Intense and localized export of selected marine snow types at eddy

2 edges in the South Atlantic Ocean

- Alexandre Accardo¹, Rémi Laxenaire^{4,5,6}, Alberto Baudena¹, Sabrina Speich^{3,4}, Rainer Kiko², Lars
 Stemmann^{1,7}
- 5 ¹Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, UMR 7093 LOV, Villefranche-sur-Mer, France
- 6 ²GEOMAR Helmholtz Center for Ocean Research Kiel, Germany
- 7 ³Ecole Normale Supérieure, PSL Research University, France
- 8 ⁴UMR 8539 Laboratoire de météorologie dynamique (LMD), France
- 9 ⁵UMR 8105 Laboratoire de l'Atmosphère et des Cyclones, Saint-Denis de La Réunion, France
- 10 ⁶Center for Ocean-Atmospheric Prediction Studies, Florida State University, Tallahassee, FL, United States

11 ⁷Institut Universitaire de France (IUF), France

12 Correspondence to: Alexandre Accardo (alexandre.accardo@imev-mer.fr)

13 Abstract

- 14 The Biological Carbon Pump (BCP) comprises a wide variety of processes involved in transferring organic carbon from the
- 15 surface to the deep ocean. This results in long-term carbon sequestration. Without BCP, atmospheric CO2 concentrations would
- 16 be around 200 ppm higher. This study reveals that ocean dynamics at mesoscale and submesoscale could have a major impact
- 17 on particulate organic matter (POM) vertical distribution. Our results suggest that intense submesoscale frontal regions, such
- 18 as those between mesoscale eddies, could lead to an important accumulation and transport of particulate organic matter (POM)
- 19 from the mixed layer depth (MLD) down to the mesopelagic zone. To reach these conclusions, a multifaceted approach was
- 20 applied. It included in-situ measurements and marine snow images from a BGC Argo float equipped with an Underwater
- 21 Vision Profiler (UVP6), satellite altimetry data, and Lagrangian physics diagnostics. We focused our study on three intense
- 22 features in marine snow distribution observed during the 17-month long float mission in the Cape Basin, southwest of Africa.
- 23 These features were located in the frontal region between mesoscale eddies. Our study suggests that a particle injection pump
- 24 induced by a frontogenesis-driven mechanism has the potential to enhance the effectiveness of the biological pump by
- 25 increasing the depth at which carbon is injected into the water column. This work also emphasizes the importance of
- 26 establishing repeated sampling campaigns targeting the interface zones between eddies. This could improve our understanding
- 27 of the mechanisms involved in the deep accumulation of marine snow observed at eddy interfaces.

a supprimé: Massive

a mis en forme : Français

a mis en forme : Français

a supprimé: The open ocean plays a critical role in mitigating climate change by sequestering carbon dioxide (CO₂) from the atmosphere for long periods of time. This carbon storage occurs over decades to millennia and relies on the physical pump that transports cold, dense, and DIC-rich waters to the deep ocean, as part of the ocean's overturning circulation, and the biological carbon pump (BCP). The BCP encompasses a wide range of processes, from the fixation of atmospheric CO₂ by phytoplankton activity to carbon sequestration in the deep ocean. Atmospheric CO₂ concentrations would be about 200 ppm higher than in a world without biology, and the global climate would be much warmer by default. This study highlights the idea that BCP efficiency is enhanced by the ocean dynamics at mesoscale and submesoscale. In fact,

a supprimé: o

a supprimé: depths of about 600 meters

46 1 Introduction

47 The open ocean plays a critical role in mitigating climate change by storing carbon dioxide (CO₂) away from the atmosphere 48 for long periods of time (Boyd et al., 2019). This carbon storage occurs over decades to thousands of years and relies on two 49 well-established mechanisms that create a gradient of dissolved inorganic carbon (DIC) between the surface and deep regions 50 of the ocean and enhances DIC concentrations at depth. These mechanisms are known as the biological pump and the solubility 51 pump (or physical pump). The solubility pump transports cold, dense, and DIC-rich waters to the deep ocean, as part of the 52 ocean's overturning circulation, primarily in high-latitude regions (Sarmiento and Gruber, 2006). The biological carbon pump 53 (BCP), on the other hand, involves the export of particulate organic carbon (POC) from surface waters below the euphotic 54 depth, and operates worldwide. The BCP encompasses a wide range of processes, from the fixation of atmospheric CO2 by 55 phytoplankton activity, to carbon sequestration into the deep ocean (Le Moigne, 2019). The BCP contributes also to 56 approximately 90% of the dissolved inorganic carbon (DIC) gradient between surface and deep ocean (Boyd et al., 2019). 57 Without the BCP atmospheric concentrations of the greenhouse gas CO2 would be approximately 200 ppm higher than in a 58 world without biology (Maier-Reimer et al. 1996) and the global climate would be much warmer by default.

59 A key component of the BCP is the biological gravitational pump (BGP). The BGP is the process by which large and/or dense 60 aggregates of POC sink due to gravity. Large particles of POC (> 500 µm), also called marine snow, can consist of aggregated phytoplankton cells such as diatoms, different types of aggregates resulting from coagulation processes (Le Moigne, 2019), 61 62 and zooplankton activity, such as phytoplankton grazing and faecal pellet egestion (Turner, 2015). This mechanism is 63 estimated, through empirical and food web models, to export about 3 to 10 Pg of carbon per year below the euphotic zone or 64 100 meters depth depending on the study (Dunne et al., 2005; Henson et al., 2012; Siegel et al., 2014; Bisson et al., 2020), The 65 speed at which surface aggregates sink to the deep ocean depends on their individual sinking rates, which are influenced by 66 their combined morphological (size, porosity, etc.) and chemical properties (ratio of organic versus mineral, mineral type, etc.) (Stemmann et al., 2004; Cael et al., 2021; Trudnowska et al., 2021; Soviadan et al., submitted). Laboratory experiments have 67 68 estimated that the sinking velocity of marine snow range from a few meters to several hundred meters per day (Shanks and 69 Trent, 1980; Azetsu-Scott and Johnson, 1992; Ploug et al., 2008; Laurenceau-Cornec et al., 2015; Cael et al., 2021) and, in a 70 few cases, from in situ imaging time series (Alldredge and Gotschalk, 1988; Stemmann et al., 2002; Trudnowska et al., 2021; 71 Soviadan et al., 2024). In situ imagery has proven to be a valuable tool for estimating sinking speeds. This can improve our 72 understanding of particle dynamics, which affect the BGP,

Another important component of the BCP that can occur concurrently with the BGP, are the particle injection pumps (PIPs).
These consist of the export of carbon mediated by plankton migrations or physical vertical movement and can also play a significant role in the ocean's capacity to store carbon. PIPs encompass a variety of mechanisms, temporal-spatial scales, and geographical extent, and can affect all types of particles, in the water column. They typically transport particles below the euphotic zone. Depending on the specific injection mechanism, PIPs can reach depths greater than 1000 m (Boyd et al. 2019).

a supprimé: particulate organic carbon (

a **supprimé:**), typically produced by phytoplankton activity, sink under gravity

a supprimé: POC

a supprimé: (for particles >500µm),

a supprimé:

a supprimé: faecal pellets (Turner, 2015)

a supprimé: This mechanism is estimated to export about 6 Pg of carbon per year below the mixed layer depth (MLD; Boyd et al., 2019)

a supprimé: rate

a supprimé: s

a supprimé: (Stemmann et al., 2004; Cael et al., 2021).

a supprimé: Sinking rates of different types of marine snow types have been estimated to range from 10 to 100 m d-1 from laboratory experiments (Shanks and Trent, 1980; Azetsu-Scott and Johnson, 1992) and, in a few cases, from in situ imaging time series (Alldredge and Gotschalk, 1988; Stemmann et al., 2002; Trudnowska et al., 2022).

a supprimé: In situ imaging of marine snow allows us to observe the change in size and morphology of aggregates as they progress through the ocean interior. This can improve our understanding of particle dynamics and, hopefully, their sinking rates, which affect the BGP.

a supprimé: , from those suspended in the water column to sinking particles

The physical processes that make up the PIPs include subduction resulting from the mixed-layer shallowing (referred to as the mixed-layer pump), subduction caused by the large-scale ocean circulation over distances of 100-1000 km (referred to as the large-scale subduction pump), and subduction mediated by mesoscale (10-100 km, few weeks to several months) to submesoscale (100 m to 10 km, hours to days) ocean dynamics (Thomas et al., 2008; McWilliams, 2016),

108 In particular, the influence of mesoscale eddies on particle production, aggregation and export (Stemmann et al., 2008; Guidi 109 et al., 2012; McGillicuddy, 2016; Stuckel et al., 2017) is a very active area of research because these structures are ubiquitous 110 in the global ocean and are the largest source of ocean variability (Stammer, 1997; Wunsch, 1999). For example, spatial 111 patterns of particles, differentiated by size, have been shown to be associated with anticyclonic circulation (Gorsky et al., 2002; 112 Waite et al., 2016). Upwelling at eddy's interfaces can enhance phytoplankton productivity and particle production (Shih et 113 al., 2020) while downwelling, contributes to oblique transport of dissolved, and particulate (both sinking and suspended) 114 carbon to depth (Stemmann et al., 2008; Guidi et al., 2012) in a process called the Eddy Subduction Pump (ESP; Omand et al. 115 2015). Vertical transport has been suggested to be increased by sub-mesoscale vertical velocities associated with fronts (Guidi 116 et al., 2007). Understanding the mechanisms associated with physical-biological biogeochemical interaction is challenging due 117 to the transient nature of the underlying processes. Therefore, it is essential to employ multidisciplinary approaches, including 118 in situ observations, to elucidate these intricate phenomena (McGillicuddy, 2016). 119 This work is based on the deployment of a new prototype of BGC Argo float (part of the Argo international program:

120 https://argo.ucsd.edu) equipped with an Underwater Vision Profiler 6 (UVP6; Picheral et al., 2022) and several physical-121 biogeochemical sensors in the Southeast Atlantic Ocean. The float was deployed in the Cape Basin, a region southwest of 122 Africa, known for its intense eddy activity, which is mainly controlled by a complex interaction between the Benguela 123 Upwelling, the Agulhas Current System and the South Atlantic Current (Richardson et al., 2003; Boebel et al., 2003). The 124 float was recovered after one year of operation and the collected images were analyzed and classified into plankton categories 125 and morphological types of marine snow (Trudnowska et al., 2022). Hydrological and particle data collected by the float were 126 then combined with satellite altimetry to identify frontal structures and mesoscale eddies (Chaigneau et al., 2009; Laxenaire et 127 al., 2018; 2019; 2020; 2024). Based on recurrent observations of marine snow concentration "hot spots" at mesopelagic depth 128 during the productive season, we discuss the role of horizontal and vertical circulation at fronts on marine snow production 129 and export to the deep sea.

130 2 Material and Methods

131 1.1 Observing strategy

During the SO283 cruise, a BGC Argo float (WMO: 6903095) was deployed, from the RV Sonne, on April 14, 2021, in a cyclonic eddy in the southeastern region of the Atlantic Ocean, near the Benguela upwelling system at 33.0978°S and

a supprimé: Due to their dynamic nature, which includes physical transport or the patchy distribution of animals, the interaction between the vertical and horizontal components of PIPs, as well as their temporal scales, can vary significantly (Boyd et al., 2019).

a supprimé: to submesoscale (1-10 km, hours to days) ocean dynamics.

a supprimé: (McGillicuddy, 2016)

a supprimé: They also play an important role in the vertical distribution of water mass properties as they are associated with upwelling and downwelling. Upwelling results in the transport of nutrients to the surface mixed layer which normally enhances productivity. Downwelling results in the physical transport of dissolved, and particulate (both sinking and suspended) carbon to depth.

a supprimé: The aim of the present work is to understand how frontogenesis mechanisms induced by mesoscale activity coupled with the gravitational carbon pump can lead to the rapid accumulation of diverse particulate matter ranging from $5 \ \mu m$ to 16 mm in size at depths exceeding 600 meters. 154 13.8673°E (Fig₄1.<u>A</u>). The float remained within the eddy for about 5 months. During this period, the eddy merged with another

155 cyclone (Baudena et al., 2023), until it disappeared from satellite altimetry maps probably due to subduction (Ioannou et al., 156 2022). A detailed analysis of this timeframe of the dataset is provided in Baudena et al., (2023). It then sampled different

156 2022). <u>A detailed analysis of this timeframe of the dataset is provided in Baudena et al.</u>, (2023). It then sampled different 157 mesoscale features within the region, and after a sampling period of about 1.5 years, it was retrieved by the S.A. Agulhas II

158 on September 19, 2022. During its deployment, the float completed a total of 183 profiles, the majority of which were acquired

159 from the surface down to 600- or 1000-meter depth.

160 1.2 Environmental data

161 The float was equipped with several sensors to quantify seawater properties along the water column. The float was instrumented with pressure (DRUCK 2900PSIA, SN: 11587115), temperature and salinity sensors (SBE41CP V7.2.5, SN: 162 163 13100) to measure the hydrological water properties. The biogeochemical properties were measured with oxygen 164 (AANDERAA OPTODE 4330, SN: 3489), fluorescence and backscattering (700 nm) sensors (ECO FLBB 2K, SN: 6310). 165 All the BGC Argo data that were used in this work, are made freely available by the International Argo Program (https://fleetmonitoring.euro-argo.eu/float/6903095). Before analysis, some derived variables were calculated based on a 166 167 Python implementation of the Gibbs SeaWater (GSW) Oceanographic Toolbox of TEOS-10 (http://www.teos-10.org/). Firstly, 168 Absolute Salinity (SA) was computed from Practical Salinity (PSAL) and pressure (dbar) measurements and Conservative 169 Temperature (CT, °C) was computed from in-situ Temperature (T, °C). These two variables were then used to calculate the 170 Potential Density (kg.m⁻³) with a reference pressure of 0 dbar (Roquet et al., 2015). Regarding the oxygen parameter, the Apparent Oxygen Utilization (AOU, µmol.kg⁻³) was computed as the difference between the oxygen concentration expected 171 172 at equilibrium with air and the in-situ oxygen concentrations. The expected oxygen concentration was computed from 173 solubility coefficients derived from the data of Benson and Krause (1984), as fitted by Garcia and Gordon (1992). Finally, the 174 mixed layer depth (MLD), which is the upper part of the water column where salinity, temperature, and density remain 175 vertically constant, was detected following De Boyer Montégut (2004). A reference value for density was taken at 5 dbar and 176 the water column was considered to be mixed until the depth at which density deviates from this reference by more than 0.03 177 kg.m⁻³

178 1.2 Living and non-living particle data

179 1.1.1 Small phytoplanktonic and bulk particles

To estimate chlorophyll-a concentrations emitted by phytoplanktonic cells, the float was equipped with a fluorescence sensor (ECO_FLBB_2K, SN: 6310). The backscattering (700 nm) sensor (ECO_FLBB_2K, SN: 6310) was used to quantify the amount of all particles (including detritus and phytoplankton). The backscattering coefficient signal (*bbp*) was decomposed to extract the signal of small particles (*bbsr*) from the raw signal which also contained spikes triggered by rare large aggregates

passing in the flow field. This was done by applying the method proposed by Briggs et al., 2020 (see supplementary materials)

(a supprimé: .

a supprimé: the eddy

a supprimé: because

a supprimé: of

a supprimé: in the ocean interior

a supprimé: labile and refractory

that decomposes the backscattering signal into its baseline (as a proxy of small particles, *bbsr*) and intermittent pulses (as
 proxy of larger aggregates). The *bbsr* signal represented the distribution of particles between 5 to 20 μm.

194 **1.2.2 Underwater Vision Profiler 6 (UVP6-LP)**

195 The float was also equipped with an in-situ camera, the Underwater Vision Profiler 6 Low-Power (UVP6-LP, SN: 000101)

196 specifically designed to be deployed on autonomous platforms. The UVP6 detects and measures the size (from 0.102 to 16.40

197 mm in Equivalent Spherical Diameter, ESD) of zooplankton and various organic/biogenic matter such as marine snow and

198 fecal pellets. Thanks to the float recovery, images of objects >500 µm could be retrieved as well and therefore, taxonomic

199 identification of macrozooplankton and large particle classification could be conducted on the Ecotaxa platform

200 (http://ecotaxa.obs-vlfr.fr). Taxonomic classification was initially assisted by a CNN (Convolutional Neural Network)

algorithm to extract descriptive features from the images. From these, the taxonomic group of each image was predicted using

a Random Forest algorithm. Then, living organisms' predictions have all been manually validated by taxonomic experts. All

203 the images used during this work can be found here: https://ecotaxa.obs-vlfr.fr/prj/8801. A more detailed description of the

204 UVP6-LP can be found in Picheral et al., 2022.

205 **1.2.3** A broad size classification of particles (MiP and MaP)

To conduct a community analysis of marine snow and examine their spatio-temporal distribution, we applied a rough size 206 207 classification on raw size- spectra data (>100 µm) provided by the UVP6 (without any plankton identification). In this case the assumption was made that zooplankton represents only a small fraction of objects sampled by the UVP6 (14.5% of images) 208 209 compared to particles (85.5%). Hence, we consider its contribution as neglectable for this purpose. Then, all size-spectra were 210 divided into two sub-classes: MiP (Micrometric Particles) and MaP (Macroscopic Particles). MiP concentrations were obtained 211 by integrating the concentrations overall size classes between 0.1- and 0.5-mm. MaP concentrations were computed exactly in 212 the same way but considering all size classes between 0.5- and 16-mm. The 0.5 mm threshold was used as detrital aggregates 213 > 0.5 mm are considered marine snow (i.e., aggregates, Alldredge and Gotschalk, 1988) and was chosen for visualization 214 purposes. However, the count/size measurements of the objects seen by the UVP6 contain zooplanktons and it is not possible, 215 from the images, to determine whether an object smaller than 0.5 mm is a living organism or detritus due to the limited 216 resolution. As a result, the MiP and MaP signals could be influenced by zooplankton abundances. However, the proportion of 217 living organisms to the total particle counts (ESD > 500µm) are usually smaller than 10% (Stemmann and Boss, 2012).

Organic carbon content of MiPs and MaPs was calculated assuming that particle mass can be estimated using an empirically derived relationship for marine aggregates (Alldredge, 1998; Kriest, 2002 reference 2a of Table 1). Assuming a carbon:nitrogen ratio of 106:16, this yields an expression for the carbon content of a particle in a given size class characterized by its diameter ESD (in cm). Moreover, this formula is dedicated to estimate POC content of miscellaneous marine snow, including components such as fecal pellets. Multiplying the carbon content with the particle number in this size class (in a supprimé: POC (Particulate Organic Carbon),

a supprimé:

particles.m⁻³), and integrating over the MiP and MaP size classes, respectively, we obtain the total POC content (mgC.m⁻³) for
 MiPs and MaPs.

Our study suggests the presence of vertical velocities within the water column which could significantly influence the marine snow distribution (MiPs and MaPs) at depth. The literature provides various methods for estimating POC fluxes from imaging devices. However, these approaches are based on particle size, sinking speed, and carbon content relationships which do not include the influence of physical processes such as water masses vertical movement. Therefore, a simple POC fluxes estimates from particle size would not accurately represent the actual fluxes in our study area. Furthermore, we couldn't disentangle the contributions of particle sinking speeds from the vertical displacement of the water mass. Given these limitations, we chose not to provide flux estimates.

The raw data corresponding to this section can be found on the Ecopart platform (https://ecopart.obs-vlfr.fr, project: uvp6 sn0001011p 2021 WMO6903095 recovery).

236 1.2.4 Unsupervised morphological classification of marine snow

237 To better characterize the marine snow dynamics, an unsupervised classification method was used, following the previous 238 study on particle dynamics in the Arctic Ocean (Trudnowska et al., 2021). This provides information on particle size, shape, 239 gray level, and heterogeneity. This method allows one to classify rapidly and efficiently particle images in objective categories. 240 In summary, firstly, zooplankton and detrital particle images were separated, by manual validation and treated independently. 241 After this separation, a PCA was performed on morphological traits of the detrital particle images. Those specific traits 242 represented their size (e.g., area, perimeter), shade intensity (e.g., mean/median gray level), shape (e.g., symmetry, elongation), 243 and structure (i.e., homogeneity or heterogeneity, mostly based on the variability in gray level). To obtain a normal distribution 244 for each variable, extreme values (in that they were below or above the first and 95th percentile) were removed and each 245 variable was transformed by the Yeo-Johnson transformation (Yeo, 2000). This PCA led to the creation of a morphospace in 246 which each particle image can be located based on their morphological features. Then, a K-means clustering was performed 247 on this new morphospace using the first five principal components. The number of clusters, "k", was set to four. This specific 248 number, after several simulations, was chosen because it conducted the best partitioning with four clearly different groups of 249 particle morphology.

- Finally, the concentration (nb.m⁻³) of each morphotype was computed by multiplying the number of particles found in each cluster and depth bin by the volume sampled by the UVP6. To study their spatio-temporal distributions, group concentrations were interpolated according to depth and time with a resolution of 5 meters and one day respectively.
- 253 Since some groups in the morphospace partially overlap (Fig. 5_B), potentially affecting the quality of the classification, a
- 254 further selection process was implemented. This involved calculating the Euclidean distance between individual particle
- images and their respective cluster centers. Subsequently, for each group, the first quartile of the Euclidean distance distribution

was computed, and only individuals with a distance smaller than the first quartile were included in the selection. The
 concentrations of the different morphotypes shown in figure 6 correspond to those of these 'exclusive members'. Objects with
 a too large distance (out of the first quartile) were not included in the further analysis,

259 1.2.5 Selection of profiles corresponding to deep massive exports

To characterize in an objective way significant changes in the deep marine snow spatio-temporal distribution, the Sequential T-test Analysis of Regime Shifts (STARS) method was used (Rodionov, 2004). This method, based on the Student's t-test2, analyses a dataset in a sequential manner. It compares each new observation with all the entries in the current 'regime' or group. If an entry significantly deviates from the average of that regime, it is marked as a potential 'shift point'. The algorithm then tests whether this detected shift is persistent over time. To characterize significant changes in the water column, marine snow concentrations were integrated, for each UVP6 profile, between 150 and 600 meters. Then, profiles detected in each significant 'shift' were selected and considered as belonging to (or 'inside') those features in marine snow distribution (see Fig. S1).

Afterward, to compare the aggregates distribution outside and inside each feature, profiles one month before and one month after each feature were selected and merged, providing the mean of particle concentrations 'outside' each feature. The same protocol was applied to study the morphotype proportions according to depth. The latter were computed in four depth layers, between 0-100, 100-300, 300-600 and 600-1000 meters to see the evolution of the morphotypes relative abundance overall the water column.

272 1.2.6 Eddy subduction detection

273 To compare our findings with the literature, we applied the algorithm proposed by Llort et al., 2018 to detect ESP events from 274 AOU and spiciness anomalies derived from BGC-Argo float data. Spiciness was defined as in Flament, 2002 and allows 275 differentiating water masses with distinct thermohaline properties but with similar density. Then, we compared each profile's 276 3-bin smoothed values to a 20-bin average to detect anomalies for both AOU and spiciness. An event was classified as 277 subduction-driven only if AOU and spiciness anomalies occurred at the same depth, which helped differentiate subduction 278 effects from horizontal mixing. Thresholds of AOU anomaly \leq -8 μ mol/kg and spiciness \leq -0.05 were set to detect these kinds 279 of events. Finally, we compared the ESP occurrence with the export features spatial distribution detected with the STARS 280 method. We also considered calculating vertical velocities according to Siegelman et al. (2020), but the temporal resolution of 281 our data was not sufficient to enable this (pers. communication L. Siegelman).

282 1.3 Satellite data and the TOEddies algorithm

- 283 To identify mesoscale eddies, we implemented the TOEddies algorithm (The Ocean Eddy Detection and Tracking Algorithm,
- Laxenaire et al., 2024). TOEddies is based on the identification of mesoscale eddies as closed contours of Sea Surface Height
- (SSH) surrounding an extremum. This relies on the principle that in a geostrophic balance, SSH isolines align with current
- streamlines. As a result, a maximum (minimum) SSH that is surrounded by a closed circulation is classified as an anticyclonic

a supprimé: Subsequently, for each group, the first quartile distance was computed, and only individuals with a distance smaller than the first quartile were included in the selection. These 'new' members (called 'exclusive members') were then used as indicators to see potential differences in the distribution pattern of each morphotype.

a mis en forme : Titre 3

a supprimé: 2018

(cyclonic) eddy. To track the eddies over time, the algorithm takes advantage of the fact that daily eddy displacements are small compared to their dimensions, resulting in overlapping areas between successive days. This methodology allows the derivation of trajectories and the detection of events where eddies merge or split, providing a mechanism for tracing the origin of sampled water masses which is a critical component for the objectives of this study.

298 For the purposes of this study, the TOEddies algorithm was applied to the Absolute Dynamic Topography (ADT, a proxy for

299 SSH) and its associated with geostrophic currents. These 1/4 gridded daily maps are produced by Ssalto/Duacs and distributed

300 by the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu/) in the version released in April 2018

301 (DT18; Pujol et al., 2016; Ballarotta et al., 2019). Each identified eddy was characterized by two radii associated to the two

B02 eddy boundaries defined in TOEddies: the outermost contour (R_{gent}), and the contour with the maximum averaged geostrophic

303 velocities (<u>Rvmax</u> and associated velocity V_{max}).

Eddies identified by the algorithm were collocated with float profiles (Chaigneau et al., 2011; Laxenaire et al., 2019; 2020). This allows us to categorize the profiles according to whether they sampled a cyclone, an anticyclone, a region outside of the influence of mesoscale eddies, or an area at the interface of two eddies. The application of TOEddies to ADT maps, coupled with the collocation of detected eddies with Argo profiles, has proven to be a successful combination for exploring eddy

dynamics in the southeast Atlantic (Laxenaire et al., 2019, 2020; Ioannou et al., 2022; Baudena et al., 2023).

309 1.4 Lagrangian diagnostics

310 Several Lagrangian diagnostics have been computed at the location of each profile using satellite-derived currents and 311 environmental variables. First, for each station (i.e., profile location), a region was defined as representative of the water parcel 312 sampled by the float. In this study, this region was a circular neighborhood with a radius r of 0.1° around each profile location. 313 This distance allowed us to smooth the satellite uncertainties and has been used in previous studies (Chambault et al., 2019; 314 Baudena et al., 2021; Ser-Giacomi et al., 2021; Fabri-Ruiz et al., 2023). This circular shape was then filled with virtual particles 315 (nearly 300) separated by 0.01°. Then, for each virtual particle, a given Lagrangian diagnostic was computed (detailed below). 316 This resulted in about 300 values for each sampling station. These have been averaged, leading to a value of a given Lagrangian 317 diagnostic for each profile. The velocity field we used have been derived from both altimetry and delayed-time model 318 assimilation data and includes both the geostrophic and the Ekman components (Copernicus CMEMS product MULTIOBS 319 GLO PHY REP 015 004-TDS). It has been used backward in time to advect each virtual particle (within the representative 320 water parcel) from the profile day until an advective time (τ). Different τ values were used, ranging from 5 to 45 days. Hence, 321 for each profile, each diagnostic has been calculated using different advective times. The first diagnostic we implemented was 322 the Finite-Time Lyapunov Exponent (FTLE, days-1; Shadden et al., 2005). By construction, intense FTLE values (typically 323 disposed in filament shapes) are found at the edge between two water masses that have been widely separated in the preceding 324 days. As these two water masses come from distant locations, they are likely to share different hydrological characteristics, 325 such as temperature, primary production or biological activity (d'Ovidio et al., 2010; Haller, 2015; Lehahn et al., 2018). For 326 these reasons, FTLE is useful to identify oceanic fronts and can be considered as proxies for water masses convergence and **a supprimé:** the origin of sampled water masses—a critical component for the objectives of this study

a mis en forme : Indice

a supprimé: Rmax

a mis en forme : Indice

a supprimé: The first diagnostic we implemented was the Finite-Time Lyapunov Exponents (FTLE, days-1; Shadden et al., 2005). ...

thus, possibly, associated vertical downwelling (McWilliams, 2016), FTLEs were computed as in Shadden et al., (2005), with an initial separation of 0.1°. We implemented as a second diagnostic the Lagrangian chlorophyll-a (mg.m⁻³), which is the mean chlorophyll content calculated along the backward virtual particle trajectory. This diagnostic determines whether the seawater parcel sampled at a profile location was rich in chlorophyll in the preceding days. For the chlorophyll, we used the delayedtime satellite product "OCEANCOLOUR GLO BGC L4 MY 009 104-TDS" provided by CMEMS Copernicus website (0.25° resolution, provided daily).

339 2 Results

340 2.1 Circulation and water mass spatio-temporal distribution

341 The lateral variability in thermohaline properties (Fig. 2) is driven by mesoscale eddies and submesoscale features, which carry 342 distinct signatures and interact dynamically, creating spatio-temporal heterogeneity in water masses. Visual inspection of the 343 TOEddies algorithm results, coupled with analysis of hydrological data provided important information about the history and 344 origin of the water masses sampled by the float. In the following, we separate the life history of the float trajectory in different 345 periods. During April to October 2021 (fall and winter), the float was trapped within a cyclonic eddy shed from the southern Benguela upwelling front (Baudena et al., 2023, preprint). During this period, temperature, salinity, and density were relatively 346 347 stable. Figure 2 shows that the MLD varied between near-surface depths and 200 m. Analysis of the AOU time series shows 348 predominantly weak positive or even negative values only above the MLD (Fig. 2.F). Regarding the FTLE time series, values 349 remained low compared to the entire time series (less than 0.25 days¹) except around August 2021 when the targeted eddy 350 merged with another Benguela Upwelling cyclone (0.45 days⁻¹). Overall, the float remained near the center of the cyclonic 351 eddy, which explains the low FTLE values. After the merging, the float continued to move within the new cyclonic structure. 352 This cyclonic eddy merged again (in early October 2021) with an Agulhas cyclone that formed along the Agulhas Bank, the 353 southern shelf-edge of Africa (Penven et al., 2001; Lutjeharms et al., 2003). This type of cyclone originates from the southern 354 African continental slope from barotropic instabilities and enters the ocean interior at the northern edge of the Agulhas Current 355 Retroflection (Duncombe Rae, 1991) with very different hydrographic characteristics (warmer and saltier water masses, 356 Giulivi and Gordon, 2006) compared with the Benguela upwelling cyclones.

After exiting the cyclone, the float remained within its periphery. In mid-October, the float was at the interface between the cyclone and an anticyclonic eddy. Then, the float moved southward until May 2022. The water column was more stratified and characterized by a shallower MLD (typical for spring and summer). During this period, two phases of the life history of the float can be identified. During the first phase, warmer and saltier waters were observed between 200 and 800 m depth. These waters clearly originate from Agulhas Current water masses, very likely originating from an injection in the region of the Agulhas rings generated at the Agulhas Current Retroflection (Laxenaire et al., 2018). The second phase is characterized by colder and fresher water masses. Indeed, between January and March 2022, the float crossed the Subantarctic front and a supprimé: This metric is useful for identifying fronts. A front is defined as a physical barrier that separates two adjacent water masses that have been widely separated in the preceding days and are likely to have different hydrographic properties....

a supprimé:

a supprimé: The study area exhibits significant environmental variability, in terms of water masses and their spatio-temporal variability in relation to intense mesoscale activity (Fig. 2). continued to move southward along the edge of an Agulhas ring, a relatively old Agulhas cyclone, as well as a Subantarctic Front cyclone. Finally, in April 2022, the float passed next to another Subantarctic Front cyclone, which could explain the colder and less salty water masses during this period. Moreover, specific patterns in the AOU and the density time series are also observed during the transition between these two phases. Indeed, the AOU time series shows smaller values (close to 0 μ mol.m⁻³) at depths between 200 and 1000 m. The latter are also associated with important horizontal isopycnal variations (steep slopes), reaching depths close to 900 m and coinciding with high FTLE values (above 0.45 days⁻¹).

The final period spans May to September 2022 and is marked by three high-intensity mesoscale features that influence the water column down to about 800 to 1000 m depth. These features are characterized by a deeper MLD and the presence of much warmer and saltier water masses all over the water column. The AOU time series shows a strong signal during this period, with negative values observed at depths around 800 m. This period was also characterized by intense FTLE values throughout. The TOEddies analysis showed that the float profiled different cyclones and anticyclones during this period.

In summary, during its deployment, the float sampled water masses with significantly different hydrological characteristics and from multiple geographical zones. At this stage, one of the main results to keep in mind is that the float sampled interface zones between anticyclonic and cyclonic structure. Overall, these observations highlight the dynamic nature of the study area, characterized by contrasting water mass properties and their temporal variations throughout the year.

389 2.2 Spatio-temporal distribution of marine snow during the survey

390 From April to October 2021 (Fall and Winter), surface chlorophyll-a concentrations and the bbsr coefficient remained relatively low (Fig. 2.E.F). Afterwards, a significant change occurred between the end of October 2021 and May 2022 (Spring 391 392 and Summer). This period coincided with the seasonal production of phytoplankton, as evident in the chlorophyll-a 393 concentration time series. Also, a noticeable increase in the bbsr coefficient indicates greater concentrations of small particles 394 in the surface (Fig. 2.E), Moving forward to the period between May and September 2022, there was a noticeable decline in 395 chlorophyll-a concentration. Consequently, weaker concentrations were observed at the surface, and the bbsr coefficient was 396 also reduced. In general, the spatio-temporal dynamics of MiP and MaP exhibit notable differences (Fig. 3). MiPs were 397 generally more abundant than MaPs, ranging between 1.5- and 7.5 part.L⁻¹, while MaP concentrations ranged from 0 to 1.6 398 part.L-1 (Fig. 3). Both types of particles displayed higher mean concentrations above the MLD than below. MiP were 399 consistently present throughout the float deployment, with a slightly higher abundance observed between October 2021 and 400 May 2022. Conversely, the distribution pattern of MaPs differed. Their concentration was relatively low from the beginning 401 of the time series until October 2021. Subsequently, their surface abundance significantly increased during the phytoplankton 402 production period between the end of October 2021 and May 2022. Overall, these observations highlight the distinct spatio-403 temporal dynamics of MiP and MaP. A key result in the marine snow spatial distribution is that three different "columns" of 404 increased particle concentration (in particular MaPs) were observed between the surface down to 600 meters. These features

a supprimé: There was also an observable increase in the concentration of small, labile, and refractory particles in the surface, as reflected by the *bbsr* coefficient (Fig. 2.E).

lasted for approximately a month. The first one took place between October 8 and 23, 2021, the second one occurred from
 November 25 to December 22, 2021, and finally, the last one spanned approximately between March 3 and April 28, 2022.

410 2.3 Spatio-temporal distribution of MaP morphological groups during the survey

411 The unsupervised clustering method led to the identification of four morphotypes distinguished by their size, circularity,

412 brightness, and homogeneity (Fig. 5.A.B). The first morphotype was characterized by small, dark, and predominantly circular 413 particles. The second morphotype comprised elongated objects with varying degrees of brightness. The third morphotype

414 consisted of bright, fluffy, and diverse marine snow particles. The fourth morphotype encompassed larger marine snow

415 particles, often with the form of aggregated structures with some heterogeneity. All the identified morphotypes were

416 predominantly found in the surface layer. Specifically, the elongated particles (Fig. 6.B) exhibited a distinct concentration 417 increase from late September 2021, maintaining a stable abundance until early May 2022. Before and after this period, their

418 presence was considerably smaller. Additionally, these elongated particles displayed a strong positive correlation with

- 419 chlorophyll-a concentration in the surface layer (0-100m), as evidenced by a significant Spearman correlation coefficient of
- 420 0.65 (p-value = 9.3.10⁻²², Fig. S₃). In contrast, the other three morphotypes (small, bright, and aggregates, Fig. 6.A.C.D)
- 421 exhibited different dynamics. They were present in all three MaP features described above, whereas the elongated particles
- 422 did not appear to be extensively involved. The dense aggregates morphotype (purple in Fig. 5.C) is the most abundant during
- 423 these three features (Fig. 6.A-C).

424 2.4 Vertical distribution of particle community composition inside and outside massive export features

Here we analyze the distribution of the four morphotypes in the water column during the three export features (Fig. 5.D).
Indeed, a shift is observed in their relative proportion between the surface and the layers below. Specifically, the abundance of small particles (salmon pink in Fig. 5.D) and dense aggregates (purple) increases, while the proportion of elongated and bright morphotypes decreases. For example, in column 3, the proportion of small morphotypes incremented from 12% to 23% and from 25% to 47% in dense aggregates. Furthermore, the distribution of morphotypes within each export feature did not

430 change considerably, except perhaps in the case of column 2.

431 2.5 The eddy dynamic context

432 The first and the second export feature occurred at the boundary between a cyclonic and an anticyclonic eddy (Fig. 1. B.Q.

433 This region was therefore characterized by very intense submesoscale frontal dynamics. During the second feature (Fig. 1. C),

434 the position of the cyclone did not change significantly. The float entered the cyclone but remained close to its Rvmax boundary

435 and thus within the submesoscale frontal region of the cyclone edge. Indeed, the eddy frontal regions extend over an area of

436 10-20 km across the region of eddy maximum azimuthal velocity (i.e., across Rvmax) as shown in Barabinot et al., (2023). This

437 second feature ended when the float was expelled from the cyclone and began to be advected southward, leaving the frontal

a supprimé: 2

a supprimé: . 7

a supprimé: . 8

region. The third export occurred when the float was advected around the southern edge of a large anticyclone (Fig. 1.D), again a submesoscale frontal region.

443 2.6 Impact of the three features on the upper 600m water column

- Figure 4 clearly illustrates the high abundance of particulate carbon associated with the three export events, with their influence
- 445 extending down to 600 m depth. The abundance increased by a factor of 2-3 (with a factor of more than 7 during the first
- 446 feature) compared to periods when the Argo float was moving 'outside' these frontal regions. An average increase in MiP POC
- 447 of about 25% is also observed for the first and the second features. Importantly, the three features occurred during the surface
- 448 production period and do not show a signature in smaller particle abundances (as indicated by the absence of such a pattern in 449 fluorescence and *bbsr*, Fig. 2.D.E). In particular, MiP and MaP abundances between 100 and 1000 m were significantly
- 450 correlated with intense FTLE values (Spearman's rank correlation coefficient of 0.4, p-value = 4.10^4 and 0.49, p-value =
- 451 1.3.10⁻⁵ respectively, Fig. S4-S5). Mean MiP abundance, at this depth, was also significantly correlated with low AOU values
- 452 (coefficient correlation of -0.59, p-value = $1.6.10^{-8}$, Fig. S6).

453 3 Discussion

454 3.1 Drivers of marine snow production in the surface layer

The analysis of the chlorophyll-a time series helped to characterize the seasonality of primary production in our study area. In particular, from the end of October 2021 to May 2022 (spanning spring and summer), there was a significant increase in surface layer chlorophyll-a concentrations (Fig. 2.D). This observation is consistent with the existing knowledge on the seasonality of phytoplankton in the southern part of the Atlantic Ocean (Thomalla et al., 2011) and led us to consider this period as the productive period.

Regarding the spatiotemporal distribution of MiP and MaP (Fig. 3.B), the abundance of MaP (i.e. aggregates) in the surface layer (0-100m) was significantly correlated with the surface <u>Lagrangian chlorophyll-a 15 days backward (see Fig. S2) and</u>

high FTLE, indicating a strong biophysical coupling via several synergistic mechanisms (enhanced primary production, coagulation, transport). Ocean eddies, especially cyclones, have the potential to enhance primary production by upwelling

- nutrient-rich water from deeper layers to the surface (Benitez-Nelson et al., 2007; Ascani et al., 2013; Cornec et al., 2021).
- 465 This leads to the biomass accumulation at the edges of cyclones due to water mass divergence (water mass flow from the
- 466 center to the cyclone periphery), resulting in aggregate formation between submesoscale structures (Lima, 2002). Eddies can
- 467 also move phytoplankton patches through eddy stirring or trapping (McGillicuddy, 2016), leading to the accumulation of
- 468 organic matter at the eddy boundaries (Fig. 7.1). This implies that actively growing phytoplankton transported by the water
- body in the previous days could have contributed to increase the abundance of MaPs by aggregation of organic matter and
- 470 biological activity. Among the MaP, large particles classified as elongated type were mostly found at the surface and they were
- the best correlated with surface chlorophyll-a. Their origin is difficult to determine. Their filamentous morphology suggests a

a supprimé: . 9

a supprimé: columns

a supprimé: 4 a supprimé: 5

a supprimé: -

a supprimé: 3

a supprimé: Lagrangian chlorophyll

a supprimé: Cornec et al., 2021; Ascani et al., 2013;

a supprimé: 10.1

481 resemblance to chain-forming diatom colonies. The average size of particles classified under the 'elongated' morphotype is 482 approximately 820 µm (±96 µm). Given their size and the study area, it's likely that some of these particles could include 483 colonies of Chaetoceros sp., which are known to form filamentous structures and to dominate phytoplanktonic blooms during 484 the austral summer (Laubscher et al., 1993). They could also be Euphausiid fecal pellets, however, this kind of organisms was 485 not observed at the surface by the UVP6 which could be attributed to their potential avoidance behavior, making their 486 identification challenging. However, given their size (>500 µm), it is unlikely that they are copeped fecal pellets, most of 487 which are smaller than 200 µm (Møller et al., 2011), The other categories of MaPs are also abundant and could be the result 488 of the aggregation into larger particles by biophysical coagulation or trophic activities. Coagulation is responsible for the 489 production of large particles when both particle concentrations and stickiness are high. Additionally, a heterogeneous particle 490 size distribution enhances coagulation, as smaller particles have a higher probability of colliding with larger particles (Hunt, 491 1982; McCave, 1984; Jackson, 1990). Through this mechanism, particle encounter rates are enhanced by Brownian motion, 492 shear and/or differential settling resulting in the formation of a single, larger particle (Jackson, 1990; Stemmann et al., 2004) 493 on a timescale of a few days, as already suggested in the Southern Ocean (Jouandet et al., 2014). By affecting photosynthesis 494 and water movement, the observed intense mesoscale and submesoscale dynamics, (Fig. 1.B.C.D.), could significantly affect 495 particle concentration and the probability of aggregation. The second aggregation mechanism by zooplankton grazing, sloppy 496 feeding (Lampitt et al., 1990) and fecal pellet production (Turner, 2015), occurs at long temporal scales due to the slower 497 growth time of zooplankton. Our observation strategy with a float cannot rule this aggregation mechanism out. However, it 498 seems that typical mesozooplankton fecal pellets (a few hundred um) were not observed in abundance in, at least, three of the 499 four morphotypes. We haven't also observed a clear increase in zooplankton abundance during the three particle distribution 500events. However, a slight increase in copepod abundance was noted during the first and third features within the first 100 501 meters (see Fig. S7). In our case, it is more likely that physical coagulation had a greater influence on aggregate formation, 502 however, we cannot rule out trophic biological aggregation, In fact, MaP were present at the surface only during the period of 503 maximum chlorophyll-a concentration and were associated with intense FTLE values (greater than 0.45 days-1), which can be 504 used as a proxy of water masses convergence (i.e. frontal zones as in Prants, 2013; Hernández-Carrasco et al., 2018). In other 505 words, MaP concentrations may have been enhanced due to the combination of two important factors for coagulation according 506 to the model of Jackson (1990), increased shear associated with high hydrodynamics at front and enhanced phytoplankton 507 biomass.

508 3.2 Coupling between massive export of large aggregates and regional ocean dynamics

Analysis of the spatio-temporal distribution of particles has revealed three regions of enhanced concentration of particles at depth, suggesting that vertical export of organic matter occurred in these areas during the productive season. These were characterized by intense MaP and MiP abundances extending vertically from the surface to depths of about 600 m. These export regions were associated with high FTLE values suggesting frontogenesis-driven mechanisms during which there could be a strong coupling between gravitational sinking of particles and intensified physical vertical velocities. a supprimé: Their origin is difficult to assess, but their filamentous morphology makes them resemble chain-forming diatoms or other phytoplankton colonies.

a supprimé: Coagulation is responsible for the production of large particles when particle concentrations become important in the water column (Jackson et al. 1990)

a supprimé: s. 7-9

a supprimé: However, typical mesozooplankton fecal pellets (a few hundred µm) were not observed in abundance in any of the four morphological categories. We haven't also observed a zooplankton abundance increase during the three particle distribution events (see Figure S6). In our case, it is more likely that physical coagulation had a greater influence on aggregate formation than trophic biological aggregation.

a supprimé: (i.e. frontal zones). In other words, they could benefit from a combination of high hydrodynamic and strong phytoplankton production, consistent with the model analysis proposed by Jackson (1990) for coagulation.

532 3.2.1 A submesoscale frontogenesis-driven mechanism

533 The abundance of particles such as MaP and MiP below the MLD (100-600m) was positively correlated with the surface 534 Lagrangian FTLE as well as for the small, bright and aggregated morphotypes. Large FTLE values can identify convergence 535 of water masses with different hydrological properties, creating intense density gradients. It is known that intense velocity and 536 density gradients arise in correspondence with mesoscale (geostrophic) and submesoscale (ageostrophic) frontogenesis, e.g. at 537 the edge of mesoscale features (Freilich and Mahadevan, 2021). At such fronts upper-ocean waters converge and subduct 538 beneath the mixed layer into the stratified pycnocline (e.g. Omand et al. 2015) or also in deeper layers (e.g. Llort et al., 2018). 539 These regions are typically associated with significant vertical velocities (up to 20 m/day). Frontal patterns, in the potential 540 density time series, are clearly seen extending into the ocean interior (Fig. 2.C) and are also found to correspond to the three 541 intense export features. During these features, the signal reached about 1000 m. All of them were located at the periphery of 542 mesoscale eddies (Fig. 1. B.C.D.), where the vertical velocity is expected to be higher (Thomas et al., 2008; Freilich and 543 Mahadevan, 2019). Unfortunately, it was not possible to calculate vertical velocities from the data provided by the BGC Argo 544 profiler.

545 Previous studies in a similar mesoscale physical context have shown that mesoscale activity can result in the intrusion of small 546 POM-rich water masses into the mesopelagic layers (Omand et al., 2015; Llort et al., 2018). In our study, the three features 547 described, occurred from the MLD to a depth of about 600 m or deeper (i.e. over a large part of the water column), whereas 548 the subduction described in Llort et al. (2018) occurred well below the MLD in the mesopelagic in depth layers thickness of 549 about 50-100 m. We applied the Llort et al. (2018) algorithm to identify ESP events across all profiles. Only 28 profiles were 550 classified as ESP events (see Figure 1.A, yellow dots). Of these, seven were located near export features described in this 551 study. However, increases in bbsr, chlorophyll-a, MiP, and MaP were not consistently observed across these ESP events. 552 Furthermore, the ESP events were generally less than 100 meters thick, whereas the export features we identified extended 553 through much of the water column. These findings suggest that while some export features may be linked to ESP events, the 554 ESP alone does not appear to be a fundamental trigger for these features. This suggests that we are describing a slightly 555 different mechanism compared to Omand et al. (2015) and Llort et al. (2018) responsible for the accumulation of organic 556 matter at depth, but also one related to mesoscale and submesoscale processes. This highlights the fact that the influence of 557 these physical mechanisms is a challenging area of research.

558 3.2.2 The key role of the gravitational carbon pump and the MLD

Historically, particle size has been considered as the primary factor influencing settling velocity (Guidi et al., 2008). However,
with advances in imaging systems, it has become increasingly clear that particle morphology has a significant effect on settling
velocities (Iversen and Lampitt, 2020; Cael et al., 2021; Williams and Giering, 2022). This process supports the idea that larger
(large ESD, size characteristic) and more compact (non-porous, morphological property) particles will sink faster. In this study,
direct estimates of settling particle velocity (e.g. export plume methodology; Stemmann et al., 2002; Briggs et al., 2020;

a supprimé: Figs. 7-9

a supprimé: 2

Trudnowska et al., 2021) could not be computed due to the non-completely Lagrangian nature of the float. However, it is possible to assume that the morphotypes identified in this work have different sinking velocities with the highest for small/dense and dark aggregate morphotypes (which dominate in the deepest water column, Fig. 5.D) and the lowest for the elongated morphotypes because they are only found at the surface (Fig. 5.B). In addition, the particles with the higher velocities should be rapidly exported to depth, so they should spend less time in the upper water column than particles with

571 the lowest sinking velocity. In other words, the latter will be more exposed to remineralization.

Furthermore, the analysis of the morphotype distribution during the three export features showed a shift in the group proportions between the surface layer (0-100m, which is approximately the mean depth of the MLD, all profiles included) and

574 deeper layers (100-1000m). This shift favored small and dense aggregate groups (in terms of proportion) between these two

575 layers. These morphotypes probably have the highest sinking speed (Soviadan et al., 2024), This supports the idea that the

576 MLD could act as a physical barrier (Hosoda et al., 2010) and only sinking particles were able to cross it. This conclusion is

577 also supported by the fact that, in most profiles, only MiP and especially MaP are located below the MLD, while small labile

s78 and refractory particles (bbsr) and chlorophyll-containing particles were rarely found below the MLD. Among the MaP, the

579 sinking explanation is valid for three morphotypes (small particles, bright and dense aggregates), but not for the elongated

580 types that we hypothesized to be chain-forming diatom colonies (*Chaetoceros sp.*). This result further emphasizes the critical

581 importance of considering morphology and not just particle size when analyzing the size of particles in marine snow dynamics

582 and when calculating vertical fluxes using only allometric relationships.

Another result is that features 1 and 3 show minimal changes in morphotype proportions between layer depths. In fact, it would be expected that the relative proportion of each morphotype would vary with depth due to their presumed different settling rates. It is possible that the morphotypes do not have different settling rates and settle at similar rates. Alternatively, there may be some other mechanism at work that is significantly more important than settling velocity and is responsible for transporting particles to deeper regions, which will be discussed below.

588 3.2.3 Possible coupling with vertical velocities

During the three described features, MiP abundance between 100 and 1000 meters was significantly correlated with low AOU values. AOU is a proxy for the age of water masses (Sarmiento, 2006), with lower AOU values indicating that the water masses had a more recent contact with the surface. The significant negative correlation between AOU and 100-1000 m MiP abundance suggests a physical downward transport leading to the formation of these features. In addition, we know from the eddy detection algorithm that each export feature was detected in the frontal region separating two adjacent eddies of opposite polarity. Mesoscale activity is known to play an important role in the vertical distribution of water masses.

In addition, surface frontal regions develop ageostrophic secondary circulations (Lévy et al., 2018) that lead to intense vertical velocities, which can be stronger at the edges of cyclonic structures and can be on the order of 100 m d⁻¹ or more (Mahadevan

a **supprimé:** These morphotypes should have the highest sinking rate.

a supprimé: be large phytoplankton

a supprimé: C

a supprimé: (Capó et al., 2021; Freilich & Mahadevan, 2021; Tarry et al., 2021; Siegelman et al., 2020; Mahadevan et al., 2016; McWilliams, 2016; 604 & Archer, 2000; Mahadevan et al., 2016; McWilliams, 2016; Freilich & Mahadevan, 2019; Siegelman et al., 2020; Capó et 605 al., 2021; Tarry et al., 2021). This is further supported by several studies that show that the presence of mesoscale eddies 606 greatly enhances the vertical transport of water properties (Omand et al., 2015, Llort et al., 2018, Couespel et al., 2024). In the 607 study region, mesoscale ocean dynamics are particularly active, with eddies generated by the Agulhas Current (the Agulhas 608 rings), the Agulhas Bank (the Agulhas lee cyclones), the Benguela upwelling, and subantarctic front cyclones. All can influence 609 the water column to depths of up to 1600 meters (Schmid et al., 2003). While these dynamics are known to exist, their impact 610 on the vertical exchange of properties through the water column remains to be assessed. However, a recent study (Siegelman 611 et al., 2020) has shown that such vertical velocities are enhanced below the MLD, which acts as a buffer for them, by relatively 612 deep submesoscale fronts. This result may explain why only large particles (i.e., MiP, MaP, and morphotypes) involved in the 613 gravitational pump and capable of crossing the physical barrier represented by the MLD are entrained in this process. However, 614 we lack information on the 3D context of the water mass, both in terms of currents and biogeochemical properties, which 615 makes it impossible to determine what happened at depth before the float passed. Consequently, it's impossible to rule out the 616 action of lateral advection on the mechanism described in this study. Nevertheless, the strong correlation between the described 617 events, the FTLE, and the positions of the eddies suggests a significant link to vertical rather than lateral advection. In addition, 618 previous studies have shown that frontal structures identified by Lyapunov Exponents ridges at the surface can persist in the 619 water column (Bettencourt et al., 2012), corroborating our findings. The hypothesis that the gravitational pump may be 620 associated with physical processes related to mesoscale activity has already been proposed by Guidi et al. (2007). The authors 621 found that the natural gravitational settling of particles combined with the associated vertical velocities of the water masses 622 triggered the export of particles into the deep Atlantic. Such a physical mechanism associated with the gravitational pump 623 would be a key process of carbon export to the deep ocean observed in our study.

624 4 Conclusion

625 As described in the conceptual schematic (Fig. 2), mesoscale frontal dynamics between cyclones and anticyclones seem to 626 have a profound effect on particle distribution down to 600 m depth. We propose that particle concentration at these locations 627 is enhanced by increased primary production and/or horizontal convergence induced by frontal activity or trapping. As a result, 628 coagulation processes may have been enhanced, with the ultimate result being the formation of larger aggregates. These 629 particles could have sunk below the MLD, in particular the large and/or dense ones, due to their higher sinking velocities. The 630 consistently observed vertical distribution of particles from the surface to a depth of 600 m suggests that their downward 631 transport is extremely rapid. We propose that such features result from the combination of the relatively large sinking speed 632 of such particles (likely due to their great density), and the enhanced vertical motion of the water induced by submesoscale 633 frontal dynamics, in particular below the MLD. If such a phenomenon is influenced by deeper mesoscale structures, it is likely 634 to extend into deeper layers. Such vertical transport is an integral part of the physical particle injection pump, particularly a unique frontal subduction pump, characterized by intense vertical velocities that might materialize in intense frontal regions. 635

a supprimé: 10

a supprimé: turbulence

a supprimé: a coupling between their own sedimentation rate (the gravitational carbon pump)

However, the relatively coarse temporal resolution of our dataset did not enable us to calculate the according vertical velocities,
 and we hence could not disentangle the gravitational and subduction pump in more detail.

642 Our study suggests that small-scale ocean dynamics represent an efficient particle injection pump that can enhance the 643 efficiency of the biological pump by increasing the depth of carbon transport. It is crucial to note that the explicit mechanisms 644 underlying these features are not fully defined due to the temporal and spatial limitations imposed by the Argo float's lack of 645 resolution. Additionally, the submesoscale nature of these features introduces high variability in both space and time. This study underscores the significance of implementing repeated sampling campaigns or the use of gliders equipped with UVP6 646 647 and further sensors (e.g. microstructure) and focusing on the interface zones between eddies. Such studies would help to 648 validate our proposed mechanism, and to disentangle the relative contribution of the various PIPs processes (such as ESP). In 649 particular, focus on such studies needs to be put on resolving the water movements (e.g. the vertical velocities) to enable the 650 separation of the passive sinking and vertical translocation of particles. Since mesoscale and submesoscale structures are 651 ubiquitous in the ocean, it would also be interesting to quantify the influence of this type of process on the overall carbon 652 budget and to determine the extent to which it contributes to carbon sequestration in the deep ocean, information that is crucial

653 in the context of global change.

654 5 Author contribution

- 655 A.A., R.K.; SS and L.S.: designed the study
- 656 A.A.: conducted data analysis, interpreted results, drafted the manuscript, under guidance of RK and LS
- 657 AB and RL: supported the study by environmental background data analysis, revised manuscript.
- 658 R.K. and S.S.: contributed to the conception of the study, revised manuscript.
- 659 R.K.: coordinated the recapture of the float
- 660 L.S.: contributed to the conception and design of the study, supervised the analysis, substantively revised the manuscript.

661 6 Competing interests

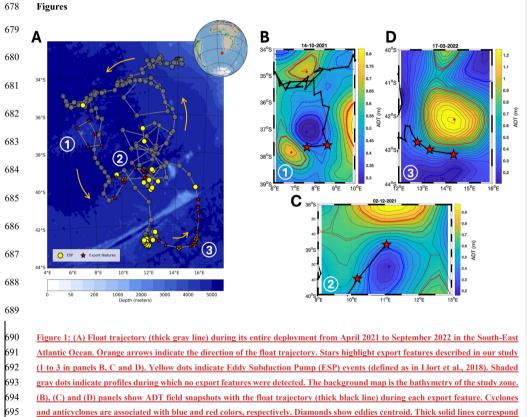
662 The authors declare that they have no conflict of interest.

663 7 Acknowledgments

664 This study would not have been possible without the support of the crews of the Research Vessel Sonne from Germany and 665 the SA Agulhas II from South Africa. We acknowledge the work of Marc Picheral, Edouard Laymarie, Antoine Poteau and 666 Camille Catalano from the Laboratory of Villefranche sur Mer in helping with the UVP6 logistic and quality control. We also 667 thank the Quantitative Imaging Platform of Villefranche-sur-Mer (PIQv) for providing us with their taxonomic expertise. This a supprimé: s

a supprimé: and would improve our understanding of the mechanisms involved in this process. Since mesoscale and submesoscale structures are ubiquitous in the ocean, it would also be interesting to quantify the influence of this type of process on the overall carbon budget

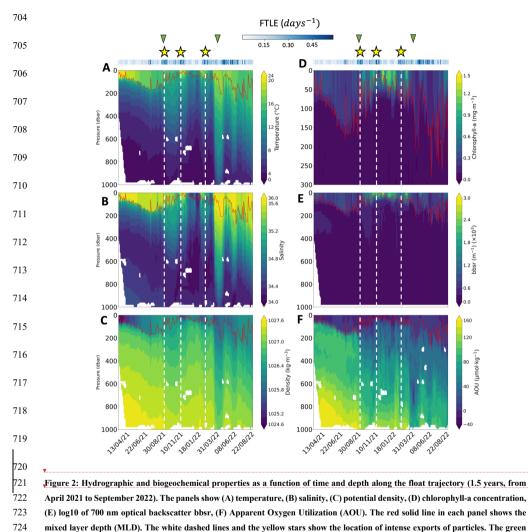
674	work was supported by the TRIATLAS project, which has received funding from the European Union's Horizon 2020 research
675	and innovation program under grant agreement No 817578. RK furthermore acknowledges support via a Make Our Planet
676	Great Again grant from the French National Research Agency (ANR) within the Programme d'Investissements d'Avenir ANR-
677	19-MPGA-0012 and funding from the Heisenberg Programme of the German Science Foundation KI 1387/5-1.



695 and anticvious are associated with blue and red colors, respectively. Diamonds show edules centrold. Thick solid lines of
 696 to eddies maximum speed. Thin solid lines correspond to ADT isolines. Dashed lines to eddies outer limit definition.

697

a supprimé: Figure 1: Float trajectory (thick black line) with profiles realized (185; black dots) during its deployment from April 2021 to September 2022. The map background is a snapshot of the ADT field in September 2022 showcasing the intense mesoscale activity of the study zone.¶



725 triangles indicate the start and the end of the production period. Blue dots on top of the panel show the mean five days backward

726 FTLE (days-1) for each profile location.

🧹 a supprimé: ¶

a supprimé: ¶

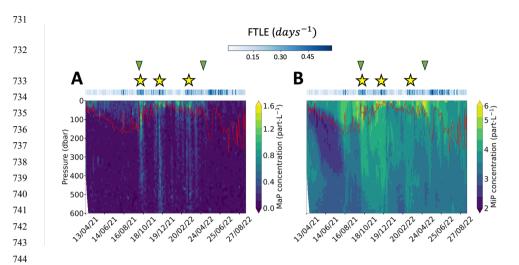


Figure 3: Particles spatio-temporal distribution. The panels show, (A) MiP (Micrometric Particles 0.1 < ESD < 0.5 mm)
 concentrations, (B) MaP (Macrometric Particles 0.6 < ESD < 16 mm) concentrations. Both concentrations were log transformed.
 Red solid line represents the MLD. Yellow stars show the location of intense exports of particles. Green triangles give the start and
 the end of the production period. Blue dots on top of the panels show five days backward FTLE (days⁻¹) for each profile location.

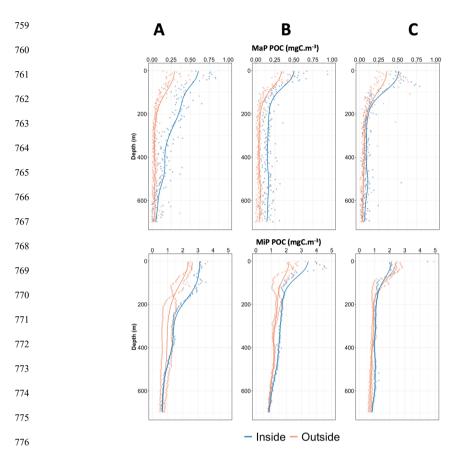


Figure 4: Comparison of MiP POC (top panels) and MaP POC (bottom panels) in the water column both outside and inside each export feature. The panels show, (A) the first export feature (01-10-2021 – 17/10/2021), (B) the second one (01-12-2021 – 19-12-2021) and (C) the last one (01/03/2022 – 28/03/2022). The dots on the graph represent the data averaged over 5-meter bins. The solid lines are a moving average of the 5-meter bins data. The orange signal corresponds to the average of profiles recorded one month prior to and after each feature (outside), while the blue signal corresponds to the average profiles recorded during each feature (inside).

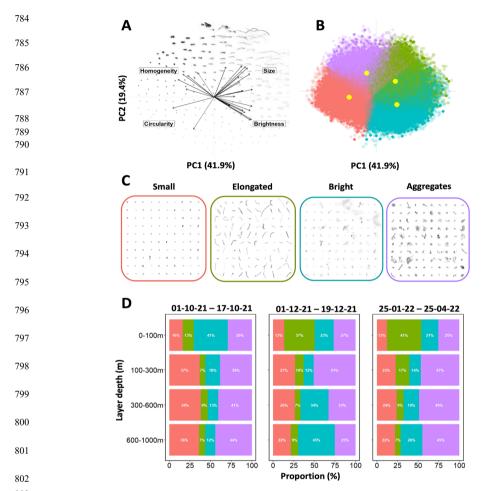
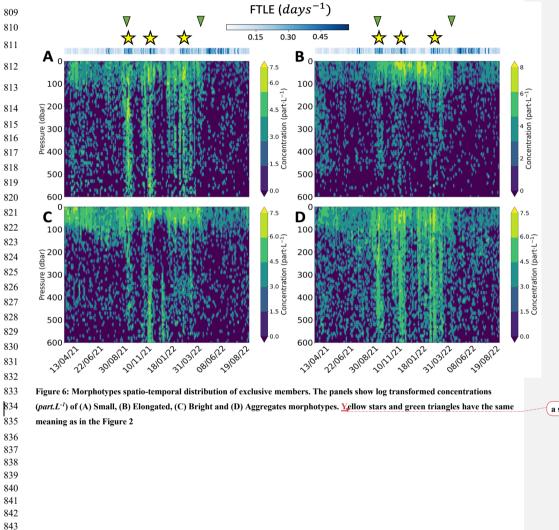


Figure 5: Results of PCA/K-means clustering on morphological traits of particles. Panels show, (A) the distribution of particle images in the morphospace built by PCA, (B) the K-means clustering classification where each point represents an image, and each cluster is colored independently. The yellow dots represent the center of each cluster. The most transparent dots represent images not retained in the analysis, (C) Representative subset of each morphotype and (D) the proportion (%) of each group according to depth layers during the three export features observed in the morphotypes spatio-temporal distribution. The color code is the same for (B), (C) and (D).



a supprimé: White dashed lines, y

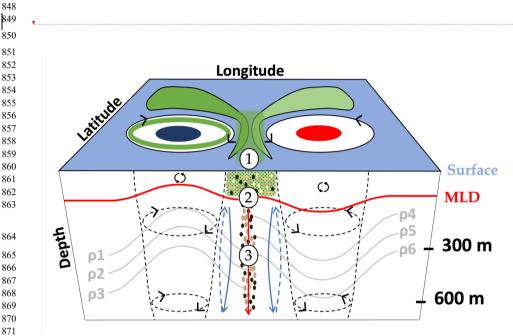


Figure 7: Snapshot of ADT field with the float trajectory (thick black line) during each export feature (A, B and C). Cyclones and anticyclones are associated with blue and red colors, respectively. Diamonds show eddy centr(...[1])

a mis en forme : Justifié, Interligne : 1,5 ligne

a supprimé: Figure 8: Schematic view of the proposed mechanism for the deep observed accumulation of particulate carbon in the mesoscale context of the study. (1) Aggregation and coagulation of surface organic matter, facilitated by eddy trapping or stirring. (2) Influence of the Gravitational Carbon Pump (represented by the red vertical arrow) that transporting particles with sufficient downward speed beneath the Mixed Layer Depth (MLD). (3) Coupling with a frontogenesis mechanism inducing enhanced physical vertical speeds (represented by blue arrows), particularly below the MLD and in interface zones between mesoscale structures. The coupling between (1), (2) and (3) can lead to the transport of particles down to significant depths (600 meters in our study). Black arrows in the MLD represent the physical mixing.



872

873

874

875

876

877

878

879

880

881

882

883

884

885

a supprimé: <object>

Figure 7: Schematic view of the proposed mechanism for the deep observed accumulation of particulate carbon in the mesoscale⁴⁴ context of the study. (1) Aggregation and coagulation of surface organic matter (green shapes around eddies), facilitated by eddy trapping or stirring. The green circle in the cyclone represents the accumulation of POM at its periphery (resulting from the divergence of the water masses) (2) Influence of the Gravitational Carbon Pump (represented by the red vertical arrow) that transporting selected marine snow types with sufficient downward speed beneath the Mixed Layer Depth (MLD). (3) Coupling with a frontogenesis mechanism inducing enhanced physical vertical speeds (represented by blue arrows), particularly below the MLD and in interface zones between mesoscale structures. The coupling between (1), (2) and (3) can lead to the transport of particles down to significant depths (600 meters in our study). Black arrows in the MLD represent the physical mixing₂

980 References

- Alldredge, A.: The carbon, nitrogen and mass content of marine snow as a function of aggregate size, Deep Sea Research Part
 I: Oceanographic Research Papers, 45, 529–541, https://doi.org/10.1016/S0967-0637(97)00048-4, 1998.
- Alldredge, A. L. and Gotschalk, C.: In situ settling behavior of marine snow1: Sinking rates of marine snow, Limnol.
 Oceanogr., 33, 339–351, https://doi.org/10.4319/lo.1988.33.3.0339, 1988.
- Ascani, F., Richards, K. J., Firing, E., Grant, S., Johnson, K. S., Jia, Y., Lukas, R., and Karl, D. M.: Physical and biological controls of nitrate concentrations in the upper subtropical North Pacific Ocean, Deep Sea Research Part II: Topical Studies in Oceanography, 93, 119–134, https://doi.org/10.1016/j.dsr2.2013.01.034, 2013.
- Azetsu-Scott, K. and Johnson, B. D.: Measuring physical characteristics of particles: a new method of simultaneous
 measurement for size, settling velocity and density of constituent matter, Deep Sea Research Part A. Oceanographic Research
 Papers, 39, 1057–1066, https://doi.org/10.1016/0198-0149(92)90039-V, 1992.
- Ballarotta, M., Ubelmann, C., Pujol, M.-I., Taburet, G., Fournier, F., Legeais, J.-F., Faugère, Y., Delepoulle, A., Chelton, D.,
 Dibarboure, G., and Picot, N.: On the resolutions of ocean altimetry maps, Ocean Sci., 15, 1091–1109, https://doi.org/10.5194/os-15-1091-2019, 2019.
- Barabinot, Y., Speich, S., and Carton, X. J.: Defining Mesoscale Eddies Boundaries from In-situ Data and a Theoretical
 Framework, Preprints, https://doi.org/10.22541/essoar.167870447.76933252/v1, 2023.
- Baudena, A., Ser-Giacomi, E., D'Onofrio, D., Capet, X., Cotté, C., Cherel, Y., and D'Ovidio, F.: Fine-scale structures as spots
 of increased fish concentration in the open ocean, Sci Rep, 11, 15805, <u>https://doi.org/10.1038/s41598-021-94368-1</u>, 2021.
- Baudena, A., Laxenaire, R., Catalano, C., Claustre, H., Ioannou, A., Leymarie, E., Picheral, M., Poteau, A., Speich, S.,
 Stemmann, L., and Kiko, R.: A Lagrangian perspective on the carbon and oxygen budget of an oceanic eddy, preprint,
 https://doi.org/10.21203/rs.3.rs-3014931/v1, 2023.
- Benitez-Nelson, C. R., Bidigare, R. R., Dickey, T. D., Landry, M. R., Leonard, C. L., Brown, S. L., Nencioli, F., Rii, Y. M.,
 Maiti, K., Becker, J. W., Bibby, T. S., Black, W., Cai, W.-J., Carlson, C. A., Chen, F., Kuwahara, V. S., Mahaffey, C.,
 McAndrew, P. M., Quay, P. D., Rappé, M. S., Selph, K. E., Simmons, M. P., and Yang, E. J.: Mesoscale Eddies Drive Increased
 Silica Export in the Subtropical Pacific Ocean, Science, 316, 1017–1021, https://doi.org/10.1126/science.1136221, 2007.
- Benson, B. B. and Krause, D.: The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in
 equilibrium with the atmosphere1: Oxygen solubility in seawater, Limnol. Oceanogr., 29, 620–632,
 https://doi.org/10.4319/lo.1984.29.3.0620, 1984.

- Bettencourt, J. H., López, C., and Hernández-García, E.: Oceanic three-dimensional Lagrangian coherent structures: A study
 of a mesoscale eddy in the Benguela upwelling region, Ocean Modelling, 51, 73–83,
 https://doi.org/10.1016/j.ocemod.2012.04.004, 2012.
- Bisson, K., Siegel, D. A., and DeVries, T.: Diagnosing Mechanisms of Ocean Carbon Export in a Satellite-Based Food Web
 Model, Front. Mar. Sci., 7, 505, https://doi.org/10.3389/fmars.2020.00505, 2020.
- Boebel, O., Lutjeharms, J., Schmid, C., Zenk, W., Rossby, T., and Barron, C.: The Cape Cauldron: a regime of turbulent interocean exchange, Deep Sea Research Part II: Topical Studies in Oceanography, 50, 57–86, https://doi.org/10.1016/S0967 0645(02)00379-X, 2003.
- Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., and Weber, T.: Multi-faceted particle pumps drive carbon sequestration in
- 1017 the ocean, Nature, 568, 327–335, https://doi.org/10.1038/s41586-019-1098-2, 2019.
- Briggs, N., Dall'Olmo, G., and Claustre, H.: Major role of particle fragmentation in regulating biological sequestration of CO
 ² by the oceans, Science, 367, 791–793, <u>https://doi.org/10.1126/science.aay1790</u>, 2020.
- Cael, B. B., Cavan, E. L., and Britten, G. L.: Reconciling the Size-Dependence of Marine Particle Sinking Speed, Geophysical
 Research Letters, 48, <u>https://doi.org/10.1029/2020GL091771</u>, 2021.
- Capó, E., McWilliams, J. C., Mason, E., and Orfila, A.: Intermittent Frontogenesis in the Alboran Sea, Journal of Physical
 Oceanography, 51, 1417–1439, <u>https://doi.org/10.1175/JPO-D-20-0277.1</u>, 2021.
- 1024 Chaigneau, A., Eldin, G., and Dewitte, B.: Eddy activity in the four major upwelling systems from satellite altimetry (1992–
 1025 2007), Progress in Oceanography, 83, 117–123, <u>https://doi.org/10.1016/j.pocean.2009.07.012</u>, 2009.
- Chaigneau, A., Le Texier, M., Eldin, G., Grados, C., and Pizarro, O.: Vertical structure of mesoscale eddies in the eastern
 South Pacific Ocean: A composite analysis from altimetry and Argo profiling floats, J. Geophys. Res., 116, 2011JC007134, https://doi.org/10.1029/2011JC007134, 2011.
- 1029 Chambault, P., Baudena, A., Bjorndal, K. A., Santos, M. A. R., Bolten, A. B., and Vandeperre, F.: Swirling in the ocean:
- 1030 Immature loggerhead turtles seasonally target old anticyclonic eddies at the fringe of the North Atlantic gyre, Progress in 1031 Oceanography, 175, 345–358, https://doi.org/10.1016/j.pocean.2019.05.005, 2019.
- Cornec, M., Laxenaire, R., Speich, S., and Claustre, H.: Impact of Mesoscale Eddies on Deep Chlorophyll Maxima,
 Geophysical Research Letters, 48, e2021GL093470, <u>https://doi.org/10.1029/2021GL093470</u>, 2021.
- Couespel, D., Lévy, M., and Bopp, L.: Stronger oceanic CO₂ sink in eddy-resolving simulations of global warming,
 Geophysical Research Letters, <u>https://hal.science/hal-04396517/</u>, 2024.

(a mis en forme : Anglais (E.U.)
(a mis en forme : Anglais (E.U.)
\sim	Code de champ modifié
-(a mis en forme : Anglais (E.U.)

a mis en forme : Anglais (E.U.)

a mis en forme : Anglais (E.U.)	
a mis en forme : Anglais (E.U.)	
Code de champ modifié	

- d'Ovidio, F., De Monte, S., Alvain, S., Dandonneau, Y., and Lévy, M.: Fluid dynamical niches of phytoplankton types, Proc.
 Natl. Acad. Sci. U.S.A., 107, 18366–18370, <u>https://doi.org/10.1073/pnas.1004620107</u>, 2010.
- De Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A., and Iudicone, D.: Mixed layer depth over the global ocean: An
 examination of profile data and a profile-based climatology, J. Geophys. Res., 109, 2004JC002378,
 https://doi.org/10.1029/2004JC002378, 2004.
- Duncombe Rae, C. M.: Agulhas retroflection rings in the South Atlantic Ocean: an overview, South African Journal of Marine
 Science, 11, 327–344, https://doi.org/10.2989/025776191784287574, 1991.
- Dunne, J. P., Armstrong, R. A., Gnanadesikan, A., and Sarmiento, J. L.: Empirical and mechanistic models for the particle
 export ratio, Global Biogeochemical Cycles, 19, 2004GB002390, https://doi.org/10.1029/2004GB002390, 2005.
- Fabri-Ruiz, S., Baudena, A., Moullec, F., Lombard, F., Irisson, J.-O., and Pedrotti, M. L.: Mistaking plastic for zooplankton:
 Risk assessment of plastic ingestion in the Mediterranean sea, Science of The Total Environment, 856, 159011,
 https://doi.org/10.1016/j.scitotenv.2022.159011, 2023.
- Flament, P.: A state variable for characterizing water masses and their diffusive stability: spiciness, Progress in Oceanography,
 54, 493–501, <u>https://doi.org/10.1016/S0079-6611(02)00065-4</u>, 2002.
- Freilich, M. A. and Mahadevan, A.: Decomposition of Vertical Velocity for Nutrient Transport in the Upper Ocean, Journal
 of Physical Oceanography, 49, 1561–1575, <u>https://doi.org/10.1175/JPO-D-19-0002.1</u>, 2019.
- Garcia, H. E. and Gordon, L. I.: Oxygen solubility in seawater: Better fitting equations, Limnol. Oceanogr., 37, 1307–1312, https://doi.org/10.4319/lo.1992.37.6.1307, 1992.
- ID54
 Giulivi, C. F. and Gordon, A. L.: Isopycnal displacements within the Cape Basin thermocline as revealed by the Hydrographic

 ID55
 Data
 Archive, Deep Sea
 Research Part I: Oceanographic
 Research Papers, 53, 1285–1300,
- 1056 https://doi.org/10.1016/j.dsr.2006.05.011, 2006.
- Gorsky, G., Prieur, L., Taupier-Letage, I., Stemmann, L., and Picheral, M.: Large particulate matter in the Western Mediterranean, Journal of Marine Systems, 33–34, 289–311, https://doi.org/10.1016/S0924-7963(02)00063-5, 2002.
- Guidi, L., Stemmann, L., Legendre, L., Picheral, M., Prieur, L., and Gorsky, G.: Vertical distribution of aggregates (>110 μm)
 and mesoscale activity in the northeastern Atlantic: Effects on the deep vertical export of surface carbon, Limnol. Oceanogr.,
 52, 7–18, https://doi.org/10.4319/lo.2007.52.1.0007, 2007.
- Guidi, L., Jackson, G. A., Stemmann, L., Miquel, J. C., Picheral, M., and Gorsky, G.: Relationship between particle size
 distribution and flux in the mesopelagic zone, Deep Sea Research Part I: Oceanographic Research Papers, 55, 1364–1374,
 https://doi.org/10.1016/j.dsr.2008.05.014, 2008.

a mis en forme : Anglais (E.U.)

a mis en forme : Anglais (E.U.)	
a mis en forme : Anglais (E.U.)	
Code de champ modifié	
a mis en forme : Anglais (E.U.)	
a mis en forme : Anglais (E.U.)	
Code de champ modifié	

- Guidi, L., Calil, P. H. R., Duhamel, S., Björkman, K. M., Doney, S. C., Jackson, G. A., Li, B., Church, M. J., Tozzi, S., Kolber,
 Z. S., Richards, K. J., Fong, A. A., Letelier, R. M., Gorsky, G., Stemmann, L., and Karl, D. M.: Does eddy-eddy interaction
 control surface phytoplankton distribution and carbon export in the North Pacific Subtropical Gyre?, J. Geophys. Res., 117,
 2012JG001984, https://doi.org/10.1029/2012JG001984, 2012.
- Haller, G.: Lagrangian Coherent Structures, Annu. Rev. Fluid Mech., 47, 137–162, <u>https://doi.org/10.1146/annurev-fluid-</u>
 010313-141322, 2015.
- Henson, S. A., Sanders, R., and Madsen, E.: Global patterns in efficiency of particulate organic carbon export and transfer to
 the deep ocean, Global Biogeochemical Cycles, 26, 2011GB004099, <u>https://doi.org/10.1029/2011GB004099</u>, 2012.
- Hernández-Carrasco, I., Orfila, A., Rossi, V., and Garçon, V.: Effect of small scale transport processes on phytoplankton
 distribution in coastal seas, Sci Rep, 8, 8613, <u>https://doi.org/10.1038/s41598-018-26857-9</u>, 2018.
- Hosoda, S., Ohira, T., Sato, K., and Suga, T.: Improved description of global mixed-layer depth using Argo profiling floats, J
 Oceanogr, 66, 773–787, <u>https://doi.org/10.1007/s10872-010-0063-3</u>, 2010.
- Hunt, J. R.: Self-similar particle-size distributions during coagulation: theory and experimental verification, J. Fluid Mech.,
 122, 169, https://doi.org/10.1017/S0022112082002158, 1982.
- Ioannou, A., Speich, S., and Laxenaire, R.: Characterizing Mesoscale Eddies of Eastern Upwelling Origins in the Atlantic
 Ocean and Their Role in Offshore Transport, Front. Mar. Sci., 9, 835260, https://doi.org/10.3389/fmars.2022.835260, 2022.
- Iversen, M. H. and Lampitt, R. S.: Size does not matter after all: No evidence for a size-sinking relationship for marine snow,
 Progress in Oceanography, 189, 102445, <u>https://doi.org/10.1016/j.pocean.2020.102445</u>, 2020.
- Jackson, G. A.: A model of the formation of marine algal flocs by physical coagulation processes, Deep Sea Research Part A.
 Oceanographic Research Papers, 37, 1197–1211, <u>https://doi.org/10.1016/0198-0149(90)90038-W</u>, 1990.
- Jackson, G. A. and Checkley, D. M.: Particle size distributions in the upper 100m water column and their implications for
 animal feeding in the plankton, Deep Sea Research Part I: Oceanographic Research Papers, 58, 283–297,
 https://doi.org/10.1016/j.dsr.2010.12.008, 2011.
- 1088Jouandet, M.-P., Jackson, G. A., Carlotti, F., Picheral, M., Stemmann, L., and Blain, S.: Rapid formation of large aggregates1089during the spring bloom of Kerguelen Island: observations and model comparisons, Biogeosciences, 11, 4393-4406,
- 1090 <u>https://doi.org/10.5194/bg-11-4393-2014</u>, 2014.
- 1091 Kriest, I.: Different parameterizations of marine snow in a 1D-model and their influence on representation of marine snow,
- nitrogen budget and sedimentation, Deep Sea Research Part I: Oceanographic Research Papers, 49, 2133–2162,
 https://doi.org/10.1016/S0967-0637(02)00127-9, 2002.

я	mis	en	forme	:	Anglais	(E.U.))

-(a mis en forme : Anglais (E.U.)
•(a mis en forme : Anglais (E.U.)
•(Code de champ modifié

- Lampitt, R. S., Noji, T., and Von Bodungen, B.: What happens to zooplankton faecal pellets? Implications for material flux,
 Mar. Biol., 104, 15–23, https://doi.org/10.1007/BF01313152, 1990.
- Ib96
 Laubscher, R. K., Perissinotto, R., and McQuaid, C. D.: Phytoplankton production and biomass at frontal zones in the Atlantic

 1097
 sector of the Southern Ocean, Polar Biol, 13, https://doi.org/10.1007/BF00233138, 1993.
- Laurenceau-Cornec, E., Trull, T., Davies, D., De La Rocha, C., and Blain, S.: Phytoplankton morphology controls on marine
 snow sinking velocity, Mar. Ecol. Prog. Ser., 520, 35–56, https://doi.org/10.3354/meps11116, 2015.
- Laxenaire, R., Speich, S., Blanke, B., Chaigneau, A., Pegliasco, C., and Stegner, A.: Anticyclonic Eddies Connecting the
 Western Boundaries of Indian and Atlantic Oceans, J. Geophys. Res. Oceans, 123, 7651–7677,
 https://doi.org/10.1029/2018JC014270, 2018.
- Laxenaire, R., Speich, S., and Stegner, A.: Evolution of the Thermohaline Structure of One Agulhas Ring Reconstructed from
 Satellite Altimetry and Argo Floats, J. Geophys. Res. Oceans, 124, 8969–9003, https://doi.org/10.1029/2018JC014426, 2019.
- Laxenaire, R., Speich, S., and Stegner, A.: Agulhas Ring Heat Content and Transport in the South Atlantic Estimated by
 Combining Satellite Altimetry and Argo Profiling Floats Data, JGR Oceans, 125, e2019JC015511,
 https://doi.org/10.1029/2019JC015511, 2020.
- Laxenaire, R., Guez, L., Chaigneau, A., Isic, M., Ioannou, A., and Speich, S.: TOEddies Global Mesoscale Eddy Atlas
 Colocated with Argo Float Profiles, https://doi.org/10.17882/102877, 2024.
- Le Moigne, F. A. C.: Pathways of Organic Carbon Downward Transport by the Oceanic Biological Carbon Pump, Front. Mar.
 Sci., 6, 634, <u>https://doi.org/10.3389/fmars.2019.00634</u>, 2019.
- Lehahn, Y., d'Ovidio, F., and Koren, I.: A Satellite-Based Lagrangian View on Phytoplankton Dynamics, Annu. Rev. Mar.
 Sci., 10, 99–119, <u>https://doi.org/10.1146/annurev-marine-121916-063204</u>, 2018.
- Lévy, M., Franks, P. J. S., and Smith, K. S.: The role of submesoscale currents in structuring marine ecosystems, Nat Commun,
 9, 4758, https://doi.org/10.1038/s41467-018-07059-3, 2018.
- Lima, I. D.: Biological response to frontal dynamics and mesoscale variability in oligotrophic environments: Biological production and community structure, J. Geophys. Res., 107, 3111, https://doi.org/10.1029/2000JC000393, 2002.
- Llort, J., Langlais, C., Matear, R., Moreau, S., Lenton, A., and Strutton, P. G.: Evaluating Southern Ocean Carbon Eddy-Pump
 From Biogeochemical-Argo Floats, JGR Oceans, 123, 971–984, https://doi.org/10.1002/2017JC012861, 2018.
- Lutjeharms, J. R. E., Boebel, O., and Rossby, H. T.: Agulhas cyclones, Deep Sea Research Part II: Topical Studies in
 Oceanography, 50, 13–34, https://doi.org/10.1016/S0967-0645(02)00378-8, 2003.

-(a mis en forme : Anglais (E.U.)
-(a mis en forme : Anglais (E.U.)
•	a mis en forme : Anglais (E.U.)
	Code de champ modifié

Mahadevan, A.: The Impact of Submesoscale Physics on Primary Productivity of Plankton, Annu. Rev. Mar. Sci., 8, 161–184,
 https://doi.org/10.1146/annurev-marine-010814-015912, 2016.

- 1124 Mahadevan, A. and Archer, D.: Modeling the impact of fronts and mesoscale circulation on the nutrient supply and 1125 biogeochemistry of the upper ocean, J. Geophys. Res., 105, 1209–1225, https://doi.org/10.1029/1999JC900216, 2000.
- Maier-Reimer, E., Mikolajewicz, U., and Winguth, A.: Future ocean uptake of CO2: interaction between ocean circulation and biology;, Climate Dynamics, 12, 711–722, https://doi.org/10.1007/s003820050138, 1996.
- McCave, I. N.: Size spectra and aggregation of suspended particles in the deep ocean, Deep Sea Research Part A.
 Oceanographic Research Papers, 31, 329–352, https://doi.org/10.1016/0198-0149(84)90088-8, 1984.
- McGillicuddy, D. J.: Mechanisms of Physical-Biological-Biogeochemical Interaction at the Oceanic Mesoscale, Annu. Rev.
 Mar. Sci., 8, 125–159, <u>https://doi.org/10.1146/annurev-marine-010814-015606</u>, 2016.
- 1132
 McWilliams, J. C.:
 Submesoscale
 currents
 in
 the
 ocean,
 Proc.
 R.
 Soc.
 A.,
 472,
 20160117,

 1133
 https://doi.org/10.1098/rspa.2016.0117, 2016.
 113
 https://doi.org/10.1098/rspa.2016.0117,
 113
 https://doi.org/10.1098/rspa.2016.0117,
 2016.
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 113
 <t
- Møller, E. F., Borg, C. M. A., Jónasdóttir, S. H., Satapoomin, S., Jaspers, C., and Nielsen, T. G.: Production and fate of copepod
 fecal pellets across the Southern Indian Ocean, Mar Biol, 158, 677–688, https://doi.org/10.1007/s00227-010-1591-5, 2011.
- Omand, M. M., D'Asaro, E. A., Lee, C. M., Perry, M. J., Briggs, N., Cetinić, I., and Mahadevan, A.: Eddy-driven subduction
 exports particulate organic carbon from the spring bloom, Science, 348, 222–225, <u>https://doi.org/10.1126/science.1260062</u>,
 2015.
- Penven, P., Lutjeharms, J. R. E., Marchesiello, P., Roy, C., and Weeks, S. J.: Generation of cyclonic eddies by the Agulhas
 Current in the Lee of the Agulhas Bank, Geophys. Res. Lett., 28, 1055–1058, <u>https://doi.org/10.1029/2000GL011760</u>, 2001.
- Picheral, M., Catalano, C., Brousseau, D., Claustre, H., Coppola, L., Leymarie, E., Coindat, J., Dias, F., Fevre, S., Guidi, L.,
 Irisson, J. O., Legendre, L., Lombard, F., Mortier, L., Penkerch, C., Rogge, A., Schmechtig, C., Thibault, S., Tixier, T., Waite,
 A., and Stemmann, L.: THE UNDERWATER VISION PROFILER 6: AN IMAGING SENSOR OF PARTICLE SIZE SPECTRA AND PLANKTON,
- FOR AUTONOMOUS AND CABLED PLATFORMS, Limnology & Ocean Methods, 20, 115–129, <u>https://doi.org/10.1002/lom3.10475</u>,
 2022.
- 1146 Picheral, M., Colin, S., Irisson, J-O.: EcoTaxa, a tool for the taxonomic classification of images, http://ecotaxa.obs-vlfr.fr
- Ploug, H., Iversen, M. H., and Fischer, G.: Ballast, sinking velocity, and apparent diffusivity within marine snow and
 zooplankton fecal pellets: Implications for substrate turnover by attached bacteria, Limnology & Oceanography, 53, 1878–
 1886, https://doi.org/10.4319/lo.2008.53.5.1878, 2008.

(a mis en forme : Anglais (E.U.)
(a mis en forme : Anglais (E.U.)
~(a mis en forme : Anglais (E.U.)
\geq	Code de champ modifié

 Prants, S. V.: Dynamical systems theory methods to study mixing and transport in the ocean, Phys. Scr., 87, 038115, https://doi.org/10.1088/0031-8949/87/03/038115, 2013.

- Pujol, M.-I., Faugère, Y., Taburet, G., Dupuy, S., Pelloquin, C., Ablain, M., and Picot, N.: DUACS DT2014: the new multimission altimeter data set reprocessed over 20 years, Ocean Sci., 12, 1067–1090, <u>https://doi.org/10.5194/os-12-1067-2016</u>,
 2016.
- Richardson, P. L., Lutjeharms, J. R. E., and Boebel, O.: Introduction to the "Inter-ocean exchange around southern Africa,"
 Deep Sea Research Part II: Topical Studies in Oceanography, 50, 1–12, <u>https://doi.org/10.1016/S0967-0645(02)00376-4</u>,
 2003.
- Rodionov, S. N.: A sequential algorithm for testing climate regime shifts: ALGORITHM FOR TESTING REGIME SHIFTS,
 Geophys. Res. Lett., 31, n/a-n/a, https://doi.org/10.1029/2004GL019448, 2004.
- Roquet, F., Madec, G., McDougall, T. J., and Barker, P. M.: Accurate polynomial expressions for the density and specific
 volume of seawater using the TEOS-10 standard, Ocean Modelling, 90, 29–43, <u>https://doi.org/10.1016/j.ocemod.2015.04.002</u>,
 2015.
- 1163 Sarmiento, J. L. and Gruber, N.: Ocean biogeochemical dynamics, Princeton University Press, Princeton, 503 pp., 2006.
- Schmid, C., Boebel, O., Zenk, W., Lutjeharms, J. R. E., Garzoli, S. L., Richardson, P. L., and Barron, C.: Early evolution of
 an Agulhas Ring, Deep Sea Research Part II: Topical Studies in Oceanography, 50, 141–166, <u>https://doi.org/10.1016/S0967-</u>
 0645(02)00382-X, 2003.
- Ser-Giacomi, E., Baudena, A., Rossi, V., Follows, M., Clayton, S., Vasile, R., López, C., and Hernández-García, E.:
 Lagrangian betweenness as a measure of bottlenecks in dynamical systems with oceanographic examples, Nat Commun, 12,
 4935, https://doi.org/10.1038/s41467-021-25155-9, 2021.
- Shadden, S. C., Lekien, F., and Marsden, J. E.: Definition and properties of Lagrangian coherent structures from finite-time
 Lyapunov exponents in two-dimensional aperiodic flows, Physica D: Nonlinear Phenomena, 212, 271–304,
 https://doi.org/10.1016/j.physd.2005.10.007, 2005.
- Shanks, A. L. and Trent, J. D.: Marine snow: sinking rates and potential role in vertical flux, Deep Sea Research Part A.
 Oceanographic Research Papers, 27, 137–143, https://doi.org/10.1016/0198-0149(80)90092-8, 1980.
- Shih, Y., Hung, C., Tuo, S., Shao, H., Chow, C. H., Muller, F. L. L., and Cai, Y.: The Impact of Eddies on Nutrient Supply,
 Diatom Biomass and Carbon Export in the Northern South China Sea, Front. Earth Sci., 8, 537332,
 https://doi.org/10.3389/feart.2020.537332, 2020.

- Siegel, D. A., Buesseler, K. O., Doney, S. C., Sailley, S. F., Behrenfeld, M. J., and Boyd, P. W.: Global assessment of ocean
 carbon export by combining satellite observations and food-web models, Global Biogeochemical Cycles, 28, 181–196,
 https://doi.org/10.1002/2013GB004743, 2014.
- 1181 Siegelman, L., Klein, P., Rivière, P., Thompson, A. F., Torres, H. S., Flexas, M., and Menemenlis, D.: Enhanced upward heat 1182 transport at deep submesoscale ocean fronts, Nat. Geosci., 13, 50–55, https://doi.org/10.1038/s41561-019-0489-1, 2020.
- Soviadan, Y. D., Beck, M., Habib, J., Baudena, A., Drago, L., Accardo, A., Laxenaire, R., Speich, S., Brandt, P., Kiko, R., and
 Stemmann, L.: Marine snow morphology drives sinking and attenuation in the ocean interior,
 <u>https://doi.org/10.5194/egusphere-2024-3302</u>, 7 November 2024.
- Stammer, D.: Global Characteristics of Ocean Variability Estimated from Regional TOPEX/POSEIDON Altimeter
 Measurements, J. Phys. Oceanogr., 27, 1743–1769, <u>https://doi.org/10.1175/1520-0485(1997)027<1743:GCOOVE>2.0.CO;2</u>,
 1188 1997.
- Stemmann, L. and Boss, E.: Plankton and Particle Size and Packaging: From Determining Optical Properties to Driving the
 Biological Pump, Annu. Rev. Mar. Sci., 4, 263–290, <u>https://doi.org/10.1146/annurev-marine-120710-100853</u>, 2012.
- II91
 Stemmann, L., Gorsky, G., Marty, J.-C., Picheral, M., and Miquel, J.-C.: Four-year study of large-particle vertical distribution

 II92
 (0–1000m) in the NW Mediterranean in relation to hydrology, phytoplankton, and vertical flux, Deep Sea Research Part II:
- 103
 Topical Studies in Oceanography, 49, 2143–2162, https://doi.org/10.1016/S0967-0645(02)00032-2, 2002.

Stemmann, L., Jackson, G. A., and Ianson, D.: A vertical model of particle size distributions and fluxes in the midwater column
 that includes biological and physical processes—Part I: model formulation, Deep Sea Research Part I: Oceanographic Research
 Papers, 51, 865–884, https://doi.org/10.1016/j.dsr.2004.03.001, 2004.

Stemmann, L., Prieur, L., Legendre, L., Taupier-Letage, I., Picheral, M., Guidi, L., and Gorsky, G.: Effects of frontal processes
 on marine aggregate dynamics and fluxes: An interannual study in a permanent geostrophic front (NW Mediterranean), Journal
 of Marine Systems, 70, 1–20, https://doi.org/10.1016/j.jmarsys.2007.02.014, 2008.

- Stukel, M. R., Aluwihare, L. I., Barbeau, K. A., Chekalyuk, A. M., Goericke, R., Miller, A. J., Ohman, M. D., Ruacho, A.,
 Song, H., Stephens, B. M., and Landry, M. R.: Mesoscale ocean fronts enhance carbon export due to gravitational sinking and
- 1202 subduction, Proc. Natl. Acad. Sci. U.S.A., 114, 1252–1257, https://doi.org/10.1073/pnas.1609435114, 2017.
- Tarry, D. R., Essink, S., Pascual, A., Ruiz, S., Poulain, P., Özgökmen, T., Centurioni, L. R., Farrar, J. T., Shcherbina, A.,
 Mahadevan, A., and D'Asaro, E.: Frontal Convergence and Vertical Velocity Measured by Drifters in the Alboran Sea, J.
 Geophys. Res. Oceans, 126, <u>https://doi.org/10.1029/2020JC016614</u>, 2021.
- 1206 Thomalla, S. J., Fauchereau, N., Swart, S., and Monteiro, P. M. S.: Regional scale characteristics of the seasonal cycle of chlorophyll in the Southern Ocean, Biogeosciences, 8, 2849–2866, https://doi.org/10.5194/bg-8-2849-2011, 2011.

a mis en forme : Anglais (E.U.)

a mis en forme : Anglais (E.U.) a mis en forme : Anglais (E.U.) Code de champ modifié

a mis en forme : Anglais (E.U.)

a mis en forme : Anglais (E.U.) a mis en forme : Anglais (E.U.) Code de champ modifié

c	ode	de	champ modifié
a	mis	en	forme : Anglais (E.U.)
a	mis	en	forme : Anglais (E.U.)

(a mis en forme : Anglais (E.U.)
(a mis en forme : Anglais (E.U.)
-(a mis en forme : Anglais (E.U.)
•(Code de champ modifié

1210	https://doi.org/10.1029/177GM04, 2008.		
1211	Trudnowska, E., Lacour, L., Ardyna, M., Rogge, A., Irisson, J. O., Waite, A. M., Babin, M., and Stemmann, L.: Marine snow		
1212	morphology illuminates the evolution of phytoplankton blooms and determines their subsequent vertical export, Nat Commun,		
1213	12, 2816, https://doi.org/10.1038/s41467-021-22994-4, 2021.		
1214	Turner, J. T.: Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump, Progress in		
1215	Oceanography, 130, 205–248, https://doi.org/10.1016/j.pocean.2014.08.005, 2015.		
1215	occanography, 150, 205–240, <u>https://doi.org/10.1010/j.poccan.2014.08.005</u> , 2015.		
1216	Waite, A. M., Stemmann, L., Guidi, L., Calil, P. H. R., Hogg, A. M. C., Feng, M., Thompson, P. A., Picheral, M., and Gorsky,		
1217	G.: The wineglass effect shapes particle export to the deep ocean in mesoscale eddies, Geophysical Research Letters, 43, 9791-		
1218	9800, https://doi.org/10.1002/2015GL066463, 2016.		
1219	Williams, J. R. and Giering, S. L. C.: In Situ Particle Measurements Deemphasize the Role of Size in Governing the Sinking		a mis en forme : Anglais (E.U.)
1220	Velocity of Marine Particles, Geophysical Research Letters, 49, e2022GL099563, https://doi.org/10.1029/2022GL099563,	<pre></pre>	a mis en forme : Anglais (E.U.)
1221	<u>2022.</u>		a mis en forme : Anglais (E.U.)
		Y	Code de champ modifié
1222	Wunsch, C.: Where do ocean eddy heat fluxes matter?, J. Geophys. Res., 104, 13235-13249,		
1223	https://doi.org/10.1029/1999JC900062, 1999.		
1224	Yeo, IK.: A new family of power transformations to improve normality or symmetry, Biometrika, 87, 954-959,		a mis en forme : Espace Après : 0 pt
1225			· · · · ·
1223	https://doi.org/10.1093/biomet/87.4.954, 2000		a supprimé: ¶

Thomas, L. N., Tandon, A., and Mahadevan, A.: Submesoscale processes and dynamics, in: Geophysical Monograph Series,

vol. 177, edited by: Hecht, M. W. and Hasumi, H., American Geophysical Union, Washington, D. C., 17-38,

1208