_{ziS}^* = 0.004O_2 + 0.05]$, $R^2 = 0.98$, Fig. 7D; $N=4$, $p<0.01$). We also found a robust correlation between AOU-based loss rates and oxygen ($[L_{zi}^{AOU} = 0.094O_2 - 1.02]$, $R^2 = 0.92$, Fig. 8B; $N=4$, $p<0.01$). While oxygen was strongly correlated with temperature (Fig. S8), given the greater dynamic range of oxygen with respect to temperature, we have more confidence in relating oxygen than temperature with organic carbon losses rates as a function of depth. This is consistent with previous studies that observed remineralization processes taking place mainly in the upper layer of the mesopelagic zone and slower remineralization rates under lower oxygen concentration (Laufkötter et al., 2017; Le Moigne et al., 2017; Robinson, 2019). Based on these observations, we surmise that temperature and oxygen might be key parameters controlling the respiration of the organic carbon pool entering the mesopelagic zone by heterotrophic organisms. Hence, the sensitivity of heterotrophic organisms to variations in ocean temperature and oxygen concentration may have implications for controlling concentration of atmospheric CO_2 and thus regulating the climate.

Although, oxygen was strongly related to carbon loss rates, the stoichiometry of organic matter could also explain the variability observed in loss rates. The C:N ratio of organic matter increases with depth in the Red Sea (Roder et al., 2013; Calleja et al., 2019) indicating that organic matter becomes more recalcitrant at depth (Thomas, 2002; Paulmier et al., 2009). As

consequence, we would expect lower remineralization rates deeper in the water column. Unfortunately, we do not have coincident particulate or dissolved organic nitrogen measurements to test this hypothesis.

Why are there fast and slow net POC loss rates from small slowly-sinking particles? --

- Small slowly-sinking particles ($<10\ \mu\text{m}$) can be degraded rapidly by mesozooplankton and bacteria, or degraded slowly (weeks to months) by bacteria (Semperé et al., 2000; Goutx et al., 2007). Our results showed that more than 85% of the POC exported to the mesopelagic was degraded within a few days, while the remaining portion of POC (less than 15%) was degraded over the course of weeks to months. We also showed that the fast loss of POC occurred at temperatures similar to those measured during the slow decline. Thus, we can infer that the observed differences in fast and slow loss rates are not due to temperature, but most likely to variations in the organisms consuming the carbon (e.g., zooplankton and bacteria) within the mesopelagic zone (Calleja et al., 2018) and/or to changes in the lability of the POC. In other words, we may have observed slow loss rates of POC over the spring-summer seasons, because after the recorded fast losses, the remaining small particles might have become less nutritious and thus less palatable for bacteria. Moreover, the bacteria and zooplankton communities consuming particles during the periods of fast and slow loss rates might have been different.

Mesopelagic carbon budget --- Closing the mesopelagic carbon budget has been challenging due to the complexity of the mesopelagic food web and the numerous processes involved in the export and remineralization of organic carbon. Numerous studies have found a strong imbalance in the mesopelagic zone by up to an order of magnitude between heterotrophic carbon demand and the flux of sinking carbon (Steinberg et al., 2008; Anderson & Ryabchenko, 2009; Burd et al., 2010). We found that the POC exported via small particles was balanced by its consumption (sum of the fast and slow small-particle POC losses) over the seasonal cycle (Fig. S9). Our results regarding export and losses of POC are consistent with the findings of

Giering et al. (2014) for the Northeast Atlantic Ocean, where they suggest that the main role of zooplankton is to fragment aggregates into smaller particles that are easy degradable by prokaryotes. Recently, Briggs et al. (2020) mentioned that fragmentation of particles into smaller slowly-sinking particles by zooplankton could play an important role in supplying organic carbon to balance the carbon demand by bacteria in the mesopelagic zone. Additional studies are needed to look at the role of zooplankton in mesopelagic waters and to determine particle size and composition in the Red Sea.

Red Sea waters vs other oceanic regions --- Our mean transfer efficiency at 100 m depth below z_p , (T_{100}) and remineralization exponent b were significantly different from values reported in the literature for different oceanic regions (Fig. 10A, B). T_{100} was lower than other values reported in some of the oceanic regions of the global ocean (Fig. 10B). Consistently, b was higher than those reported in different environments, even in other tropical and oligotrophic ecosystems (Fig. 10A). The POC flux just below the productive layer (E_{z_p}) was lower than those reported in other areas of the global ocean except for the eastern part of the Mediterranean Sea (Fig. 10C). Recent studies showed that most of the biomass of zooplankton in the Red Sea is mainly found in the upper layer of the water column (0 - 100 m) due to the presence of low oxygenated waters below 100 m (Karati et al., 2019). The scenario of low abundance of meso-zooplankton in Red Sea waters may explain these differences. We can assume that most of the particles within the productive layer are fragmented into smaller size by zooplankton and are then degraded by bacteria in the mesopelagic zone. Regarding the TOC remineralization rates, our values agree well with those reported for some oceanic regions of the global ocean (Fig. 10D). However, no clear information regarding the temporal and spatial variability of the $\Delta C:\Delta O_2$ Redfield ratios in the Red Sea is known. Uncertainties should be considered when using a conversion factors to estimate TOC based on the Redfield ratio. It is known that temporal and regional differences in $\Delta C:\Delta O_2$ Redfield ratio may appear depending on which

biogeochemical processes pre-dominate (Reinthal et al., 2006; Burd et al., 2010). The common value 0.688 has been used to convert AOU into TOC here, which might not be appropriate of the Red sea and could result in higher or lower estimates of TOC consumption. Thus, while our estimates are within the range of those reported in other areas of the global ocean, they should be considered with caution. Future work should investigate quantitatively how these uncertainties affect our understanding of the carbon fluxes in the mesopelagic layer. We also investigated the relationship between the median temperature within the upper layer of the water column (0-500 m) (where the remineralization of particles mainly occurs) using the dataset from the World Ocean Atlas climatology (WOA13) and the Martin's curve exponent b for various regions of the global ocean (Fig. 11A; Marsay et al. 2015). Both parameters were significantly correlated ($[b = 0.05T + 0.25]$, $R^2 = 0.85$, $N=7$, $p<0.001$), suggesting that temperature may be used as a proxy to predict the effect of climate change on carbon fluxes in the Red Sea. However, we also observed a strong correlation between organic carbon loss rates and oxygen (Fig. 7 and 8), which suggests that temperature changes might mask variations in oxygen (Fig. S8). Indeed, we also found a significant relationship between b and the median AOU ($[b = -0.01\text{AOU} + 0.45]$, $R^2 = 0.90$, $N=7$, $p<0.001$, Fig. 11B) as well as the median oxygen ($[b = -0.03\text{O}_2 + 7]$, $R^2 = 0.90$, $N=7$, $p<0.001$, Fig. 11C) using the dataset from the World Ocean Atlas climatology (WOA09) within the upper layer of the water column (0-500 m) and for various regions of the global ocean. Oxygen is known to be a critical factor affecting growth rates of the heterotrophic communities and remineralization processes, and thus the observed oxygen-dependence of b may be as useful a parameter as the temperature-dependence for future projections in the context of climate change. Interestingly, because oxygen concentrations depend strongly on temperature, oxygen might be used as a proxy for flux attenuation that combines both the effects of oxygen availability and temperature. Further studies to confirm this hypothesis are needed.

While it is known that POC remineralization varies with time and space in the oceans (Buesseler and Boyd, 2009), little is known about this variability and most global biogeochemical models use a constant $b = 0.86$ and a fixed remineralization rate (in depth and time) (0.025 d^{-1}) to estimate ocean carbon sequestration from sinking POC (Dutkiewicz et al., 2005; Seigschneider & Bendsten, 2013; DeVries & Weber, 2017). A constant b value and a fixed remineralization rate are clearly not representative of natural conditions and thus likely lead to uncertainties in predictions of global carbon sequestration. Our observed TOC remineralization rates (loss rates) converge with previous estimates using different approaches reported in the literature (Fig. 10D). However, many of those depend on conversion parameters which may vary in time and space as well inducing high variability. Future work should investigate quantitatively how these uncertainties affect our understanding of the ocean carbon cycle.

Conclusion

In this study, we found that POC exported in the mesopelagic zone was rapidly degraded in a first stage and slowly in a second stage likely by heterotrophic organisms. We hypothesized that these differences in POC loss rates may depend on the palatability of the organic matter (from labile and nutritive at the start *vs.* recalcitrant and less palatable later). Regarding the TOC degradation (AOU-based), we found higher loss rates compared to POC loss rates, which are likely due to the consumption of dissolved organic carbon tracked by AOU and perhaps on the differences observed in the timing between POC and TOC loss.

We then observed that organic loss rates could be potentially expressed as a function of temperature and/or oxygen and thus, could be used to predict their changes in response to climate change. We also showed a significant correlation between b values and the median upper 500 m water temperature and AOU with greater b values in warm waters where we observed high respiration processes by heterotrophs. Such regional variability in b showed that

a uniform b value in the open ocean might not be necessarily appropriate to estimate or predict the feedback of ocean carbon remineralization on atmospheric carbon in the future as suggested by Marsay et al. (2015) and Weber et al. (2016). As we observed a rapid remineralization of the organic matter within the upper layer of the mesopelagic zone, further studies of the processes controlling the size and nature of the particles between 0-500 m depth are necessary to study the size and the nature of the particles in such environment. Currently, BGC-Argo floats do not provide this information. The next configuration of the BGC-Argo floats will enable a better understanding of the nature of the particles and the role of the heterotrophic organisms (zooplankton and bacteria) with a particular focus on the upper mesopelagic layer (Boyd et al., 2019). We also found that the sum of fast and slow POC losses led to a balanced budget for the small slowly-sinking particles in the mesopelagic zone. The contribution of these particles could be a supplementary carbon source capable of balancing carbon budgets in the mesopelagic zone. Heterotrophic communities play an important role in regulating the efficiency of the biological carbon pump through controlling POC export by grazing, fragmenting and degrading sinking particles in the global ocean. An outstanding scientific challenge is to understand the role of the heterotrophic communities in the mesopelagic zone. This will be possible with the development of new sensors on autonomous platforms (Boyd et al., 2019).

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Figure 1: Trajectory of the BGC- Argo float over the period of deployment (A). The location of the deployment is indicated by the red star. The thick white line indicates the portion of the trajectory during the period of this study (January 1 - December 31, 2016). The coloured lines represent the average modeled trajectories of particles that were tracked within the productive layer (z_p) (B) and isopycnal layers $28.30 - 28.40 \text{ kg m}^{-3}$ (C), $28.40 - 28.52 \text{ kg m}^{-3}$ (D), $28.52 - 28.55 \text{ kg m}^{-3}$ (E) and $28.55 - 28.57 \text{ kg m}^{-3}$ (F) during the year 2016. The date (Julian day/year) is indicated on top of each trajectory. The background indicates the bathymetry along the study area.

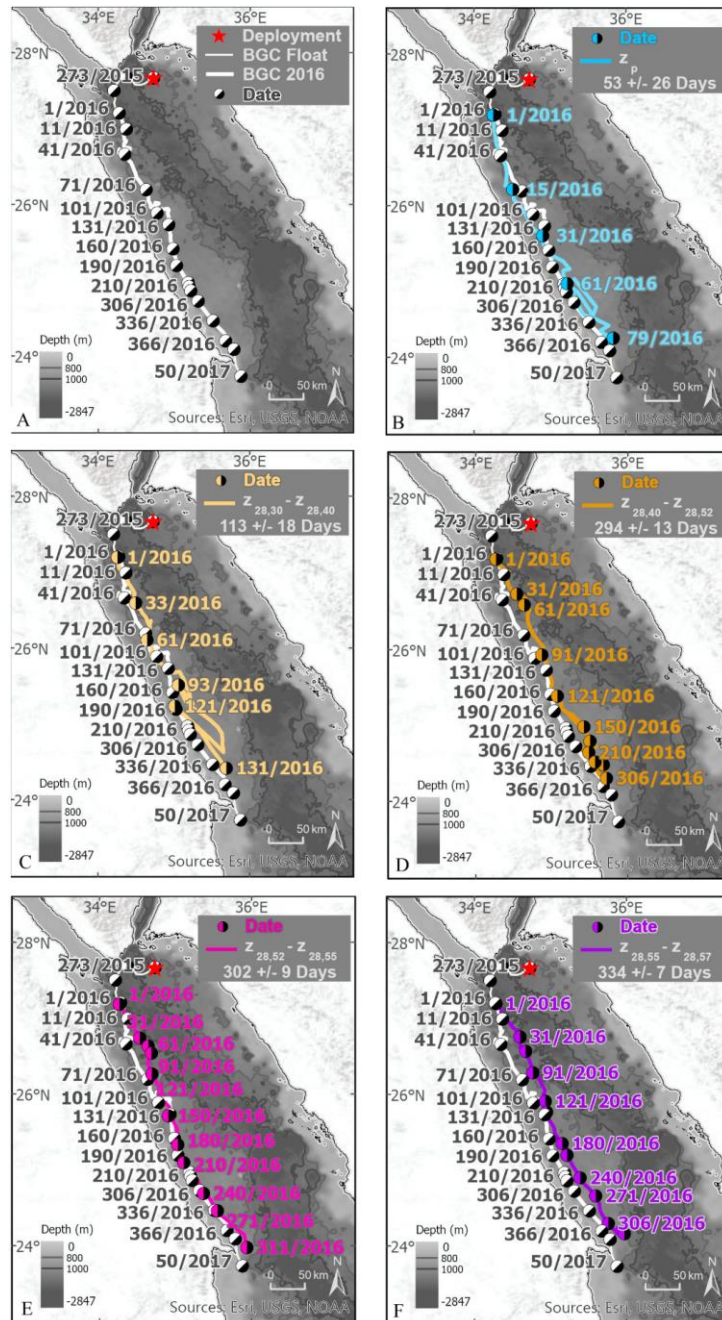


Figure 2 : Time series of the vertical distributions of chl_a (A) and b_{bp} (B) for the float data collected by the float in 2016. Grey lines are the isopycnals 28.3, 28.4, 28.52, 28.55 and 28.57 kg m⁻³. chl_a and b_{bp} (700) are plotted on a logarithmic scale. The black and cyan lines represent the mixed layer depth (MLD) and the productive layer (z_p), respectively. The symbols *, **, ***, and **** represent the isopycnal layers used in the rest of the analysis: 28.30 – 28.40 kg m⁻³, 28.40 – 28.52 kg m⁻³, 28.52 – 28.55 kg m⁻³ and 28.55 – 28.57 kg m⁻³, respectively.

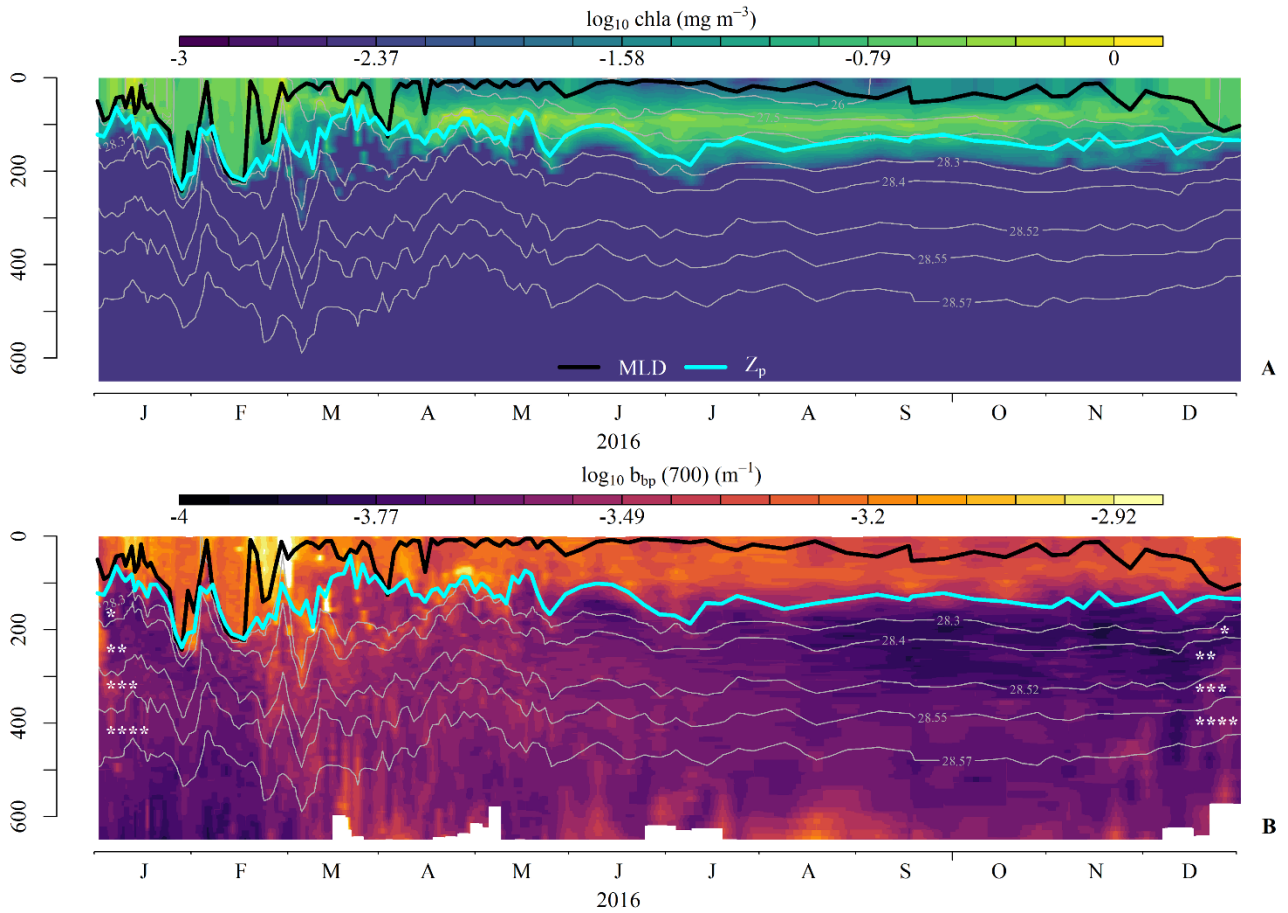


Figure 3 : Vertically integrated POC stocks ($iPOC_{Z_{28.30}+Z_i}^{Z_{28.57}}$) estimated from the float data during 2016 within the productive zone and the mesopelagic zone: the isopycnal layer 28.30 – 28.57 kg m^{-3} representing the entire mesopelagic layer and progressively deeper isopycnal layers ($iPOC_{Z_{28.30}+Z_i}^{Z_{28.57}}$, with $Z_i = 0.1, 0.22, 0.25, 0.27 \text{ kg m}^{-3}$). The symbols *, **, *** and **** refer to the same isopycnal layers presented in Figure 4. Cyan solid and dashed lines: linear regressions used to estimate seasonal and daily fast carbon export rate, E_{Z_i} and $E_{Z_{iF}}$, respectively. Grey dashed and dotted lines: linear regressions used to estimate daily fast and slow carbon loss rates, $L_{Z_{iF}}$ and $L_{Z_{iS}}$ respectively.

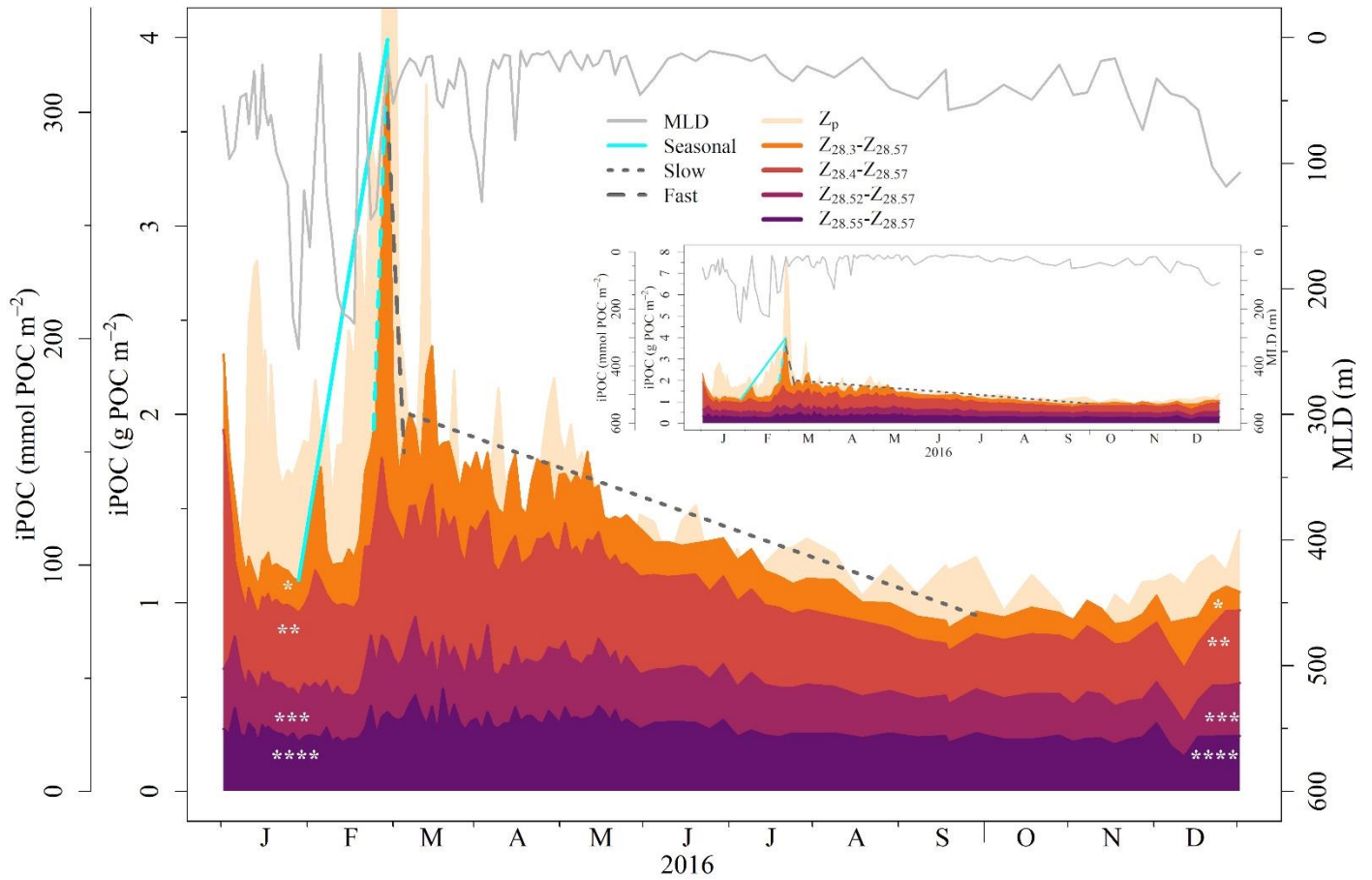


Figure 4 : Estimates of seasonal and fast export rates E_{zi} (A) and E_{ziF} (B) and transfer efficiency (T_{zi}) (C) over the analysed isopycnal layers of the mesopelagic zone. Error bars represent one standard deviation. The line in plot C represent T_{zi} and the grey area its standard deviation. The symbols *, **, *** and **** refer to the isopycnal layers 28.30 – 28.40 kg m⁻³, 28.40 – 28.52 kg m⁻³, 28.52 – 28.55 kg m⁻³ and 28.55 – 28.57 kg m⁻³, respectively (see also Figure 4).

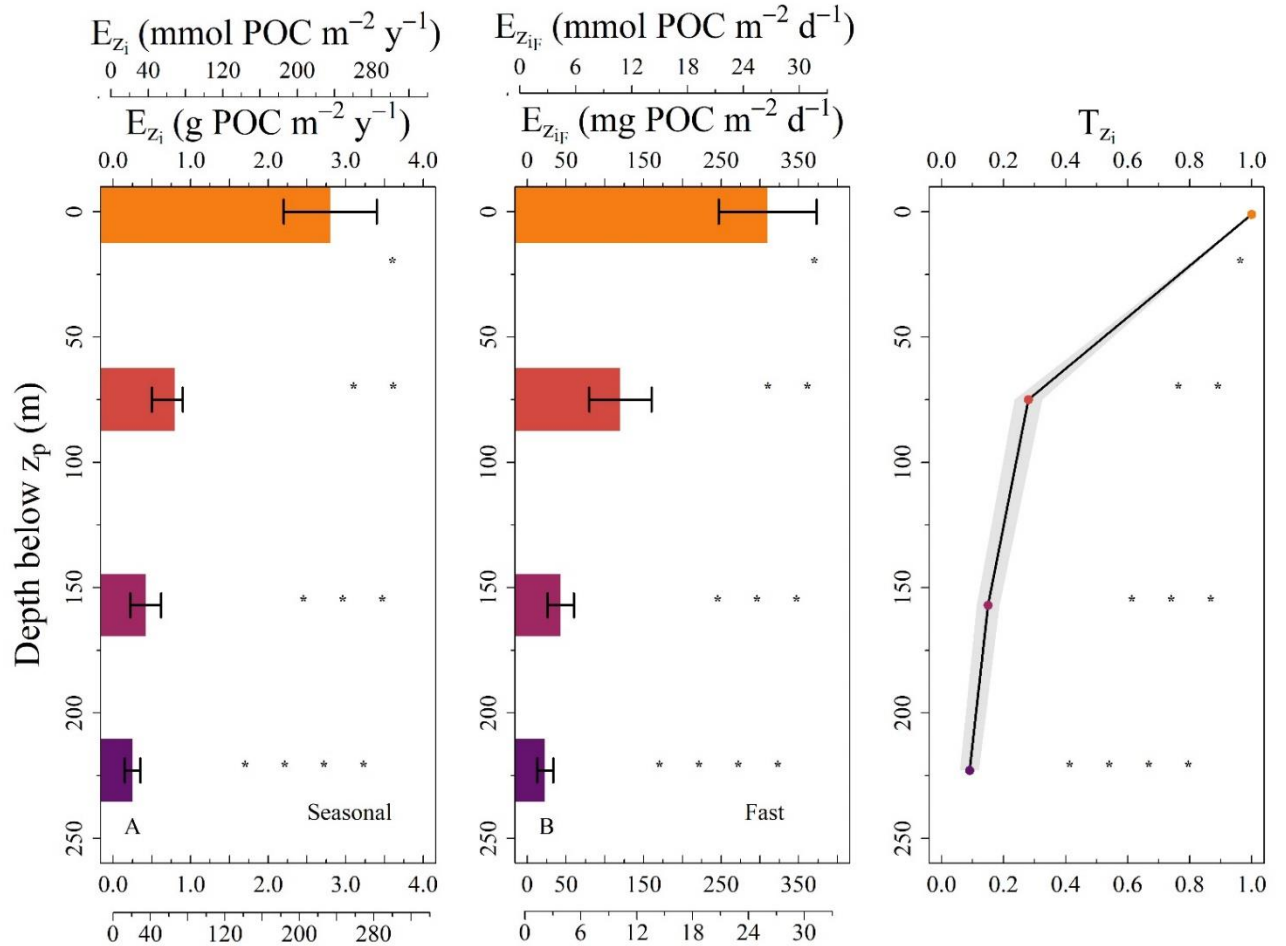


Figure 5 : Vertically averaged AOU estimated from the float data during 2016 within each isopycnal layer of the mesopelagic zone. . The symbols *, **, *** and **** refer to the same isopycnal layers presented in Figure 4. Grey dashed lines: linear regression used to estimate daily carbon loss rates, $L_{Z_i}^{AOU}$.

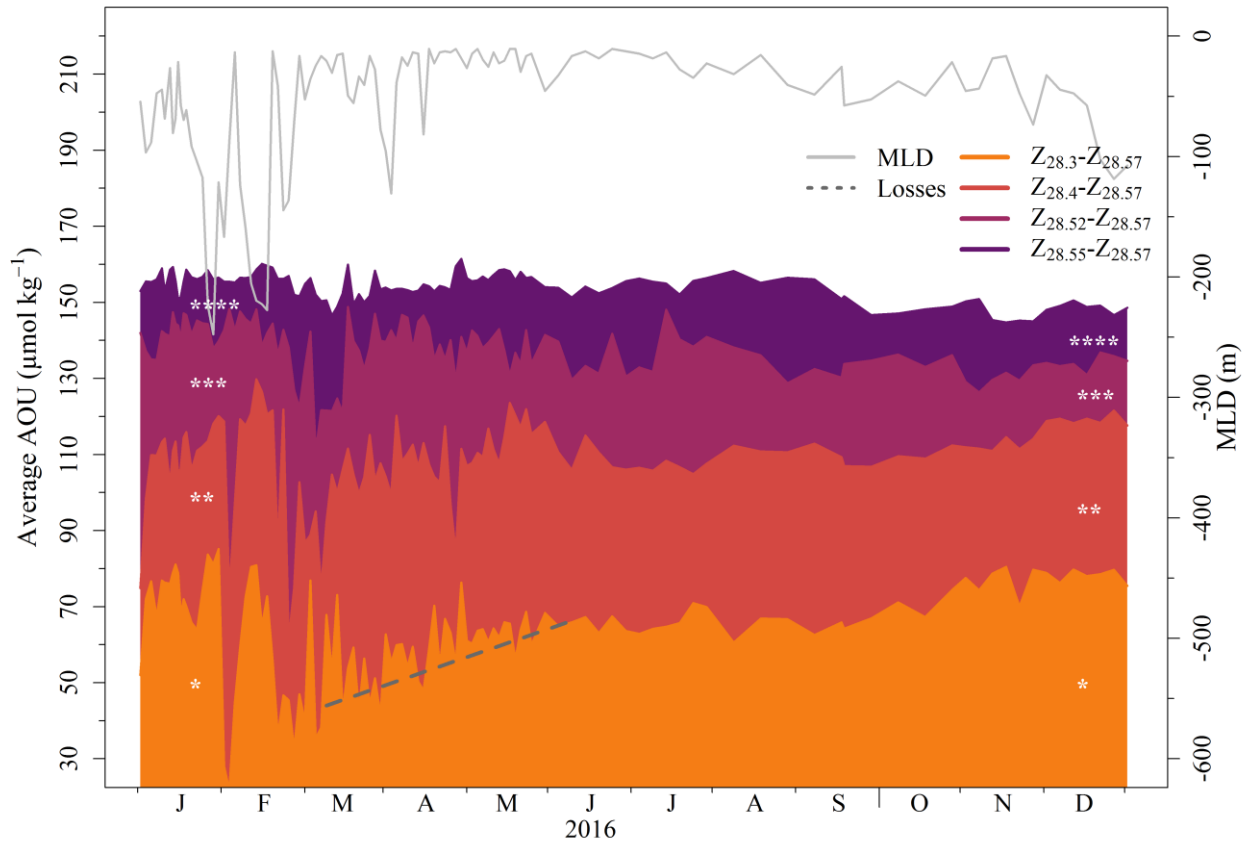


Figure 6 : Fast and slow loss rates L_{ziF} (A) and L_{ziS} (B) over gradually deeper isopycnal layers of the mesopelagic zone. Error bars represent one standard deviation. The symbols *, **, *** and **** refer to the isopycnal layers 28.30 – 28.40 kg m^{-3} , 28.40 – 28.52 kg m^{-3} , 28.52 – 28.55 kg m^{-3} and 28.55 – 28.57 kg m^{-3} , respectively (see also Figure 4).

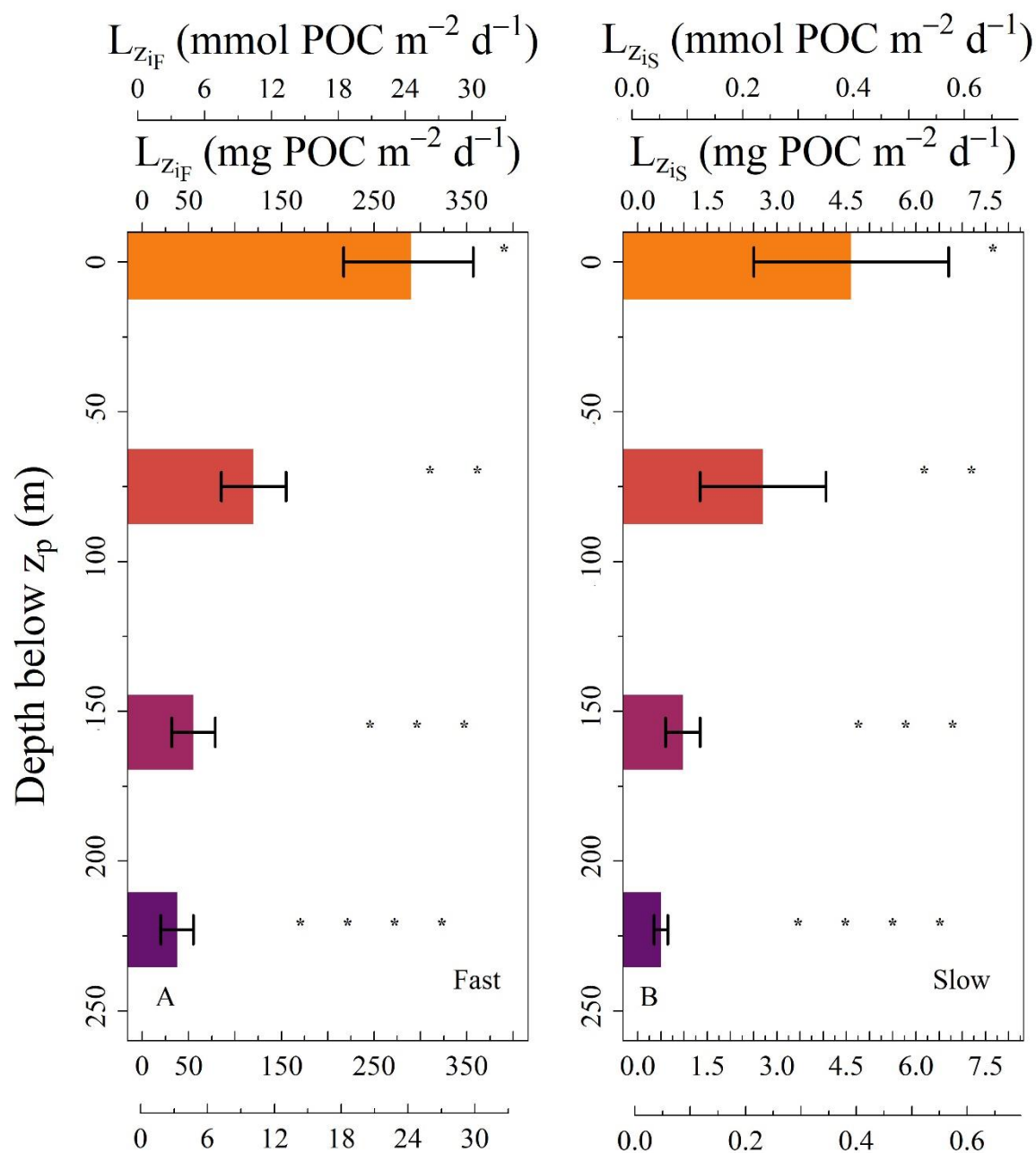


Figure 7 : POC-specific (fast and slow) loss rates as a function of the mean temperature (A, C) and oxygen concentration (B, D) over gradually deeper isopycnal layers of the mesopelagic zone. Error bars represent one standard deviation.

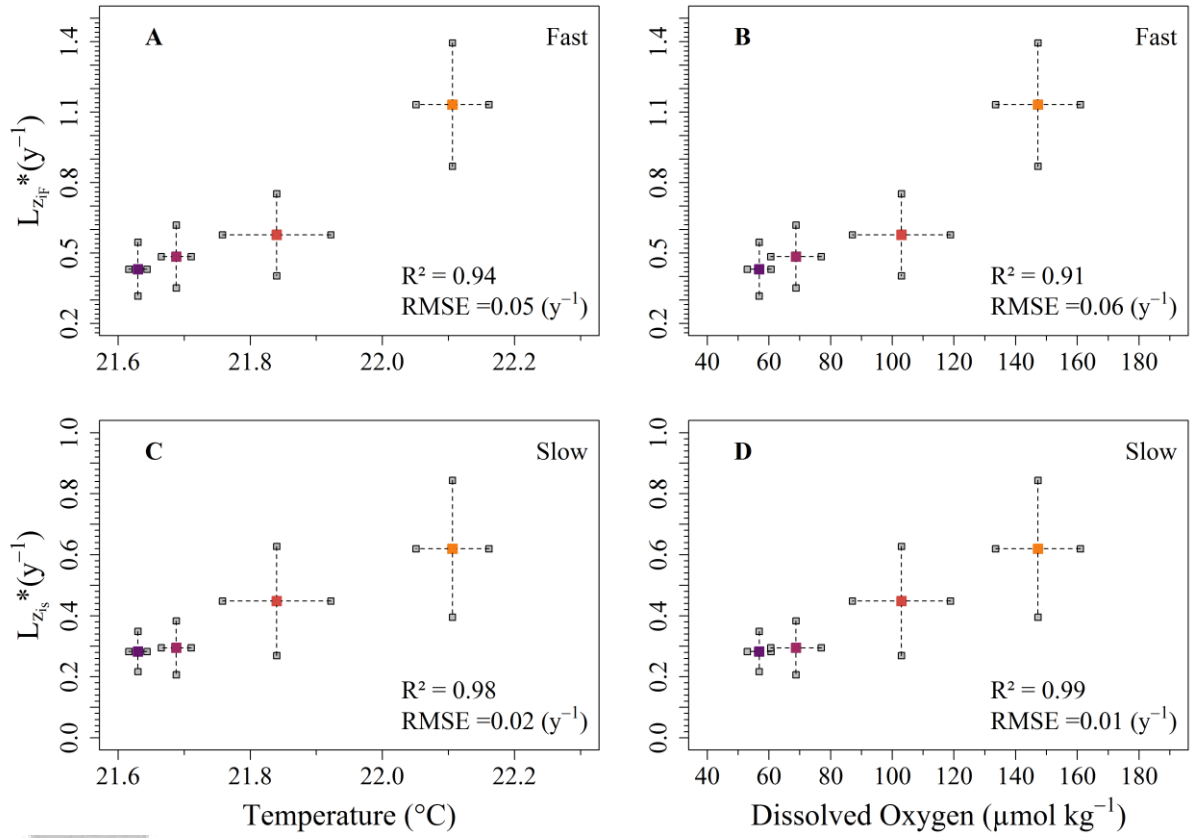


Figure 8 : AOU-based loss rates as a function of the mean temperature (A) and oxygen concentration (B) over gradual isopycnal layers of the mesopelagic zone. Error bars represent one standard deviation.

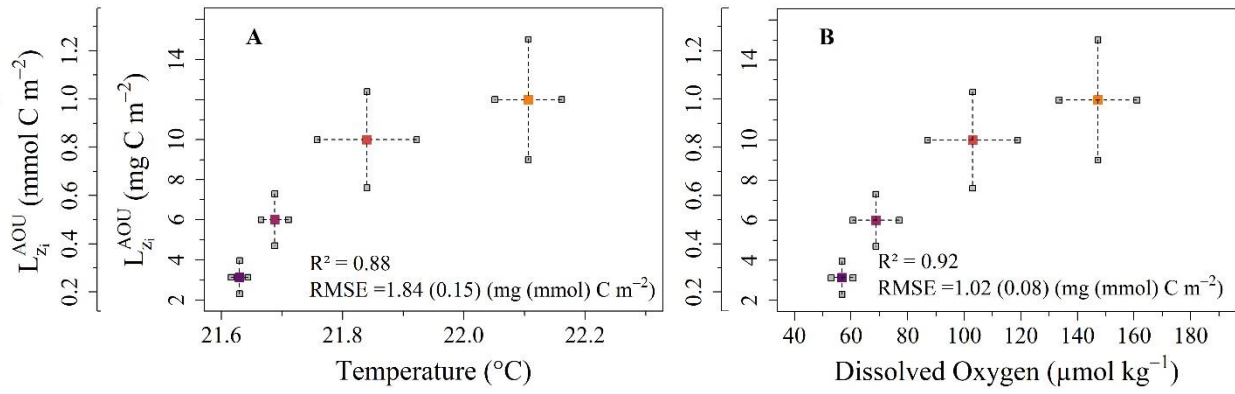


Figure 9 : Arrhenius activation energy plots for L_{zis} (A) and L_{zi}^{AOU} (B) over gradual isopycnal layers of the mesopelagic zone. Error bars represent one standard deviation.

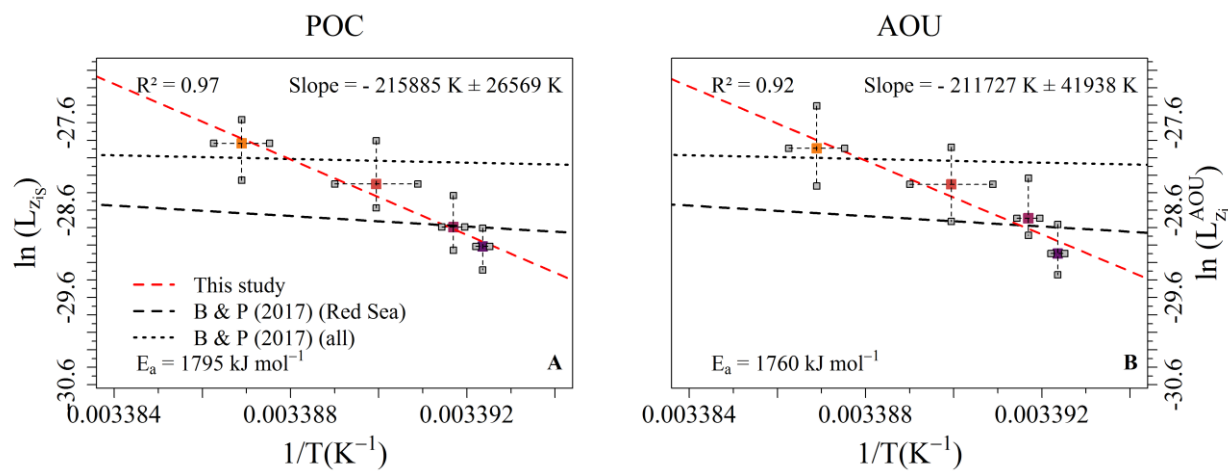
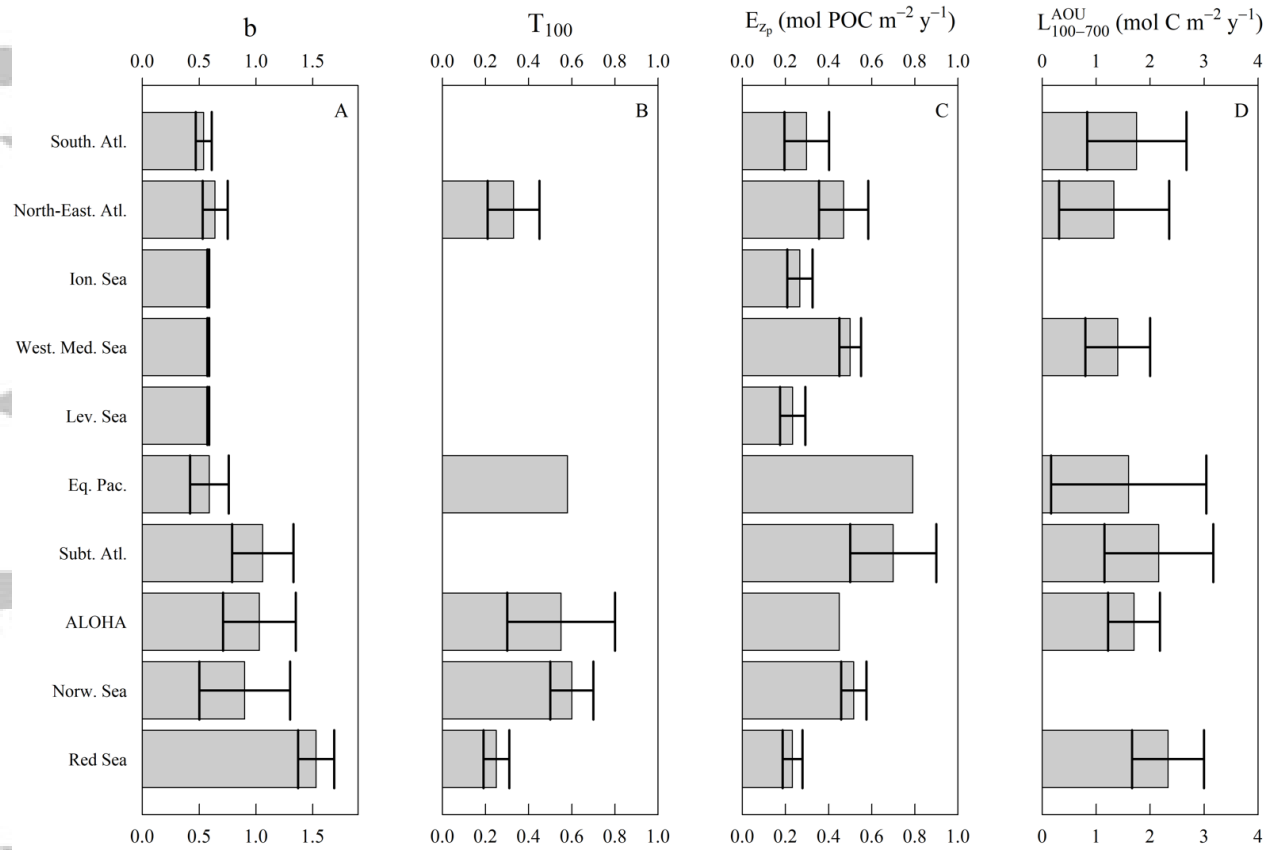
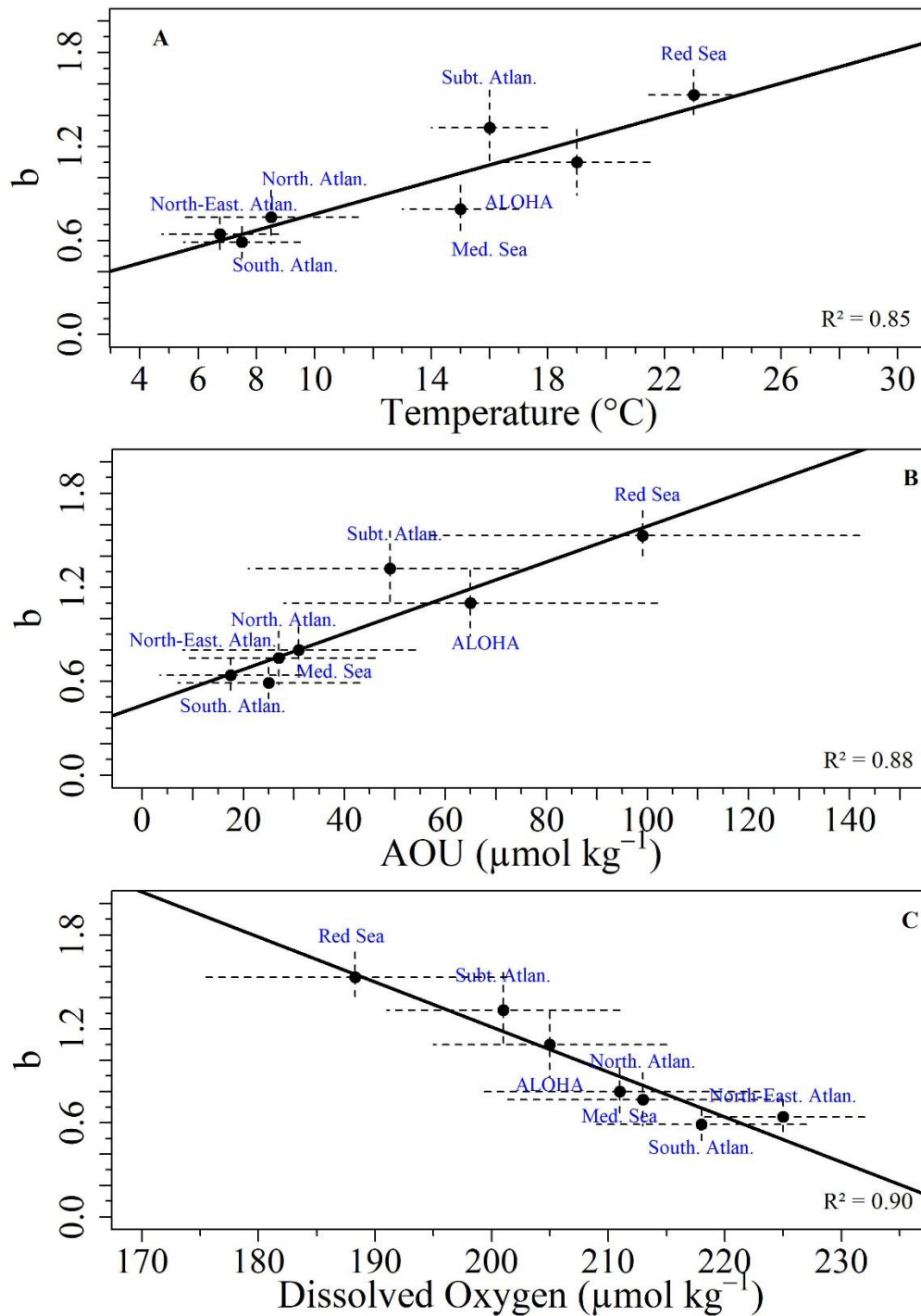


Figure 10 : Comparison of flux attenuation coefficient (b), the net POC flux just below the productive layer (E_{zp}), The transfer efficiency at 100 m depth (T_{100}), and the net TOC loss rates (L_{zi}^{AOU}) with literature values for various oceanic regions. Error bars represent one standard deviation.



Note*: b (Martin et al., 1987; Henson et al., 2012; Guidi et al., 2015; Marsay et al., 2015), T_{100} (Honjo et al., 2008; Buesseler & Boyd, 2009; Dall'Olmo & Mork, 2014; Weber et al., 2016; Devries & Weber., 2017), E_{zp} (Lohrenz et al., 1992; Boyd & Newton, 1995, 1999; Moutin & Raimbault, 2002; Guieu et al., 2005, 2014; Buesseler et al., 2007; Honjo et al., 2008; Buesseler & Boyd, 2009; Henson et al., 2012; Dall'Olmo & Mork, 2014; Emerson, 2014; Giering et al., 2014; Marsay et al., 2015; Durkin et al., 2015; Shih et al., 2015; Weber et al., 2016; Devries & Weber., 2017) and $L_{100-700}^{AOU}$ (Carlson et al., 1994; Lefèvre et al., 1996; Abell et al., 2000; Doval & Hansell, 2000; Nagata et al., 2000; Hansell and Carlson, 2001; Aristegui et al., 2003; Feely et al., 2004; Karstensen et al., 2008; Martz et al., 2008; Devries & Weber., 2017; Roshan & Devries, 2017 ; Calleja et al., 2019)

Figure 11 : Flux attenuation coefficient, b , as a function of the median temperature (A), oxygen (B) and AOU (C) of the upper 500 m of the water column for various oceanic regions. Error bars represent the standard deviation.



Float WMO#	Length of the mission	Date of deployment (dd/mm/YYYY)	Position of deployment	Date of last profile (dd/mm/YYYY)	Temporal resolution of data acquisition	Equipment
6901573	17 months	29/09/2015	33.73°N / 27.66°E	19/02/2017	<u>Daily</u> : 29/09/2015 to 05/10/2015 <u>5 days</u> : 10/10/2015 to 30/10/2015 24/05/2016 to 28/07/2016 01/11/2016 to 31/12/2016 10/01/2017 to 19/02/2017 <u>2 days</u> : 30/10/2015 to 24/05/2016 31/12/2016 to 10/01/2017 <u>10 days</u> : 28/07/2016 to 01/11/2016	CTD (Seabird SBE 41CP) Radiometry (Satlantic OCR) WET Labs ECO Puck Triplet Oxygen sensor (Aanderaa optode, model 4330)

Table 1: Summary of the mission and equipment for the profiling float used in this study.

Table 2: Symbols of variables used in this study with their definitions and units.

Symbols	Definition	Units
POC	Particulate Organic Carbon	$mg\ m^{-3}$
chl_a	Chlorophyll a fluorescence	$mg\ m^{-3}$
b_{bp}	Particulate backscattering coefficient	m^{-1}
PAR	Photosynthetically Available Radiation	$\mu mol\ quanta\ m^{-2}\ s^{-1}$
MLD	Mixed Layer Depth	m
z_p	Productive layer	m
E_{z_p}	Net POC flux just below z _p	$mmol\ POC\ m^{-2}\ y^{-1}$
E_{z_i}	Seasonal net POC export rate	$mmol\ POC\ m^{-2}\ y^{-1}$
b	Martin's exponent	<i>Dimensionless</i>
T_{z_i}	Transfer efficiency	<i>Dimensionless</i>
E_{z_{iF}}	Net Fast maximum (instantaneous) carbon export	$mmol\ POC\ m^{-2}\ d^{-1}$
L_{z_{iF}}	Net Fast POC loss rates	$mmol\ POC\ m^{-2}\ d^{-1}$
L_{z_{iS}}	Net Slow POC loss rates	$mmol\ POC\ m^{-2}\ d^{-1}$
L_{z_{iF}}[*]	Fast POC-specific loss rates	y^{-1}
L_{z_{iS}}[*]	Slow POC-specific loss rates	y^{-1}
L_{z_i}^{AOU}	Net TOC loss rates	$mol\ C\ m^{-2}\ d^{-1}$

Table 3: Average and standard deviation of spiciness metric over gradual isopycnal layers of the mesopelagic zone.

	Z28.30 - Z28.40	Z28.40 - Z28.52	Z28.52 - Z28.55	Z28.55 - Z28.57
Average \pm standard deviation	7.986 \pm 0.006	7.963 \pm 0.008	7.918 \pm 0.005	7.906 \pm 0.003

Table 4: Average and standard deviation of net carbon export and loss rates over gradual isopycnal layers of the mesopelagic zone

	L_{ZiF} (mmol POC m ⁻² d ⁻¹)	L_{ZiS} (mmol POC m ⁻² d ⁻¹)	L_{Zi}^{AOU} (mmol C m ⁻² d ⁻¹)
Z28.30 - Z28.40	24 \pm 6	0.41 \pm 0.16	10.8 \pm 2.7
Z28.40 - Z28.52	10 \pm 3	0.23 \pm 0.12	9.1 \pm 2.2
Z28.52 - Z28.55	4.6 \pm 1.9	0.08 \pm 0.03	5.4 \pm 1.2
Z28.55 - Z28.57	2.3 \pm 1.4	0.042 \pm 0.013	2.8 \pm 0.7