



1 Marine snow surface production and bathypelagic export at the

2 Equatorial Atlantic from an imaging float

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14 Abstract. The marine biological carbon pump (BCP) plays a central role in the global carbon cycle, transporting 15 carbon from the surface to the deep ocean and sequestering it for long periods. Sinking of surface-produced particles, known as the Biological Gravity Pump (BGP) constitutes the main component of the BCP. To study the 16 17 BGP in the equatorial Atlantic upwelling region, a biogeochemical (BGC) Argo float equipped with an Underwater 18 Vision Profiler 6 (UVP6) camera was deployed from July 2021 to March 2022. The float was recovered after its 19 eastward drift from 23°W to 7°W along the equator, during which it conducted profiles to 2000 m depth every 20 three days. For the first time in this oceanic region, in situ images and physical and biogeochemical data from a 21 BGC-Argo float were acquired and analyzed in combination with satellite data. During the float trajectory, two 22 blooms were recorded followed by two main export events of sinking aggregates that lasted for over a month, 23 consistently reaching 2000 m depth. A Lagrangian approach was applied to investigate the production, 24 transformation, and deep export of marine particles. Based on the characterization of the morphology of detritus 25 within and outside of the plumes, five particle morphotypes with different sinking properties were detected. Small 26 and dense aggregates were present throughout the water column while porous morphotypes, despite being larger, 27 were predominantly concentrated in the surface layer. Export was driven by small and compact particles with higher 28 particle abundance and flux during upwelling and export events. Our investigation reveals the stability of the 29 equatorial Atlantic BCP system during this period, yielding an export efficiency of 6-7% during and outside of 30 export events. This study highlights the importance of using new technologies on autonomous platforms to 31 characterize the temporal variability in the magnitude and functioning of the BCP.

32 1 Introduction

The term "biological carbon pump" (BCP) encompasses physical and biological processes responsible for the generation, export, and remineralization of organic matter from the upper ocean to depth (Boyd et al., 2019; DeVries et al., 2012; Steinberg & Landry, 2017). The biological pump connects various aspects of the carbon cycle: the upper-ocean photosynthetic carbon uptake, the alimentation of the midwater biota (Irigoien et al., 2014), and the carbon storage within the deep sea (Buesseler et al., 2007). Within the euphotic zone, organic particles are continuously generated and recycled, with only a small fraction descending into deeper layers (De La Rocha, 2004), while remineralization occurs within a few hundred meters of the surface and is facilitated by processes such as





- 40 zooplankton feeding or microbial degradation (Giering et al., 2014; Steinberg & Landry, 2017; Stemmann, Jackson,
- 41 & Ianson, 2004). Given the retroactive potential of the BCP to significantly impact anthropogenic climate warming
- 42 (Bernardello et al., 2014; Bopp et al., 2013), understanding the multitude of mechanisms governing the BCP is of
- 43 paramount importance.

44 Among the different processes of the BCP, sinking marine snow is the key component of particulate carbon 45 transport to the deep ocean, a process known as the biological gravitational pump (BGP). Marine snow consists of 46 detritus, formed from a mixture of source particles produced by the surface ecosystem and aggregated together by 47 physical (coagulation) or biological (trophic activity) mechanisms (Alldredge & Silver, 1988). Their composition 48 is determined by multiple characteristics, mainly the phytoplankton and zooplankton community composition 49 (Bach et al., 2019; Tréguer et al., 2018). In the mesopelagic layers, several biological and physical factors influence 50 their dynamics and control their size distribution and morphology, which affect their sinking (Cael et al., 2021; 51 Stemmann, Jackson, & Ianson, 2004). Shear and differential settling modulates aggregation (Jackson, 1990; 52 Stemmann et al., 2004) while fragmentation rates have been proposed to depend on shear and swimming organisms 53 (Briggs et al., 2011; Dilling & Alldredge, 2000; Jackson, 1990). Additionally, particle volume and surface area 54 condition interactions with microorganisms (e.g., colonization and degradation of particles; Bianchi et al., 2018), 55 modifying marine snow morphology by making them more porous and fragile with time (Biddanda & Pomeroy, 56 1988; Ploug & Grossart, 2000).

57 An efficient tool to track the particle morphology, study their abundance, and estimate the vertical carbon flux is 58 the Underwater Vision Profiler (UVP; Picheral et al., 2010, 2022). This imaging tool measures particle abundance 59 and distribution (Guidi et al., 2009; Kiko et al., 2022; Stemmann et al., 2002), to estimate the biological 60 gravitational pump (Forest et al., 2013; Guidi et al., 2015; Kiko et al., 2017; Ramondenc et al., 2016), and more 61 recently, to explore particle morphology (Trudnowska et al., 2021; Accardo et al., submitted). One decade of 62 observation with the UVP5 during ship surveys allowed a global monitoring (Forest et al., 2013; Guidi et al., 2008, 63 2015; Kiko et al., 2017; Stemmann et al., 2002) and enabled the reconstruction of global export fluxes from the spatially variable euphotic zone and mixed layer depths (Clements et al., 2022, 2023; Guidi et al., 2015). 64

65 Despite significant improvement in observation capacities from ships, high frequency observations during long-66 term deployment to study relevant scales of marine snow dynamics over a large depth range was not possible. 67 Autonomous platforms equipped with imaging sensors have emerged and are currently being utilized to remotely 68 record plankton and particle distributions in addition to the core parameters such as salinity, temperature, and 69 optically derived other variables (Claustre et al., 2020; Picheral et al., 2022). Recently, surface blooms followed 70 by plumes of sinking material were monitored using optical sensors (fluorescence and backscatter) mounted on 71 BGC-Argo float drifting in a quasi-Lagrangian mode (Briggs et al., 2011, 2020) and global POC standing stocks 72 have been calculated (Fox et al., 2024). Such studies with optical sensors (fluorescence, backscatter) are key to 73 understanding particle dynamics in the core of the oceans but they are not adapted to study marine snow.

We selected the equatorial Atlantic Ocean to conduct our study, as it is characterized by enhanced primary productivity concentrated within the equatorial and coastal regions (Grodsky et al., 2008). This productivity is due to the presence of upwelling zones in the central and eastern parts of the equatorial basin (Schott et al., 1998) which bring nutrients to the euphotic zone (Radenac et al., 2020). This enhanced productivity results in a stronger passive





78 and active export of particulate matter reaching up to 4000 m (Kiko et al., 2017). The strength of the equatorial 79 upwelling system is modulated by the strength of seasonally varying winds associated with the meridional 80 migration of the intertropical convergence zone (Brandt et al., 2023). At intraseasonal (20-50 days) scales, Tropical 81 Instability Waves (TIWs) are another factor influencing the equatorial local productivity. TIWs are westward-82 propagating, cusp-shaped oscillations prevalent in the central and western equatorial Atlantic generated by 83 baroclinic and barotropic instabilities (Athie & Marin, 2008). They induce strong intraseasonal variations in sea surface temperature, sea surface salinity, and ocean currents (Tuchen et al., 2022), and are associated with sharp 84 85 fronts (Warner et al., 2018). TIWs can also influence nitrate (Radenac et al., 2020) and chlorophyll distribution 86 (Menkes et al., 2002; Sherman et al., 2022).

We here focus on the equatorial Atlantic BGP, using data from a UVP6 camera mounted on a BGC-Argo float deployed at 23°W, 0° in July 2021 to study the impact of seasonal upwelling and intraseasonal TIWs on productivity and particle export. In particular, we use a plume-based approach to follow the initiation and vertical extent of export events, to characterize particle production of various morphotypes during two bloom events, and to describe the patterns of their attenuation as they are exported to the meso- and bathypelagic layers.

92 2 Material and Methods

93 2.1 Satellite data

94 2.1.1 Sea surface chlorophyll-a

95 Estimates of chlorophyll-a (chl-a) concentration and anomalies for the tropical Atlantic were obtained from the 96 combination of two different products: the Global Ocean Color product (OCEANCOLOUR_GLO_BGC_L4_MY_009_104) produced by ACRI-ST and the NOAA-VIIRS provided by 97 98 NOAA CoastWatch. Both of these data sets provide gap-free time series, with a temporal extent from 1997 till 99 2023 for the first product, while the second one only started in 2018. The temporal resolution for both products is 100 one day with a spatial resolution of 4 km for the first product and 9 km for the second one.

101 **2.1.2 Sea surface temperature**

Sea surface temperature (SST) and SST anomaly data were downloaded from the NOAA OI-SST data set (Huang et al., 2021; https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.htm). SST anomalies are computed relative to a 30-year climatological mean. The gridded data are available daily from 1981-present at a horizontal resolution of 0.25°. To isolate TIW induced SST variability from the time series, a temporal (20-50 days) and a zonal (4-20° wavelength) bandpass filter were applied in accordance with previous studies (Olivier et al., 2020; Tuchen et al., 2022).

108 2.1.3 Lagrangian diagnostics

Several Lagrangian diagnostics were computed for each sampling station using velocity data and environmental satellite products. To this aim, we defined for each station a circular region that we consider representative of the water parcel sampled by the BGC-Argo float. A radius of 0.1° was used (consistently with previous studies, Baudena et al., 2021; Fabri-Ruiz et al., 2023; Ser-Giacomi et al., 2021), and the circular region was filled with virtual particles. A given diagnostic is calculated for each virtual particle in the circular region. These values are then averaged together, providing one value of a given diagnostic per station.





- 115 The velocity field used is the Copernicus CMEMS product MULTIOBS GLO PHY REP 015 004-TDS at 15 m 116 depth. This product has a spatial resolution of 0.25° and a daily temporal resolution. It is derived from satellite altimetry and model assimilation and includes both geostrophic and Ekman components. Using the surface velocity, 117 118 each particle within the circular region of a given sampling station was advected using a Runge-Kutta scheme of 119 order 4 from the day of the sampling backward in time. Different advective times were used, from 5 to 45 days. 120 Two types of diagnostics were carried out: Eulerian and purely Lagrangian diagnostics. These groups consist of 121 calculating properties that are integrated in time: at the sampling location (Eulerian) or along the trajectory of the 122 water parcel (Lagrangian). In this study, we only present diagnostics that are relevant to our area of study, such as 123 the Lagrangian and Eulerian chl-a, divergence, and vorticity. The Lagrangian chlorophyll, the average chl-a content carried by the water parcel in the previous days, provides information on the recent primary productivity. The 124 125 Lagrangian divergence can be considered as a proxy of the upwelling (when negative) of downwelling (when 126 positive) experience by the water parcel in the previous days. This metric has been correlated with chlorophyll 127 (Hernández-Carrasco et al., 2018).
- In the following, we will report diagnostics calculated using an advective time of 15 days. This value was chosen as it showed the highest correlations between the chl-a concentrations and the abundance of micrometric particles
- 130 and macroscopic particles between 0-100m (Supplementary Fig. S8).

131 2.2 Float data

132 2.2.1 Coverage and data collection

For this study, a BGC-Argo float (WMO:6904139) was deployed at the equator during *RV Sonne* SO284 cruise traversing the transect from 23°W to 7°W migrating from west to east during the period between July 2021 and March 2022. The float was recovered during the PIRATA FR32 cruise. This float was equipped with several physical and biogeochemical sensors to measure the pressure, temperature, salinity, chlorophyll, oxygen, and particle backscattering coefficient (BBP) with a vertical resolution of 5 m. BGC-Argo float data were collected through the International Argo Program and can be found at https://argo.ucsd.edu. Chl-a and BBP both present a gap between the 1st and the 5th of January 2022.

140 2.2.2 UVP measurements

An Underwater Vision Profiler 6 (UVP6) was mounted on the BGC Argo float. This camera-based particle counter sizes and counts marine particles (Kiko et al., 2022) covering a size range from 0.102 mm to 16.4 mm. The UVP contributes to understanding sinking organic particles and carbon sequestration at global (Guidi et al., 2015) and regional scales (Ramondenc et al., 2016). More information about calibration and data processing can be found in Picheral et al. (2021). In total, our data set includes 86 profiles reaching at least 1000 m. Every 3 days, the BGC Argo float reached 2000 m. For all parameters, we interpolated the data set with a vertical resolution of 10 m and a temporal resolution of a day.

148 2.2.3 Mixed layer depth calculation

To determine the mixed layer depth, we use temperature profiles provided by the BGC-Argo float. Using the definition outlined in De Boyer Montégut et al. (2004), the mixed layer was determined by identifying the depth at





151 which the temperature decreased by 0.2°C relative to the temperature at 10 m depth. The mixed layer depth in this

152 study reached a depth of 60 m.

153 2.2.4 Particle abundance and carbon flux calculation

Particle size abundances (number of particles per liter) for depth bins of 2.5 m along the water column were 154 155 obtained by the UVP. Particles were divided into two categories based on their size: Micrometric particles (MiP) 156 for particles ranging between 0.1-0.5 mm, and Macroscopic particles (MaP) ranging between 0.5-16 mm. The 157 carbon flux was obtained by integrating all size classes and therefore represents the total carbon flux. To calculate 158 the flux for a given size class, we used the relationship provided by Kriest (2002), linking the particle size to the 159 sinking speed and its carbon content. This relationship has been used in former studies using UVP observations 160 (Kiko et al., 2017). For each parameter, we interpolated the profiles in depth with a vertical resolution of 10 m and 161 a temporal resolution of a day.

162 2.2.5 Determination of export events

We determined periods of export events, using the anomalous carbon flux. We calculated the total mean particle abundance and mean carbon flux along the water column from the interpolated fields for the deployment period. The resulting mean profile was then subtracted from the individual particle abundance and carbon flux profiles, yielding anomaly profiles. This helped us determine two different types of periods: periods with main export events and periods where no or weak export occurred.

168 2.2.6 Regime shift detection for surface export

169 A sequential algorithm for regime shift detection (Rodionov, 2004) was applied to the MaP abundance for the first 200 m to identify accurately the beginning and the end of the carbon export events. This method identifies 170 171 discontinuities in a time series without prior assumptions of the timing of the regime shifts. The algorithm requires 172 a set of parameters to specify: the target significance level and the cutoff length. The target significance used here 173 is p=0.05. The cutoff length affects the time scale of the regime by removing regimes of shorter duration than the 174 reference value. In this study, the cutoff length was set to 9 days to cover at least 3 profiles. For more details, see 175 Rodionov (2004, 2006). We determined three masks, two corresponding to periods of export 'event 1', 'event 2', 176 and a period where no main export plume was observed, hereafter referred to as the 'outside-between' mask. It 177 should be noted that 'outside-between' refers to periods that do not belong to the two main export events.

178 2.2.7 Morphological properties of detritus

179 The data set consisted of 127,000 images. Each image underwent individual classification using the Ecotaxa 180 program with the support of machine learning classifiers (Picheral et al., 2017). This classification differentiates 181 between living and non-living organisms. The automatically classified images were then manually validated or 182 reclassified. To distinguish between different types of marine snow, we examined the morphological properties of 183 individual objects such as size (area, perimeter), shade intensity (mean/median gray level), shape (elongation), and 184 structural complexity (homogeneity or heterogeneity of gray levels). This was done using a principal component 185 analysis (Fig. S6) to summarize the morphological information into a few new variables, followed by k-means 186 clustering to separate different morphotypes of particles (Trudnowska et al. 2021). Using this method, we 187 distinguish between five types of marine snow, as this number was a good compromise between the continuum of





- 188 change in morphology and a need for simplicity. Concentration in numbers (numbers m⁻³) was computed per 10 m
- 189 bins for each UVP6 profile.

190 2.2.8 Flux attenuation and biological carbon pump efficiency

191 The biological carbon pump (BCP) was computed following Engel et al. (2023), and Buesseler et al. (2020):

$$BCP = E_{eff} \times T_{eff} \tag{1}$$

193 With Eeff, as the carbon export efficiency (Eeff)

$$194 \qquad E_{eff} = \frac{F_{Z0}}{PP} \tag{2}$$

Fx0 is the carbon export flux out of the surface ocean layer, corresponding to 100 m. While PP is the amount of CO2 fixed by primary production, both in mg m⁻³ d⁻¹. Satellite-based net primary production (NPP) was downloaded from the Ocean Productivity website (www.science.oregonstate.edu/ocean.productivity) using the Vertically Generalized Production Model (VGPM)-Eppley.

199 T_{eff} represents the carbon transfer efficiency:

200
$$T_{eff} = \frac{F_Z}{F_{Z0}}$$
 (3)

F_Z is the flux at a particular depth and Z_0 is the reference depth (taken here as 100 m). T_{eff} is related to the attenuation of carbon flux with depth, over 0-1000 m, quantified by a Martin power law (Martin et al., 1987).

203
$$F_Z = F_{Z0} \times \left(\frac{Z}{Z_0}\right)^{-b}$$
 (4)

Z is the depth. The exponent b represents the attenuation with depth. An analogous equation was used to describethe particle attenuation.

$$206 n_Z = n_{Z0} \times \left(\frac{Z}{Z_0}\right)^{-b} (5)$$

207 n_Z, n_{Z0} are the concentrations of particles at depth Z or Z₀.

208 3 Results

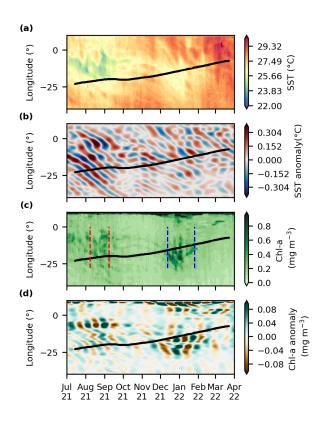
209 3.1 Satellite data analysis

Throughout the float trajectory (Fig. S1), satellite observations disclosed the presence of relatively cold surface waters during two distinct periods: August-October 2021 and December 2021 to February 2022 (Fig. 1a). The first period aligned with the seasonal development and peak of the Atlantic cold tongue with minimum surface temperatures around 23.8°C. The second period was from December to February with temperatures around 26°C. The seasonal surface warming occurring between October and December featured values reaching 27.5°C, while temperatures reached almost 29.5 during March and April (Fig. S2a). The temperatures were warmer than usual compared to the climatology from 2012-2022, especially throughout the boreal summer of 2021 (Fig. S2a).





- Before and during the cold tongue development in July to September 2021, bandpass-filtered SST anomalies
 oscillated between -0.3°C and 0.3°C and showed westward propagation (Fig. 1b), suggesting the presence of TIWs.
 A weaker TIW signal was observed during the second period when SST anomalies ranged between -0.1°C and
- 220 0.1°C.
- Peaks of chl-a were observed during both low-temperature periods reaching about 0.4 mg m⁻³ on 10 September 2021 and 2 January 2022 (Fig. 1c, S2b). The surface chl-a concentration ranged between 0.1 and 0.4 mg m⁻³ along
- the float trajectory. When comparing the chl-a to the climatology, a delay in both peaks was observed (Fig. S2b)
- with a low peak during summer 2021 and a second high peak during winter 2022 for the float compared to the
- climatology. The bandpass-filtered chl-a anomaly oscillated between -0.04 mg m⁻³ and 0.04 mg m⁻³ from August
- to October (Fig. 1d). These anomalies seem to be anti-correlated with the SST anomalies (Fig. S2 c,d). However,
- 227 westward propagation of bandpass-filtered chl-a anomalies is less obvious than for SST. From December to March,
- 228 more pronounced chl-a anomalies were observed.



229

Figure 1: Satellite-derived properties as a function of time (x-axis) and longitude (y-axis): (a) sea surface temperature (°C), (b) bandpass-filtered sea surface temperature anomaly, (c) surface chl-a concentration (mg m⁻³), and (d) bandpassfiltered chl-a anomaly along the equator from July 2021 to March 2022. The black line represents the float trajectory from west to east. The blue and red lines determine the beginning and the end of the first and the second export event,

²³⁴ respectively.





235 **3.2 Float data analysis**

236 **3.2.1** Physical parameters (Temperature, Salinity, mixed layer)

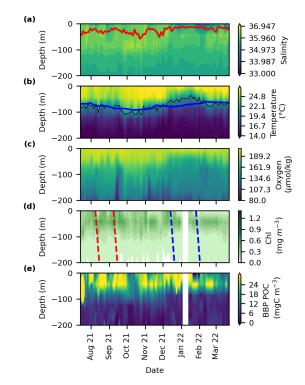
237 During August, the mixed layer depth (MLD) was at about 42 m, salinity integrated over the first 100 m showed a 238 maxima of 36 PSU (Fig. 2a, S3a) while temperature (averaged over the top 100 m) showed a first minimum of 239 21°C (Fig. 2b). Average 100-m temperature increased with the progressive deepening of the ML from September 240 to January. MLD reached a maximum of 60 m in October. Salinity was high during the same period with a maximum of 36 psu in November (Fig. 2a). A second 100-me temperature minimum of 18.8°C was also recorded 241 242 in January coinciding with the shoaling of the Deep Chlorophyll Maximum (DCM) and the presence of a salinity 243 minimum in the top 100 m (Fig 2a,b, S3a,b). A subsurface maximum was determined for the salinity between 50-244 100 m (Fig. 2a,b). The thermocline, represented by the 20°C isotherm (black line, Fig. 2,e) was unusually deep 245 during summer (80 m) compared to the Argo climatology and reached a maximum of 100 m in October. It was 246 also unusually shallow (50 m) in January 2022.

247 3.2.2 Biogeochemical parameters (chl-a, BBP, oxygen)

The chl-a concentration reported by the BGC-Argo float in the first 100 m, varied between 0 and 0.5 mg m⁻³. Peaks 248 249 reached 0.45-5 mg m⁻³ values on September 18, November 3, and 8 December (Fig. 2d, S3a). Elevated chl-a 250 concentrations were observed at 70 m depth, corresponding to the depth of the deep chl-a maximum. These values 251 varied between 0.28 and 0.8 mg m⁻³. Both satellite and float chl-a data show the presence of two blooms (Fig. S3a). 252 However, float data presented a more variable chl-a concentration compared to the satellite. This can be attributed 253 to the low resolution of satellite images compared to the float and the interpolation methods applied to ensure a 254 gap-free time series. BBP POC, calculated using a BBP-to-carbon relationship (Koestner et al., 2022), followed 255 the same pattern as chl-a and small particles were concentrated in the first 90 m (Fig. 2e). Periods of high chl-a 256 were correlated with an increase in the BBP POC. Oxygen concentrations reached values around 189 µmol kg⁻¹ 257 (Fig. 2c) in the mixed layer. Concentrations decreased with depth, with values below 134 µmol kg⁻¹ below 100 m.







258 259

Figure 2: Time-depth profiles determined from the BGC-Argo float for (a) salinity, (b) temperature (°C), (c) oxygen (µmol kg⁻¹), (d) chl-a (mg m⁻³) (e) and BBP POC (mgC m⁻³). The red line in (a) represents the mixed layer depth defined as a decrease of 0.2°C relative to temperature at 10 m depth. The black line in (b) represents the 20°C isotherm depth which is a well-known proxy for the thermocline in the tropics. The blue line in (b) is the average depth of the 20°C isotherm from the Argo climatology (2012 to 2022). The blue and red dashed lines in (d) determine the beginning and the end of the first and the second export event, respectively.

265 3.3 Carbon flux dynamics

266 **3.3.1 Surface flux and particle abundance along the trajectory (0-100m)**

267 The increase in surface chl-a in the first 100 m was linked to an increase in surface carbon flux and MiP abundance 268 (particles between 0.1-0.5 mm) (Fig. S3). Both were significantly correlated with in situ chl-a ($r^2=0.4$ and 0.3, 269 respectively, p-value<0.01). No significant correlation was found between surface chl-a and MaP abundance 270 (particles>0.5 mm). The highest integrated MiP abundance in the surface layer was recorded on the 18th of August 2021 with values reaching 316 particles L-1 (Fig. 3a,c, S3d). This also coincided with the highest MaP abundance 271 272 with around 5 particles L⁻¹. Simultaneously with the surface chl-a peak, on 3 November 2021 a peak of MiP with 273 348 particles L-1 was also observed (Fig S3d), while carbon flux increased after a 15 day delay reaching 250 mg C 274 m⁻² day⁻¹ (Fig. S3f). The peak of chl-a, in December 2021 caused an increase in carbon flux, MiP, and MaP 275 abundance.

276 **3.3.2** Flux and particle abundance pattern along the water column (averaged profile)

277 Throughout the float trajectory, the UVP6 data showcased high variability in MiP and MaP abundance, and carbon

flux in the upper 100 m, with a dominance of small particles compared to big particles (Fig. 4a, S3). MiP and MaP

increased in the surface layer peaking at 30-40 m, respectively. The maximum carbon flux, 104.1 ± 61.5 mgC m⁻³



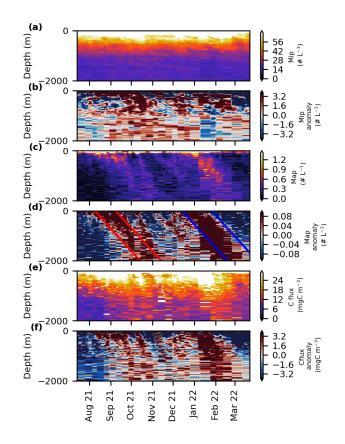


- 280 day-1, coincided with the MaP's maximum. After the surface layer peaks, MiP abundance and carbon flux declined
- 281 rapidly until 1000 m, reaching 22.5 \pm 1.3 particles $L^{\text{-1}}$ and 13.2 \pm 2.9 mgC m^{\text{-3}} day^{\text{-1}}, while MaP's abundance
- 282 decreased rapidly until 200 m with 0.3 ± 0.2 particles L⁻¹. Flux and abundance declined further with depth. The
- 283 carbon flux was dominated by MiP abundance and followed its pattern.

284 3.3.3 Evaluation of export events

To investigate two settling plumes depicted in Figure 3d, four spaced lines were drawn on the MaP abundance with a slope of 30 m day⁻¹, as suggested by Stemmann, Jackson, & Gorsky, (2004) using a model for particle size distribution. The periods of surface production and export were determined using the Rodionov algorithm (Fig. S4). The first export event, "Event 1", started at the surface on the 8th of August and lasted until the 8th of September 2021, while the second event, "Event 2", occurred from the 13th of December 2021 to the 26th of January 2022. Both events lasted one month (Fig. 3f). These events are easily discernible on the MaP abundance and carbon flux plots as two plumes that reach 2000 m depth (Fig. 3c-f) while they are less visible in the MiP

292 pattern.



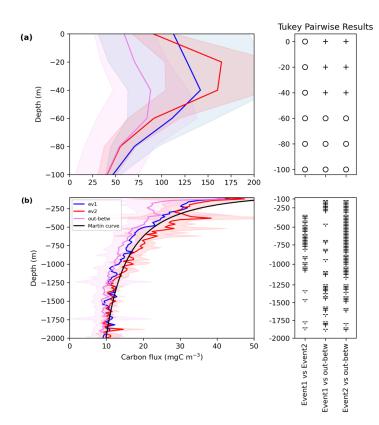
293

Figure 3: Time series of (a) MiP abundance (# L⁻¹), (b) MiP anomaly, (c) MaP abundance (# L⁻¹), (d) MaP anomaly, (e) carbon flux (mgC m⁻³ day⁻¹), and (f) carbon flux anomaly. The blue and red lines determine the beginning and the end of the first and the second export event, respectively.





297 Interestingly, the carbon flux profiles for events 1 and 2, and the 'outside-between' mask showed the same attenuation of the mean carbon flux along the water column (Fig. 4a,b). Flux at 30 m depth reached 168, 139, and 298 83 mg C m⁻³ day⁻¹ for event 2, 1 and outside-between mask, respectively (Fig. 4a). The flux then decreased with 299 300 depth during all periods. An intermediate particle maximum was observed for 'outside-between' and event 2 301 between 300-500 m (Fig. S5). The 'outside-between' mask showed the lowest carbon flux along the water column 302 compared to the two export events. Flux during event 2 was the highest from 0-60 m and then from 120 m to 2000 303 m (Fig. 4a-c). Post hoc Tukey tests showed a significant difference between the outside-between mask and the two 304 main export events for most of the layers of the water column (Fig. 4), while there was rarely a difference between 305 events 1 and 2.



306

Figure 4: Averaged carbon flux profiles (mg C m⁻³) along the plumes during event 1 (blue), event 2 (red), and the outside between mask (purple) (a) from 0-100 m, (b) from 200-2000 m. The shading represents the standard deviation. The
 Tuckey pairwise results were conducted for each depth. Plus signs indicate a significant difference, and blank space or
 empty circles indicate a non-significant difference. The black line represents the Martin curve of event 2 calculated using
 Eq. 4 with b=-0.6 and F_{x0}= 100m.

312 **3.3.4 Flux attenuation and export efficiency**

313 We parameterize the strength of the BCP pump using the export efficiency calculated at 100 m. Export efficiency

ranged between 6-7% of the NPP (from satellite data estimates) exiting the 0-100 m layer. The attenuation rate of

315 carbon flux was determined using a power law regression fit. The b values ranged between - 0.4 and - 0.6. The best





- 316 transfer efficiency was found during event 2, where 40% of the flux at 100m reaches 1000m, followed by the
- 317 between-outside mask and event 1 (31% and 29%, respectively; Table 1).
- 318 Table 1: Parameters characterizing the biological carbon pump efficiency calculated in the plumes

	Outside-between mask	event 1	event 2
Eeff	7%	7%	6%
T _{eff}	31%	29%	40%
b	-0.48	-0.53	-0.6

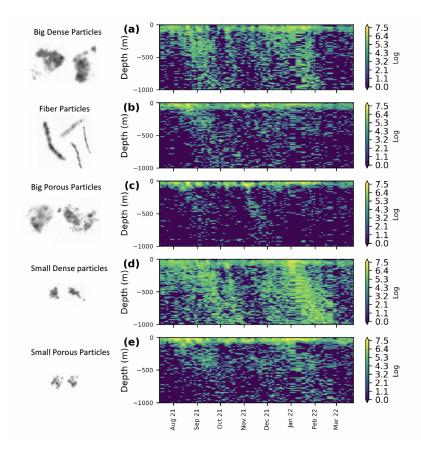
319 3.4 Particle composition

320 **3.4.1** Morphotypes of marine snow and composition of the different events

321 The k-means clustering applied to the PCA coordinates helped us to distinguish between five marine snow 322 morphotypes illustrated in Figure 5. Type 1 consisted of big and dense objects (Big Dense Particles, BDP) with an Equivalent Spherical Diameter (ESD)>0.8mm. Type 2 comprised elongated objects (Fiber particles: FP), and type 323 324 3 consisted of big, bright, and porous objects (Big Porous particles: BPP). Type 4 was mainly formed of dense, 325 small, and circular objects (Small Dense particles: SDP) and type 5 consisted of light grey, small, and porous objects (Small Porous particles: SPP). These five morphotypes were then used to characterize the distribution and 326 327 composition of marine snow. It should be noted that the terms "porous" and "dense" refer to brightness, with 328 "porous" indicating greater light transmission.







329

Figure 5: Time series of the logarithmic concentration of (a) Big Dense, (b) Fiber, (c) Big Porous, (d) Small Dense, and
 (e) Small Porous morphotypes.

332 The different detritus morphotypes showed high concentrations of particles in the surface, especially during the 333 export events (Fig. 5, S7). They shared similar temporal dynamics primarily in the surface layer: FP, BPP, BDP, 334 SDP, and SPP decreased exponentially between 0 and 150 m. While FB, BPP and SPP decreased slowly throughout 335 the water column in the mesopelagic layers, BDP and SDP increased gradually between 400-600 m and then 336 decreased again (Fig. S7). BDP and SDP presented two discernable plumes during the two delineated export events, 337 reaching 2000 m with significant concentrations all along the plumes (Fig. 6a,d, S6). Other morphotypes such as FP and SPP were sometimes present in deeper layers but with low concentrations. In the deeper mesopelagic, only 338 339 SDP showed no decrease with depth (Fig. S7).

SPP were most abundant across the different periods (Fig. S7). For the outside-between mask, these particles constituted 28% within the 0-100 m range. In events 1 and 2, their presence increased up to 50-60% within the 0-342 50 m range (Fig. S7). However, this percentage notably declined between 50-100 m for events 1 and 2 with values dropping to 25% below 100 m. It further decreased between 100-150 m outside of these events, 18% below 150 m 344 (Fig. S7). BPP and FP also exhibited high concentrations within the upper 100 m where they were primarily located.





345 Even though BDP and SDP were the least preponderant classes in the first 100 m, they dominated deeper layers 346 compared to clusters BPP, SPP, and FP which were found almost exclusively in the surface layer. Their proportions were more than 20% for events 1 and 2 and 15% outside of these export events in the first 100 m. Concentrations 347 348 of small, dark, and compact marine snow decreased until 200 m and then increased until 1000 m, while big, dark, and compact particles decreased until 400-450 m for all masks and increased afterward (Fig. S7). Small compact 349 350 particles showed a mean proportion of more than 40% for both events and 28% for the period outside of those (Fig S7). Throughout the observation period, the vertical attenuation of dark, compact, and small particles was the 351 352 lowest of all marine snow categories with visibly more dark dense morphotypes in deep waters for all periods, 353 while the highest vertical attenuation amongst all marine snow types was observed for the BPP cluster.

354 3.5 Lagrangian diagnostics

To determine the optimal advective time scale for the different particle sizes, we correlated both MiP and MaP abundance in the first 100 m with the Lagrangian chl-a (chlorophyll in the moving water mass) for the different advective times (from 0-45 days). The highest correlation was determined for t=15 days (Fig. S8). Chl-a and BBP POC were positively correlated with MiP in the first 100 m (Fig. S9). While MaP showed a low correlation with chl-a. As for the different morphotypes, FP, SDP, and SPP were significantly correlated with chl-a while no significant correlation was observed with BDP and BPP. POC flux, MiP, and MaP abundances were also significantly correlated with the Lagrangian vorticity and divergence for an advective time scale of 15 days.

362 4. Discussion

363 4.1 Cold tongue and TIW related equatorial upwelling dynamics

The equatorial Atlantic follows a pronounced seasonal cycle in upwelling activity, forced by the seasonal winds and the meridional migration of the intertropical convergence zone (Brandt et al., 2023), which translates into a respective cycle of productivity (Grodsky et al. 2008) and a slight seasonality in carbon export (Fischer et al., 2000; Wefer & Fischer, 1993).

368 Here, we use a combination of satellite data analysis and in situ biogeochemical and image-based measurements 369 from a BGC-Argo / UVP float to further our understanding of equatorial Atlantic biological pump dynamics. We 370 observed relatively cool SST between August and October corresponding to the occurrence of the Atlantic Cold Tongue (ACT; Brandt et al., 2011), and during boreal winter in December and February corresponding to a 371 372 secondary cooling period as was reported by Jouanno et al. (2011) and Okumura & Xie (2006). Seasonal cooling 373 events are largely linked to diapycnal heat flux out of the mixed layer into the deeper ocean (Hummels et al., 2013). 374 This heat flux is due to the enhancement of the vertical shear driven by the strength and the direction of the surface 375 current (Jouanno et al., 2011) and the eastward Equatorial Undercurrent (EUC) at the thermocline level (Hummels 376 et al., 2013). The equatorial Atlantic was warmer than usual at the surface throughout the boreal summer of 2021. 377 This was the result of the occurrence of a strong Atlantic Niño driven by wind and equatorial wave forcings (Lee 378 et al., 2023; Song et al., 2023; Tuchen et al., 2024). The physical processes controlling the downward heat flux out 379 of the mixed layer also control the upward supply of nitrate to the euphotic layer (Radenac et al., 2020). The equatorial Atlantic is a nitrate-limited upwelling regime (Grodsky et al., 2008; Moore et al., 2013) and modeling 380 381 studies showed that in the equatorial Atlantic, the seasonal variations in chl-a are closely linked to the seasonal 382 variability of the nitrate input via upwelling and mixing (Loukos & Mémery, 1999; Radenac et al., 2020). The chl-





383 a blooms that are normally found in the equatorial Atlantic are linked to the upwelling of nitrate-rich thermocline 384 waters during these periods and the diffusive flux of nitrate into the mixed layer through mixing (Longhurst, 1993; Radenac et al., 2020). Likewise, we found that chl-a concentration followed a pronounced semiannual cycle with 385 386 peaks in boreal summer and winter, as also described by Grodsky et al. (2008) and Brandt et al. (2023). During the 387 first peak, from August to October, the thermocline was relatively deep compared to climatology (as a consequence 388 of the presence of the Atlantic Niño), and chl-a levels were likewise relatively low. A shallower nitracline together with a shallower EUC (Tuchen et al., 2024) during the second peak in boreal winter might have favored the growth 389 390 of the phytoplankton assemblage showing anomalously high chl-a levels. These variations with respect to the 391 climatological cycle are in agreement with what was proposed by Grodsky et al. (2008) that the interannual variability of the secondary bloom in boreal winter is as large as those of the primary bloom in boreal summer, 392 393 even though its climatological expression is weaker.

394 Another process affecting local productivity at the equator is intraseasonal TIWs with a 20-50 days period range 395 as indicated by the bandpass-filtered SST and chl-a anomalies. In this study, elevated primary production was 396 located between 10°W-25°W in a region affected by TIWs. Their occurrence strongly suggests that TIWs might 397 influence the biogeochemistry of the equatorial upper-ocean system. On the one hand, TIWs are associated with 398 meridional currents at the equator modulating the boundary of the Atlantic cold tongue eventually resulting in local 399 variations of SST and chl-a. On the other hand, TIWs are associated with phases of enhanced mixing (Foltz et al., 400 2020; Heukamp et al., 2022; Inoue et al., 2019; Moum et al., 2009) or front generation (Warner et al., 2018) leading 401 to upward nutrient supply. It has been suggested that TIWs could enhance upper-ocean fertilization by promoting 402 local nitrate upwelling alleviating the nitrate depletion which usually affects this region (Radenac et al., 2020; 403 Sherman et al., 2022). Enhanced chlorophyll concentration has been associated with TIWs suggesting that TIWs 404 drive intraseasonal chl-a variability (Grodsky et al., 2008; Menkes et al., 2002; Shi & Wang, 2021). Pronounced 405 positive and negative anomalies in bandpass-filtered chl-a data were anti-correlated with anomalies in bandpass-406 filtered positive SST anomalies. The SST anomalies were moderate during the secondary bloom in boreal winter, accompanied by a shallower thermocline. However, during that period, a pronounced chl-a bloom was observed 407 408 together with the largest bandpass-filtered chl-a anomalies.

In brief, the development of the cold tongue during boreal summer, the secondary cooling during boreal winter, and the presence of TIWs in the equatorial Atlantic exert major controls on the surface ocean hydrographic characteristics and biogeochemistry on intraseasonal to seasonal time scales. We suggest that the combination of seasonal thermocline upwelling and TIWs was responsible for the observed enhanced chl-a signals indicating enhanced variability of primary productivity. Therefore, we can examine their impact on particulate matter build up and export.

415 **4.2** Upwelling events translate into size-differentiated enhanced export from the mixed layer

The timing of the two upwelling events which lead to chl-a accumulation is consistent with the objective detection of two peaks in the MaP concentration. Both MiP and MaP in top 100 m are correlated to the in situ chl-a biomass suggesting that the primary producers provided the elemental particles for the two size classes of marine snow aggregates. Stronger correlation with MiP than with MaP may indicate that MaP are formed with a delay through the transformation of MiP by aggregation. This is also supported by Lagrangian chl-a which is more correlated





- 421 with MiP and MaP (for the same advective time scale of 10 to 15 days) than with concomitant in situ chl-a biomass.
- 422 This time scale is consistent with particle aggregation by coagulation of phytoplankton cells followed by the export
- 423 of aggregates (Burd & Jackson, 2009; Jackson, 1990). Correlation between Lagrangian chl-a and MiP emphasizes
- 424 that MiP are also built up with time.
- 425 More comprehensive understanding of pelagic functioning can arise from the identification of marine snow morphotypes (Trudnowska et al., 2021). Fiber Particles (FP), Small Dense particles (SDP), and Small Porous 426 427 Particles (SPP) in the epipelagial were significantly correlated with chl-a while no significant correlation was 428 observed for BDP and BPP. This means that both fiber and porous aggregates might be of phytoplanktonic origin. 429 Elongated or porous particles in the surface layer, for example, can result from phytoplankton colonies such as 430 diatom chains or Trichodesmium colonies (Dupouy et al., 2018; Villareal et al., 2011) (Fig. S10). These diatoms were mostly detected during event 1 in our study, their presence increases in conditions of high export systems 431 432 (Henson et al., 2019). Porous aggregates might be associated with the accumulation of phytoplankton biomass. 433 When the bloom is massive enough to enhance aggregation, small porous aggregates are precursors of bigger ones. 434 As for dense particles, they could be potential fecal pellets produced by zooplankton's feeding as generally found 435 in other studies (Stemmann & Boss, 2012; Trudnowska et al., 2021).
- All morphotypes, particle size classes and POC flux were significantly correlated with Lagrangian vorticity and divergence highlighting that physical dynamics of the upper ocean (such as up- and downwelling) leading to primary production were the primary control in particle production and transformations. In their paper, Siegel et al. (2024) found that turbulence levels close to the surface tend to favor smaller particle sizes and increase fragmentation while turbulence near the base of the mixed layer encourages coagulation and the formation of larger particles.

442 POC production is associated with phytoplankton production which ultimately influences the export flux. To 443 investigate the ratio of POC flux leaving the euphotic zone, we calculated the export efficiency ratio at 100 m 444 during and outside of the events. The export efficiency (e-ratio) was 6-7% and fell within the global average e-ratio 445 range (Bam et al., 2023 and references within). These values suggest that strong remineralization occurs in surface 446 waters, aligning with existing literature (Clements et al., 2022). The same e-ratio during and outside of events 447 highlights the stability of the export efficiency of the equatorial system. One of the hypotheses explaining this 448 stability is the distribution and contribution of the morphotypes during and outside of export events. During and 449 before export events, all five morphotypes were detected, with proportions varying with depth. This suggests that 450 within our observation period, the equatorial region, during or before export events, possesses a similar 451 phytoplanktonic bloom behavior leading to the same marine snow morphotypes which might explain the similar 452 behavior of the biological pump. This is in contrast with what was observed for the Arctic system, where two 453 successive blooms of different nature occur and are associated with different morphotypes. The first bloom was an 454 ice edge bloom and was dominated by diatoms, while the second was ice free and was associated with the presence 455 of Phaeocystis leading to agglomerated morphotypes and their slow settling compared to the first bloom (Trudnowska et al., 2021). 456

Another hypothesis for the stability of the system might be related to the tight coupling between primary production
 and export. In this study, the lag between PP and particle production was estimated to be 10-15 days, corresponding





459 to a similarly short lag determined by Henson et al. (2015) usually found in upwelling regions. This lag increases 460 with the increase of seasonality and also affects the seasonality of the eeff (Henson et al., 2015). In our case, the 461 same eeff highlights the low seasonality of the carbon pump in the equatorial system: producers and grazers are 462 tightly coupled due to the low seasonality in PP and export (Owens et al., 2015). This coupling might be due to the 463 combination of euphotic-zone irradiance and the supply of nutrients: strong light penetration combined with the 464 energetic intraseasonal variability of the system bringing nutrients to the surface (Menkes et al., 2002), allows producers to be present all year long in the surface layer. Further studies on the dynamics and composition of 465 466 detrital particles in bloom situations, in combination with planktonic measurements, are necessary to understand surface dynamics of particle formation and export. 467

468 **4.3 Deep particle sequestration is driven by compact particles**

469 Particle production within the upper 100 m led to the formation of sinking plumes reaching down to 2000 m of 470 depth. Although particle concentrations were higher during export events, the vertical carbon flux, within and 471 outside the plumes followed the general asymptotic shape characteristic of particle flux observations, with rapid 472 attenuation in the surface layer transitioning to a more gradual decrease in the bathypelagic layer. This was also 473 true for the MiP and MaP abundances. More likely, the observed general decrease in small and big particles is 474 driven by biological processes such as degradation and aggregation. Yool et al. (2013), using a biogeochemical 475 model, attributed the flux of particles at deep depths of the ocean to MaPs. However, Kiko et al. (2017) found an 476 abundance of MiPs in the bathypelagic zone that can be observed down to the sea floor. They suggest that shedding 477 and other disaggregation processes might result in a more effective export of particulate matter, both actively and 478 passively. We suggest that their presence in the meso- and bathypelagic layer highlights both their important roles 479 in contributing to the flux. The difference in flux amplitude inside versus outside of the plumes, along with the 480 higher particle concentration within the plumes, suggests a seasonal pulse in flux to the deep sea, as previously 481 described by Beaulieu (2002). This rapid and deep flux is mainly associated with bloom events, consistent with 482 earlier observations of flux events reaching depths of up to 4000 m (Beaulieu, 2002; Kiko et al., 2017; Lampitt et 483 al., 1993).

484 We combined the quantitative analysis of particle mass distribution with particle image analysis to investigate the nature of particles exported to deeper layers. In this study, SDP were more deeply exported compared to other 485 486 morphotypes, indicating that most of the MaP abundance found at depth is dominated by small dense particles. 487 This trend toward more circular and less elongated aggregates with increasing depth confirms prior research 488 (Drago, 2023; Trudnowska et al., 2021; Accardo et al., submitted). SDP vertical profiles also showed a particle 489 maximum between 450 and 800 m as found by Kiko et al. (2017) and Siegel et al. (2024), unlike the rest of the 490 morphotypes which attenuated with depth. The observed increase in small particles is more likely driven by diel 491 vertical migrations of zooplankton that actively exports organic material to depth (Hidaka et al., 2001; Turner, 492 2015). This can be confirmed by the increase of zooplankton for all periods between 300-600 m (Fig. S11) 493 coinciding with the depth of increase of dense particles and the upper limit of zooplankton migration depth 494 extracted from shipboard ADCP data (shown in Fig. S11) and the range mentioned in Kiko et al., (2017) and 495 Bianchi & Mislan, (2016). Kiko et al. (2017) also found a particle maximum between 300 and 600 m in the 496 equatorial Atlantic and attributed it to migrating zooplankton. Food ingested near the surface is carried downward 497 in the guts of migrating zooplankton to be egested, eaten by consumers of zooplankton, or metabolized at depth





(Packard & Gómez, 2013). Model studies suggest that zooplankton diel vertical migration might account for 10-30% of the total vertical flux of carbon downward from epipelagic layers (Bianchi et al., 2013), enhancing the efficiency of carbon export (Gorgues et al., 2019) through the generation of fecal pellets which can be incorporated in marine snow. Kiko et al. (2020) found that gut flux and mortality might make up about 30-40% of particulate matter supply to the 300-600 m depth layer in the eastern tropical North Atlantic and that the amount of carbon supplied via these mechanisms could suffice to generate a flux and particle increase.

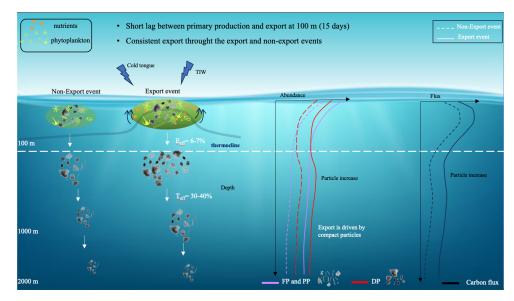
504 Because our study includes periods of both high and low export, we aimed to assess the flux attenuation rate by calculating the transfer efficiency for different periods. The transfer efficiency was estimated using flux at depths 505 of 100 m and 1000 m. Although our export reached depths of 2000 m, we selected the 1000 m layer due to the 506 507 relatively small reduction in POC flux with increasing depth, as noted by Francois et al. (2002). Teff values obtained 508 in our study indicate a high efficiency of the biological pump with up to 40% of the organic material exported at 509 100 m also reaching 1000 m, regardless of the conditions. This means that despite seasonal variation in primary production and carbon flux during and outside of export events, the biological pump exhibits a consistent response 510 in the equatorial region, rendering it a predictable system. The b values calculated (around 0.5) show a low 511 attenuation rate of the computed POC flux, suggesting that part of the particulate matter exported at the equator 512 513 and undergoes little further remineralization at mesopelagic depths (Henson et al., 2015; Omand et al., 2015). 514 Global studies showcased the seasonal and regional variability in the exponent b and showed values around 0.7 in 515 Guidi et al, (2015) and 0.6 in Henson et al., (2012) for the tropical equatorial region. The consistent low e-ratio associated with high T_{eff} aligns with the pattern proposed by Guidi et al. (2015) and Henson et al., (2012). This 516 517 means that deeper particle injection and rapid sinking result in longer carbon sequestration as the time a given water 518 parcel needs to travel from the ocean interior to the surface increases with depth.

519 For the first time, we characterized the distribution of particles within an export plume, and offered a morphological 520 description of exported particles using in situ imaging. The comparisons made with previous studies for the e-ratio 521 and the transfer efficiency show that opting for the plume method yields more accurate results and a more

522 comprehensive understanding of the fate of particles along their progression into deeper layers (Table S1).







523

Figure 6: Illustrative example of the particle export system in the Atlantic equatorial region during export and non export events. FP: fiber particles, PP: porous particles, DP: dense particles. Teff: Transfer efficiency, Eeff: Export
 efficiency, TIW: Tropical instability Wave.

527 5 Conclusion

528 The integration of the UVP on an Argo float has allowed us to study the temporal variability and the dynamics of 529 the BCP. Our study follows the particle dynamics along the water column in the equatorial Atlantic region between 530 July 2021 and March 2022 including the strong 2021 Atlantic Niño event, using the plume method and a novel 531 BGC-Argo/UVP6 dataset. Ocean dynamics in the equatorial system exhibit a seasonal cycle with a decrease in 532 temperature during boreal summer and winter leading to the presence of two distinct blooms. These blooms are 533 characterized by significant export events reaching depths of 2000 m. The production and export of carbon during 534 that year was dampened because of the strong Atlantic Niño event during boreal summer 2021. Detritus were 535 classified into five distinct morphotypes based on morphological variables. In surface waters, marine snow is 536 dominated by porous aggregates and fibers while deeper layers primarily receive big and small dense particles 537 during export events. Unlike most of the morphotypes decreasing with depth, dense particles show an increase 538 between 300-600 m. Zooplankton diel vertical migration might play a role in the generation of a particle maximum at intermediate layers consisting of the small dense cluster. The equatorial region acts as a stable export system 539 540 throughout all periods observed, with an export efficiency steadily ranging between 6-7% probably due to the short 541 lag between the primary production and the export and the same morphotype composition along the year. Regardless of the initial conditions, 30-40% of the flux at 100 m is exported to 1000 m. Such consistency highlights 542 543 the equilibrium inherent in the equatorial region's carbon dynamics along the float trajectory during this special 544 event, providing further context to the observed patterns of carbon and particle export. Moreover, it underscores 545 the necessity for additional observations to ascertain whether the system is truly stable over the long term. This 546 study contributes to a deeper understanding of the intricacies of carbon cycling in equatorial waters using 547 autonomous vehicle-derived estimates of particle fluxes. By elucidating the role of export events and different particle morphotypes, we underscore the significance of these factors in shaping the equatorial biological pump. 548





- 549 The successful combination of the UVP6 with other float sensors and the development of a continuous monitoring
- 550 strategy will provide insights that were previously unattainable with sparse and temporally limited shipboard and
- 551 moored sediment trap observations.

552 6 Code availability

553 The codes used post-data treatment are available upon request to the lead author.

554 7 Data availability

NOAA 555 The sea surface temperature data is available on the website at: https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.htm. Float data are available at https://argo.ucsd.edu. 556 Data used in this manuscript for the carbon flux and particle concentrations are available online using the following 557 558 DOI: 10.5281/zenodo.14007570. Further data can be made available by the authors upon request.

559 8 Author contribution

- 560 JH, RK, and LS developed the study's concept. RK, LS, JH, FPT, PB, and AB contributed to data acquisition; RK,
- LS, JH, PB, AA, AB, and FPT contributed substantially to the data analysis; JH wrote the initial version of the
- 562 paper. All authors contributed substantially to drafting the manuscript; All authors approved the final submitted 563 manuscript.
- 564 9 Competing interests
- 565 The authors declare that they have no conflict of interest.

566 9 Acknowledgments

567 The study was supported by EU H2020 under grant agreement 817578 TRIATLAS project. RK acknowledges

568 support via a Make Our Planet Great Again grant from the French National Research Agency (ANR) within the

569 Programme d'Investissements d'Avenir #ANR-19-MPGA-0012 and funding from the Heisenberg Programme of

- 570 the German Science Foundation #KI 1387/5-1. We thank the crews, scientists, and technicians involved in the
- 571 deployment and recovery of the Argo float during RV Sonne cruise SO284 and PIRATA FR32 cruise with RV
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