



Seasonal flux patterns and carbon transport from low oxygen eddies at the Cape Verde Ocean Observatory: lessons learned from a time series sediment trap study (2009-2016)

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15 **Abstract.** Mesoscale eddies are abundant in the eastern tropical North Atlantic and can form an oasis for phytoplankton growth due to local enrichment of nutrients in an otherwise oligotrophic ocean. It is not clear, whether these eddies can efficiently transfer organic carbon and other flux components to depth and if they are important for the marine carbon budget. Due to their transient and regionally restricted nature, measurements of eddies' contribution to bathypelagic particle flux are difficult to obtain. The rare observations of export flux associated with low oxygen eddies have suggested efficient export from the surface to the deep ocean, indicating that organic carbon flux attenuation might be low. Here we report on particle flux dynamics north of the Cape Verde Islands at the oligotrophic Cape Verde Ocean Observatory (CVOO, approx. 17°35' N/ 24°15'W). This region is a corridor for eddies and low-oxygen eddies regularly passing the position of CVOO between 2009 and 2016, while we collected biogenic and lithogenic particle flux with sediment traps moored at ca. 1 and 3 km water depth. Overall, we observed quite consistent sine-wave flux patterns during the passages of low oxygen eddies in 20 the winters of 2010, 2012 and 2016. We found flux increases in 3 km depth in October-November when the eddies approached CVOO and distinct flux peaks in February-March, clearly exceeding low oligotrophic background fluxes in winter 2011 and showing an enhanced particle flux seasonality. During spring, we observed a stepwise flux decrease leading to summer flux minima. The flux pattern of biogenic silicate (BSi) shows a stronger



30 seasonality compared to organic carbon. Additionally, the deep fluxes of total mass show an unusually higher
seasonality compared to the 1 km traps. We assume that BSi and organic carbon/lithogenics had different sources
within the eddies. BSi-rich particles may originate at the eddy boundaries where large diatom aggregates are
formed due to strong shear, resulting in gravitational settling and, additionally, in an active local downward
transport. Organic carbon associated with the lithogenic material is assumed to originate from the interior of eddies
or from mixed sources both constituting smaller, dust-ballasted particles. Our findings suggest that the regularly
35 passing low-oxygen Anticyclonic Modewater Eddies (ACME) at CVOO repeatedly release characteristic flux
signals to the bathypelagic in the winter-spring season far above the oligotrophic background fluxes and sequester
higher organic carbon than expected for oligotrophic settings. However, the reasons for a lower carbon flux
attenuation below ACMEs remain elusive.

1. Introduction

40 The eastern tropical North Atlantic hosts one of the major Oxygen Minimum Zones (OMZ) of the world oceans
(Karstensen et al. 2008; Brandt et al., 2015). The specific oxygen consumption and ventilation pattern creates two
oxygen minima in the eastern tropical North Atlantic, the shallow one at about 80 m depth mostly associated with
regional processes, and the deep one at about 450 m water depth (minimal oxygen about $40 \mu\text{mol kg}^{-1}$) associated
with the gyre scale ventilation (e.g. Karstensen et al. 2008, Fiedler et al., 2016; Brandt et al. 2015). Most energetic
45 flow features in the region are the boundary current system (Mittelstaedt, 1991; Brandt et al., 2015) and, at a local
scale, westwards propagating mesoscale eddies (e.g. Schütte et al., 2016a; Pietri and Karstensen, 2018). The two
features are connected as the mesoscale eddies spin off instabilities of the boundary current and transport water of
coastal origin offshore, with elevated nutrients and high organic carbon. The eddy origin in the Canary Current-
Eastern Boundary Upwelling Ecosystem (CC-EBUE) can be traced back to certain 'hot spots' for eddy formation,
50 one of them at Cape Vert (Senegal) where anticyclones are formed in summer and propagate westward, reaching
the Cape Verde Ocean Observatory (CVOO) site about half a year later, in winter (Fig. 1; Schütte et al., 2016a;
Karstensen et al., 2015). The eddies start with high nutrient load from the coastal upwelling while, en route,
dynamical processes support local upwelling and high productivity (Karstensen et al., 2017; Fielder et al. 2016).
The combination of high biomass, high respiration of organic matter, and the physical isolation of the eddy core
55 water masses leads to low oxygen concentration in the eddies where even suboxic conditions ($\text{O}_2 < 1 \mu\text{mol kg}^{-1}$)
have been observed at very shallow depth, just below the base of the mixed layer (Karstensen et al., 2015; Schütte
et al., 2016b).



Lowest oxygen content in mesoscale eddies in the Eastern Tropical North Atlantic have been found in Anticyclonic Modewater Eddies (ACME). These eddies can have a very isolated core related to a velocity maximum at about
60 70 to 100 m depth and the low oxygen content is found just below the mixed layer (Karstensen et al., 2015, 2017). In parallel, intense upwelling of nutrients into the euphotic zone have been reported and attributed to different concepts such as sub-mesoscale shear instabilities (Karstensen et al., 2017) or eddy-wind interaction and a resulting Ekman transport divergence (McGillicuddy et al., 2007). Dedicated surveys of ACMEs revealed rather unique ecosystem responses compared with the surrounding oligotrophic region. High phytoplankton and particle
65 concentrations, high carbon degradation and specific nitrogen cycles have been reported (Fiedler et al. 2016; Löscher et al., 2015; Grundle et al. 2017). Additionally, due to the very low oxygen availability, the diurnal migration cycle of zooplankton is for some species severely limited (e.g. Hauss et al., 2016), while species with high oxygen tolerance, e.g. the polychaete *Poebobius*, profit from the high particle flux even in the low oxygen core of the eddies (Christiansen et al. 2018).

70 For the OMZ in the eastern tropical Atlantic, it is assumed that organic carbon attenuation of larger particles in the water column is reduced, thereby increasing the efficiency of the biological carbon pump (Rasse and Dall’Olmo, 2019). In the OMZs of the Pacific Ocean and the Arabian Sea, low carbon flux attenuation has been suggested in suboxic waters at depths between 100 and 1000 m (Weber and Bianchi, 2020). However, the role of mesoscale eddies for carbon export and deep ocean carbon sequestration is still largely unexplored (see review of Benitez-
75 Nelson and McGillicuddy, 2008) and therefore not reliably resolved in global carbon cycling models (e.g. Omand et al., 2015; Shih et al., 2015).

Sediment trap flux studies in the meso- and bathypelagic associated with eddies are rare (e.g. E-Flux and EDDIES Projects: see review in Benitez-Nelson, and McGillicuddy, 2008; CVOO: Fischer et al., 2016; Romero et al., 2016) and episodic pulses of organic matter sedimentation from eddies may be largely undersampled or even missed.
80 Some studies show that carbon export was higher at the eddy edges and organic matter export occurred partly via sedimentation of large diatom frustules and zooplankton fecal pellets (Shih et al. 2015). Other studies of organic carbon export associated with eddies did not reveal higher organic carbon fluxes compared to the surrounding oligotrophic waters (e.g. Buesseler et al., 2008). Two to three fold higher biogenic silica (BSi) fluxes compared to the oligotrophic surroundings (e.g. Maiti et al., 2008; Rii et al., 2008; Verdeny et al., 2008) have been observed
85 within eddies (e.g. eddy *OPAL*). Most of these studies, however, did not differentiate between the type of eddies investigated. Benitez-Nelson and McGillicuddy (2008) pointed out that a higher phytoplankton biomass produced within eddy blooms may not necessarily result in increasing particle export and sedimentation. Instead, microzooplankton grazing (e.g. by ciliates and dinoflagellates) may be stimulated, resulting in a strong upper ocean recycling and a release of suspended and dissolved materials at shallow depths within eddies. Oxygen to total



90 nitrate stoichiometry in an ACME north of Cape Verde was found to be about twice as high (16) compared with
the surrounding waters (8.1) or the classical Redfield ratio (Redfield et al. 1963) and explained by local (mesoscale)
upper layer nitrate recycling (Karstensen et al., 2017).
Site CVOO is north of Sao Vicente (Cape Verde, approx. 17°35'N/ 24°15'W), located within one of the eddy
corridors from the west African coast at ca. 15-20°N (Schütte et al. 2016a, Fig. 1), is ideal to investigate particle
95 fluxes and deep carbon sequestration from different types of eddies characterized by variable oxygen conditions
in the epi- and mesopelagic. A great advantage are continuous oceanographic studies and surveys at this site (e.g.
Karstensen et al., 2015; Löscher et al., 2015; Schütte et al., 2016a, Pietri and Karstensen, 2018) as well as
synchronous time-series measurements of oxygen concentrations in the epi- and mesopelagic which aid in the
identification of the passing of low oxygen eddies. A detailed description of the biogeochemical responses in terms
100 of export flux in winter 2010 from an ACME with a hypoxic-anoxic core was provided by Fischer et al. (2016a).
This study discussed the impact of an hypoxic-anoxic eddy on bulk export flux, stable nitrogen isotopes, major
planktonic groups (diatoms, coccolithophores, planktonic foraminifera) and biomarkers from ca. 1300 and 3400
m depth. The most striking observation was a 2-3 fold higher organic carbon flux in the 1 km trap compared to
oligotrophic waters and a high seasonality (Berger und Wefer, 1990). Additionally, we found a massive increase
105 of organic matter flux with increasing depth, pointing to particle flux focusing (Fischer et al., 2016).
The aim of this study is to investigate the transfer of biogenic and lithogenic particles (Saharan dust) from different
types of eddies to sequestration depths at about 1 and 3 km water depth against oligotrophic background conditions.
We use a multi-year sediment trap record (2009-2016, with interruptions; Fig. 1; Table 1) of particle fluxes at the
oligotrophic site CVOO. Our emphasis is on the fall-winter flux peaks when different low oxygen eddies pass
110 through the study site and we compare these fluxes to oligotrophic, low-seasonality conditions. Data discussed are
partly based on earlier investigations from deployments CVOO-3 and 4 (2009-2012; Fischer et al., 2016, Romero
et al., 2016). We also use the deeper trap flux data to unravel organic carbon transfer to the deep CVOO site within
passing eddies and extend the flux record to 2016.

2. Materials and Methods

115 2.1. Cape Verde Ocean Observatory (CVOO)

The study site CVOO in the eastern tropical North Atlantic (approx. 17°35'N/ 24°15'W; Fig. 1) is located about
800 km off the African coast and about 80 km north of the island of São Vicente, Cape Verde (Fig. 1a). It consists



of a steel wire mooring of approx. 3600 m length, first deployed in 2006 and maintained continuously since then. The mooring is equipped with several temperature and salinity sensors at multiple depth, water current profiler
120 and single point current meters (also in conjunction with the sediment traps), and Aanderaa AADI optodes (Type 3830) oxygen sensors, typically at about 50 and 180 m depth. The optode calibration was refined over the years but followed essentially two strategies – a laboratory calibration with zero and saturated oxygen concentrations and a calibration against reference points acquired by mounting the logger to a CTD rosette and comparing the logger readings with calibrated (Winkler titration) CTD oxygen readings (see e.g. Hahn et al. 2014). For the
125 deployment period 2015 to 2016 a programming error for the logger occurred and only a record of two weeks was acquired. However, the temperature and salinity sensors were operational and were used to estimate mesoscale eddy occurrence, at least in case of the ACMEs, which are characterized by low salinity and cold waters compared to the surrounding waters.

Except for the periods when mesoscale eddies cross the CVOO site, the currents are generally sluggish as expected
130 for a site in the OMZ region. Fischer et al. (2016) reported ca. 2-6 cm s⁻¹ for about 600 m depth and around 2 cm s⁻¹ for the deep water column. As a consequence, the mooring, which has its head buoy at about 40 m depth, was mostly in an upright position and catchment was unaffected by mooring tilt. A detailed description is given by Fischer et al. (2016). Oceanography and biogeochemistry of the area around CVOO including the passages of different types of eddies is outlined elsewhere (Karstensen et al. 2015, 2017, Schütte et al. 2016a).

135 2.2. Sediment trap collections

Particle fluxes were collected with cone-shaped and large-aperture sediment traps (0.5 m²; Kiel type, Kremling et al., 1996) in ca. 1300 m (afterward 1 km) and in ca. 3000-3500 m water depths (afterward 3 km; Table 1), respectively. We used samples collected on roughly monthly intervals (Table 1). The traps were equipped with 20
140 cups, which were poisoned with HgCl₂ before and after deployment by addition of 1 mL of a saturated HgCl₂ solution in distilled water at 20°C per 100 ml. Pure NaCl was used to increase the density of water in the cups prior to the deployments (final salinity was 40‰). Large swimmers were removed manually and/or by filtering carefully through a 1 mm sieve. All fluxes therefore refer to the major size fraction of <1 mm. Samples were wet-split in the home laboratory using a rotating McLANE wet splitter and freeze-dried. Additional methods information is given elsewhere (Fischer and Wefer, 1991).

145 Deep ocean sediment traps usually collect material from a rather large catchment area, typically around 100 km in diameter or wider, depending on particle settling rates and ocean currents (Siegel and Deuser, 1997). As ocean currents are generally in a western and southwestern direction, we used a catchment area for environmental data



from GIOVANNI (<https://giovanni.gsfc.nasa.gov/giovanni/#service=TmAvMp&starttime=&endtime=>) for the surface ocean located to the NE of CVOO (17°30'-18°30' N / 23-24° W; Fig. 1a). Calculated mean seasonal and annual fluxes allow a better comparison among seasons and years to identify interannual variability. Seasons are defined using the dates of opening and closure of the sampling cups closest to the start of the astronomical seasons (March 21, June 21, September 23, December 21). To illustrate and quantify the seasonal variability of particle fluxes, we applied the Seasonality Index (SI) from Berger and Wefer (1990).

2.3. Sample Analysis of Particles

Samples were analyzed using freeze-dried and homogenized material of 1/5 wet splits. The collected material was weighed for total mass and analyzed for organic carbon, total nitrogen, carbonate and biogenic silica. Particulate organic carbon, total nitrogen and calcium carbonate were measured by combustion with a Vario EL III Elemental Analyzer in the CN mode. Carbonate was determined by subtracting organic carbon from total carbon, where the latter was measured by combustion without pre-treatment with 2N HCl. Biogenic opal was determined with a sequential 1M NaOH leaching method according to Müller and Schneider (1993). The precision of the overall method based on replicate analyses is between ± 0.2 and ± 0.4 %. Lithogenic fluxes were calculated from total mass flux by subtracting the flux of carbonate, biogenic opal and two times the flux of organic carbon (Hedges et al. 2002) to approximate organic matter. As there is no river input in the study area, we assume that all non-biogenic (= lithogenic) material was supplied via aeolian transport to site CVOO.

2.4. Diatom fluxes at CVOO (upper traps)

We used 1/125 splits of the original samples. Samples were rinsed with distilled water and prepared for diatom analysis as previously published (see details in Romero et al., 2016; 2017; 2020). Identification and counts of diatom taxa at the species level were done at x1000 magnifications using a Zeiss®Axioscop with phase-contrast illumination (MARUM, University Bremen, Bremen). Counts were carried out on permanent slides of acid cleaned material (Mountex® mounting medium). Depending on valve abundances in each slide, several traverses were examined. Total amount of counted valves per slide ranged between 300 and 600. Two cover slips per sample were scanned in this way. Diatom counts of replicate slides indicate that the analytical error of concentration estimates is 12 %. The counting procedure and definition of counting units for diatoms follows Schrader and Gersonde (1978).



175 The resulting counts yielded abundance of individual diatom taxa as well as daily fluxes of valves per m² d⁻¹ (DF), calculated according to Sancetta and Calvert (1988), as follows:

$$DF = \frac{[N] \times [A/a] \times [V] \times [\text{Split}]}{[\text{days}] \times [D]}$$

where, [N] number of valves, in an area [a], as a fraction of the total area of a petri dish [A] and the dilution volume [V] in ml. This value is multiplied by the sample split [Split], representing the fraction of total material in the trap, and then divided by the number of [days] of sample deployment and the sediment trap collection area [D].
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3. Results

3.1. Seasonal and interannual environmental variability in the CVOO eddy box

SSTs in the box northeast of CVOO (Fig. 1) show a seasonal cycle and varied between about 20.5 and 27.5°C with lowest values occurring in winter and spring (Fig 2a). Highest SSTs occurred during late summer/early fall, where after SSTs decreased rapidly until the turn of the year. Satellite-derived chlorophyll biomass (Fig. 2b) increased with decreasing SSTs and was highest during winter and spring. Modelled dust dry deposition peaked in winter and occurred ca. 1-2 months prior to the chlorophyll maxima (Fig. 2c). The years 2010 and 2011 showed higher SSTs, lower chlorophyll and reduced dust deposition compared to 2012-2016 (Fig. 2). Chlorophyll content was very low and remained below the mean value in winter 2011 and 2010 (oligotrophic conditions, Fig. 1b). During winter 2010, a high chlorophyll eddy approached the trap site CVOO (Fig. 1b, Fischer et al. 2016). During the following winter seasons from 2012 to 2016, chlorophyll was above the mean values (Fig. 1b).
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3.2. Oxygen and salinity time series at CVOO

The oxygen (Fig. 3a) and salinity (Fig. 3b) time series from 2010 to 2016 recorded between 30 and 90 m depth show different scales of variability. Note the time series are aligned with the CVOO 3-7 sediment trap particle sampling in ca. 1 and 3 km depth (Fig. 4; Table 1). For both, oxygen (one instrument only) and salinity (2 to 3 instruments), a seasonal cycle can be seen with highest oxygen and salinity in summer. Lowest oxygen values are found in February 2010, December 2013 and August 2015, and maybe in January 2016, all associated with low salinity signals (Fig. 3b). Low salinities indicate the presence of boundary current waters of South Atlantic Central Water (SACW) origin and are most likely linked to the presence of coherent and isolated eddies from the
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205 Mauritanian-Senegalese coast (Schütte et al. 2016a; Fiedler et al. 2016). The most severe and longest oxygen drawdown, with lowest values reaching almost anoxic conditions, were observed for the entire February 2010, largely overlapping with the collection period of one sampling cup of the CVOO-3 sediment traps (cup #3, Fischer et al., 2016). However, low salinity events were also obtained for January 2011, February to April 2012, August-September 2013, and April to June 2015, which indicate the presence of isolated eddies. Unfortunately, oxygen data were not available for the winter season in 2016 but the relationship to the salinity values (Fig. 3b) suggest that a low-oxygen ACME was passing in winter 2016 as well.

3.3. Time-series of sediment trap particle fluxes

210 Total mass flux was highest during winter at both 1 km and 3 km and reached $>100 \text{ mg m}^{-2} \text{ d}^{-1}$ (Fig. 4). Fluxes started to decrease in spring (except 2011) and reached a minimum in summer. Mass fluxes increased from late summer until fall, sometimes constituting a maximum during fall (e.g. in 2011, lower traps, Fig. 4b). The only winter-spring flux pattern with values below $50 \text{ mg m}^{-2} \text{ d}^{-1}$ was in 2011, observed at both depths. Between summer 2010 and spring 2011, total mass fluxes remained below $25 \text{ mg m}^{-2} \text{ d}^{-1}$ with low seasonal variability. Mean total mass fluxes for the whole time-series were 51 ± 18 and $62 \pm 49 \text{ mg m}^{-2} \text{ d}^{-1}$ for 1 km and 3 km, respectively (Fig. 4).
215 However, this overall increase with depths was mainly driven by the exceptional high mass fluxes to 3 km in 2010 (Fischer et al., 2016). Between 2015 and 2016, total particle fluxes in the upper CVOO-6 trap were above the overall mean of $\sim 51 \text{ mg m}^{-2} \text{ d}^{-1}$, however, the trap malfunctioned and the export flux for the whole deployment period was collected into one cup (Fig. 4).

220 Particle fluxes mostly decreased with increasing depth. During the CVOO-3 deployment (2009-2011), peak mass fluxes at both 1 km and 3 km were highly correlated ($R^2=0.69$, $N=16$, $p\text{-value} < 0.05$). The pattern showed no temporal shifts of flux maxima during winter 2010, the same period collected the flux maxima despite a vertical distance of 2 km between the two traps. This suggests that the material settled faster than 100 m d^{-1} (Fischer et al., 2016). During the deployment CVOO-4 (2011-2012), however, the mass flux peak in winter 2012 was delayed by one cup (26.5 days) when comparing the upper and lower traps (Fig.4) and flux correlations between the two trap
225 depths were weaker, though still statistically significant ($R^2=0.54$; $N=16$; $p\text{-value} < 0.05$). In 2016 (CVOO-7), particle settling velocities $< 100 \text{ m d}^{-1}$ were estimated from February to March due to the temporal shift in mass flux maxima by one cup (28 days, Fig. 4). Nevertheless, overall correlations between the upper and lower mass fluxes (CVOO-7) were high ($R^2=0.81$, $N=13$) and statistically significant ($p\text{-value} < 0.05$).



3.4. Diatom fluxes and composition of the assemblage

230 We here combine new with former diatom data only for the upper traps at the CVOO. In an earlier study, Romero
et al. (2016) published and discussed diatom fluxes from the mooring deployments CVOO-3 and CVOO-4 (Dec
2009-Oct 2012). Here, we add CVOO-7 (Sept 2015-Aug 2016, upper traps; Table 1). Marine diatoms delivered
most of the BSi flux. Silicoflagellates, radiolarians, the dinoflagellate *Actiniscus pentasterias* and land-derived
235 freshwater diatoms and phytoliths were sporadically present. The total diatom flux ranged from 6.2×10^5 to $2.3 \times$
 10^3 valves $\text{m}^{-2} \text{d}^{-1}$ between December 2009 and August 2016 (average = 9.4×10^4 valves $\pm 1.2 \times 10^5$). Diatom
maxima ($>9.4 \times 10^4$ valves $\text{m}^{-2} \text{d}^{-1}$) mainly occurred in winter and fall (Fig. 5c); minor peaks occur in middle spring
2010, middle spring and late summer 2011. Except for this later maximum, summer shows mostly the lowest
diatom fluxes.

The marine diatom community was composed of 118 marine species. The average relative contribution of main
240 diatom species or group of species over the whole trap experiment interval was: *Bogorovia* spp. (12.11%),
Nitzschia interruptestriata (11.64%), *Nitzschia bicapitata* (7.26%), *Nitzschia capuluspalae* (5.15%),
Thalassionema nitzschioides var. *parva* (5.00%) (sum of the average relative contribution of these five species =
41.2%). Accompanying taxa were resting spores (RS) of *Chaetoceros* spp. (3.51%), *Azpeitia tabularis* (3.49%),
Fragilariopsis doliolus (3.19%), *Thalassiosira subtilis* (2.10%), and *Roperia tessellata* (1.90%).

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3.5. Composition of settling particles and flux relationships between upper and lower traps

The overall composition of sinking materials in the upper traps was 2.1-5.9 % of BSi, 3.1-5.7 % organic carbon,
48-68 % of total carbonate and 16-36 % of lithogenic material. Lower traps collections contributed 3.1-6.4 % of
BSi, 3.2-5.7 % of organic carbon, 44-58 % of carbonate and 29-40 % of lithogenic material to total mass flux.
250 Excluding the extreme winter ACME-2010 (Fischer et al., 2016), we observe decreasing percentages of BSi and
organic carbon with increasing depth and more or less stable contributions of carbonate and lithogenic materials
to total flux.

Winter C:N ratios were between 8.9 and 10.0 for the upper traps and between 7.1 and 10.4 for the lower traps
(excluding the year 2010, Table 3), respectively, thus being in the range of partly degraded phytodetritus collected
255 in the deep ocean (Schneider et al., 2003). However, during the ACME 2010, winter C:N ratios were 13.8 for the
upper and 15.5 for the lower traps, respectively (Table 3). Winter flux compositions varied among years and
oceanographic conditions (Fig. 6). Only organic carbon content remains rather constant, despite different total



fluxes. Under oligotrophic conditions in winter 2011 (Figs. 1b, 2), lithogenic and BSi contributions were low, whereas the percentage of carbonate was high at both trap depths. Particle flux compositions in winters 2010, 2012 and 2016 during low-oxygen ACME passages (Fig. 3) showed comparable values for the upper trap collections (Fig. 6). Lithogenic content was generally high (around 1/3 of the total flux), except during oligotrophic conditions in winter 2011 (Fig. 6). Winters 2012 and 2016 showed almost similar total fluxes (98 and 96 mg m⁻² d⁻¹, respectively) and flux constituents.

Flux components of both trap depths showed no correlation during winter 2011 under oligotrophic conditions (Table 2). However, winter 2010 showed a high correlation coefficient (above 99 % c.l.) between organic carbon and lithogenic fluxes at both trap depths (Table 2), while none of the other flux components correlated. In contrast, a relatively high R² between organic carbon and lithogenic fluxes was observed during winter 2012 for the upper trap, indicating differences between both ACMEs in 2010 and 2012. In winter 2012, the correlations between organic carbon and BSi, carbonate and lithogenic fluxes become weaker with increasing depth.

270 3.6. Seasonal patterns of biogenic and lithogenic fluxes

The seasonal flux pattern for BSi, organic carbon and the lithogenic components are given in Fig. 7 on a Julian day scale. The flux signals from 2010 showed a high seasonality with discrete peaks from January to February (Fig. 7). The deep flux peak from February to March 2010 was even more clear due to flux focusing (Fischer et al. 2016). The year 2012 revealed high fluxes from January to March in the upper trap with a step-like decrease during spring (Fig. 7a). The deeper traps showed higher individual peaks for BSi, organic carbon and the lithogenic fluxes (Fig. 7). When low oxygen eddies approached, particle fluxes increased stepwise starting in fall to values of ca. 100 mg m⁻² d⁻¹ (deep traps, Figs. 4, 7), where after they declined during the turn of the year, and increased again to form a significant eddy-induced flux peak in late winter to early spring (Fig. 7).

4. Discussion

280 Biogeochemical responses in terms of organic carbon fluxes from different types of eddies in oligotrophic oceans are difficult to quantify (e.g. Fischer et al. 2016). In particular, the transfer mechanisms and processes of organic carbon sequestration associated with eddies are still a matter of controversial debate (e.g. Benitez-Nelson and McGillicuddy, 2008). Here, we discuss the flux patterns and seasonality of total fluxes and compositions of exported materials associated with the passages of different eddy types north of the Cape Verde Archipelago at site CVOO (Fig. 1a). We further examine organic carbon flux attenuation in the water column between ca. 1 and



3 km water depth at CVOO in relation to the oxygen availability at epi- and mesopelagic depth within passing eddies.

4.1. Flux patterns and seasonality associated with low oxygen eddies vs oligotrophic background sedimentation at site CVOO

290 Site CVOO is located within a corridor for mesoscale cyclonic (CE) or anticyclonic eddies (including ACME),
originated eastward off the west African coast (Fig. 1). Schütte et al. (2016b) found a large variability in oxygen
consumption between different types of eddies (CE, ACE, ACME) and surface chlorophyll. They allocated this to
(1) differences in the initial conditions in coastal waters where eddies originated, and (2) the degree of isolation as
well as the external forcing (e.g. wind, dust/iron input) occurring en route to site CVOO. As a consequence, one
295 might expect a high variability in the release of particles, seasonality and flux magnitudes derived from different
eddies, all of which are also significantly affected by zooplankton communities (e.g. Hauss et al., 2016; Goldthwait
and Steinberg, 2008).

The seasonal flux pattern influenced by low oxygen eddies that reach CVOO during late fall and winter look quite
consistent (Fig. 7). Total flux often reached values above $100 \text{ mg m}^{-2} \text{ d}^{-1}$ (Figs. 4, 8a, b) and clearly exceeded the
300 typical fluxes characteristic for oligotrophic settings of ca. $50 \text{ mg m}^{-2} \text{ d}^{-1}$ (e.g. Bory et al., 2001, Fischer et al.,
2010; Korte et al., 2017 (site M3)) and showed a low to moderate seasonality (Berger and Wefer, 1990). Fluxes
of BSi and organic carbon were very low in winter 2011 (Fig. 7) matching low chlorophyll values (Figs. 1b, 2).
The entire flux record (Figs. 4, 8), however, suggests that the oligotrophic conditions in winter 2011 is an exception
and the occurrence of low oxygen eddies delivering higher particle fluxes mainly in winter is the regular situation
305 at CVOO. This observation supports statements of an existing eddy corridor occurring north of the Cape Verdes
and that mesoscale eddies seem to be created rather regularly at the coast around summer and reach site CVOO in
late fall to winter (e.g. Karstensen et al., 2015; Schütte et al. 2016a).

Elevated fluxes in winter delivered by the different eddies are not generally correlated to a particular environmental
parameters at CVOO (Fig. 2). In winter 2010, for example SST remained relatively high, chlorophyll and dust
310 deposition were low (Fig. 2), but the resulted output of the ACME in terms of fluxes was high (Fig. 4, 7).
Comparably high fluxes were recorded for the winter ACMEs in 2012 and 2016 (Fig. 4, 7), however, under
different environmental conditions (low SST, high chlorophyll and dust deposition) (Figs. 1b, 2). Typical
oligotrophic fluxes with low seasonality were observed in winter 2011 under environmental forcing similar to that
of the extreme winter 2010-ACME. During winter 2011, however, the oxygen drawdown was less severe than
315 during the other winter seasons (Fig. 3) but salinity was low, suggesting the presence of a coastal eddy (ACME)



around CVOO (Tables 2, 3). The most severe and longest oxygen drawdown (almost anoxia) combined with a salinity low were observed for the entire February 2010 (Fig. 3), largely overlapping with the collection period of one sampling cup of the CVOO-3 sediment traps (cup #3, Fischer et al., 2016). This resulted in clear peaks in all fluxes (except carbonate) during this time interval and a significant increase of fluxes with depth (Fischer et al., 2016), suggesting that an eddy passed directly over the mooring site CVOO. Overall, only winter organic carbon fluxes showed a tendency to increase with satellite chlorophyll (Table 3) but this relationship is statistically not significant.

The deep flux pattern of all components showed more distinct peaks and a higher seasonality (SI = ca. 2.6) during the passages of low oxygen eddies than to the shallower traps (SI = ca. 2.3; Figs. 7, 8). Usually, the upper traps in the open ocean record a higher seasonality (Berger and Wefer, 1990), which is due to a smaller catchment area and a shorter vertical distance for the settling material between production in surface waters and particle transfer to 1 km compared to the deeper traps. In contrast, seasonality is generally lower in the deep traps (3–4 km) due to a larger particle catchment area (Siegel and Deuser, 1997), longer particle descent time, and a higher impact from lateral advection (McCave, 1984).

However, this typical pattern of seasonality with depth is not observed at CVOO (e.g. Fig. 7). This is most probably due to the occurrence of eddies with their different particle transport, a potential subduction of particles at frontal systems (e.g. Boyd et al., 2019) and flux focusing within funnel-like structures (Fischer et al., 2016). The BSi flux pattern of eddies in the upper traps showed a higher seasonality compared to organic carbon and lithogenic fluxes (Fig. 7), the two latter showing a significant correlation (Table 2). This suggests that BSi (mostly from diatoms) and organic carbon together with the non-biogenic components may have different particle sources within the respective eddies. Diatoms are mostly produced at the eddy edges (Shih et al., 2015) due to vertical nutrient supply (Karstensen et al., 2015), where a strong shear and high particle concentrations could result in the formation of large and fast settling diatom aggregates. At these frontal zones, a concentration threshold for diatoms to encounter each other and form aggregates may be reached (Jackson and Kjørboe, 2008). Most of the diatoms at CVOO possess small valves (ca. 10–15 μm) but produced high numbers (Fig. 5c) which could not individually sink at higher rates to form the observed sharp flux peaks (Fig. 7). Larger diatom aggregates, presumably formed at the eddy edges, sink passively (biological gravitational pump, Boyd et al., 2019), although their sinking could be accelerated by active subduction at frontal structures (eddy subduction pump, Boyd et al., 2019) to form a distinct flux signal in the 1 km traps and below.

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4.2. Diatom sedimentation at CVOO affected by eddies

The predominant occurrence of highest diatom flux maxima in winter and fall (Fig. 5) temporally matches the passage of ACMEs over site CVOO. This seasonal pattern suggests that mesoscale eddy impact diatom productivity through two primary processes, namely, (1) pulsed nutrient injections into the sunlit layer, and/or (2) horizontal advection of phytoplankton (Gaubert et al., 2014). Since ACMEs north of the Cape Verde Archipelago are a hotspot of primary productivity (Hauss et al., 2016) with elevated chlorophyll concentrations (Karstensen et al., 2015; Schütte et al., 2016a), and high content of nitrate, phosphate, and silicate in the mixed layer (Fiedler et al., 2016; Karstensen et al., 2017), we favor the scenario of nutrient injection. This promotes diatom productivity under regular, open-ocean oligotrophic conditions and translates into substantially increased productivity in surface waters of the ACME when passing through the CVOO site (Romero et al., 2016).

The seasonal dependence of diatom production on the ACME-associated nutrient delivery results in a strong seasonality of flux occurrence: independent of the year, between ca. 45 and 65 % of the total yearly diatom flux at the CVOO site was captured in intervals shorter than 70 days, leading to a strong seasonality. During episodes of nutrient injections, small diatoms reproduced fast and valves sank quickly after the formation of large diatom aggregates (see chapter above), possibly diminishing the chance of being grazed by meso-zooplankton (Smetacek, 1985). Earlier observations in the low-oxygen Cape Verde ACME in winter 2010 show that meso-zooplankton populations were reduced due to suboxia within ACMEs crossing site CVOO (Fischer et al., 2016) and, hence, grazing pressure was probably reduced (Karstensen et al., 2015; Hauss et al., 2016). The decline of the diatom maxima was likely due to the decrease nutrient availability (mainly dissolved silica) after the ACME moves further west (Fiedler et al., 2016). The diatom flux returned to values typical of the low latitude pelagic area of the oligotrophic northeastern Atlantic Ocean (Mittelstaedt, 1991; Oschlies and Garçon, 1998; Romero et al., 1999) in early spring and summer.

The obvious success of the small-sized diatoms (valve size range = 10-15 μm) during ACME passages possibly lays in their fast growth rates under high-turbulence conditions and the advantage conferred by the small cell size on their efficiency in nutrient uptake (Smetacek, 1985). Although the overall seasonality of total diatom and BSi fluxes broadly matched (winter until mid-spring, Fig. 5), the comparison of major peaks between both parameters showed some leads/lags. This is most evident in winter 2016, when the highest diatom peak occurred between mid-December 2015 and mid-January 2016, while BSi had two peaks: the first between mid-November and mid-December 2015, and the second in March 2016. The temporal difference in the occurrence of peaks of diatoms (microscope counts) and BSi fluxes (chemical analysis) could be related to the temporal contribution of species. The late 2015/early 2016 diatom peak was dominated by species with predominantly valves smaller than 12 μm



in diameter/length, such as *T. nitzschioides* var. *parva*, *N. bicapitata*, *N. capuluspalae* and RS *Chaetoceros*, while diatom with valves larger than 15 μm dominated before and after the main 2016 diatom peak.

380 4.3. Carbon flux attenuation and transport within eddies and under oligotrophic conditions

Studies from OMZ in the Eastern Tropical Atlantic showed that organic carbon flux attenuation of large particles is reduced, thereby increasing the efficiency of the biological carbon pump (Rasse and Dall'Olmo, 2019). However, small particles seem to react differently and show a normal to higher attenuation. The winter 2010-ACME show that organic carbon fluxes increased by more than two-fold with depth due to flux focusing (Fischer et al., 2016; Table 2, Figs. 7, 9). During oligotrophic conditions in winter and spring 2011, however, organic carbon
385 fluxes show a comparable slope to the Martin curve (open-ocean composite) or the log-line (Fig. 9). In winters 2012 and 2016, when other ACMEs reached site CVOO, the deep ocean fluxes clearly exceeded the projected values from the Martin curve (Fig. 9).

Low oxygen values in the epipelagic during the ACME 2012 (Schütte et al., 2016a) might have reduced organic
390 carbon degradation (Fischer et al., 2016). This decreased degradation in the epipelagic, however, would also have caused higher flux to the upper traps in 1 km. This leads to the question of the potential factors which act to reduce organic carbon degradation in the bathypelagic. According to Iversen and Ploug (2010), particle settling rates are critical for carbon flux attenuation and are primarily influenced by ballast content, composition and density of the settling particles (Ploug et al., 2008). A highly ballasted particle stock within eddies, most probably due to high
395 dust dry deposition in winter in this region (Gama et al., 2015), could contribute to lower carbon flux attenuation during eddy passages, also in the deeper water column. On the other hand, an active downward transport of particles at frontal systems, i.e. at the boundaries of these structures, should be considered ('eddy subduction pump', Boyd et al., 2019), thus reducing carbon degradation and leading to higher carbon fluxes above the predicted values (Martin et al., 1987).

400 Estimated carbon fluxes at 100 m (flux below the photic zone) from the deep traps were between ca. 5.5 and 19.5 mg C m^{-2} (winter means), including the oligotrophic background scenario of winter 2011 (ca. 12 $\text{mg C m}^{-2} \text{d}^{-1}$; Fig. 9). The highest value of 19.5 in winter 2012 is about one order of magnitude lower compared to organic carbon fluxes of 190-230 $\text{mg m}^{-2} \text{d}^{-1}$ at 100 m derived from oxygen consumption rates in March 2014 at site CVOO (Fiedler et al., 2016). This discrepancy may be due to a strong variability in productivity and export flux between
405 the different eddies (2012 and 2014) or caused by short-term seasonal changes of the oxygen consumption rates. Altogether, carbon fluxes during eddy passages (Fig. 7) seem to indicate that attenuation is reduced between ca. 1



and 3 km water depth (Fig. 9). This cannot be linked to the OMZ, which occur between ca. 75 and 400 m water depth (Schütte et al., 2016a). The increased fluxes compared to the background situations (low biomass combined with less severe oxygen drawdown; Fig. 1b, 2, 3) may be due to a combination of higher production due to local eddy upwelling, higher aggregate formation due to the concentration of small diatoms at the eddy boundaries (Shih et al., 2015), and low oxygen concentrations, limiting degradation of the organic matter. Whether the latter is due to reduced zooplankton grazing or less microbial degradation or both needs further exploration of particle formation and fluxes, and degradation in the epi- and mesopelagic.

Except during the extreme winter ACME 2010, the molar C:N ratios were between ca. 9 and 10, falling in the range for degraded marine phytoplankton detritus (Schneider et al., 2003; Fischer et al., 2010) (Table 3). Only in winter 2016, a mean value of 7.1 points to rather fresh material sinking to the 3 km trap (Table 3). Under oligotrophic conditions in winter 2011, C:N ratios were higher (10-10.4) than during the eddies in 2012 (8.7-8.9) and 2016 (7-9). This could point to a higher degradation due to zooplankton grazing in winter 2011. However, during the extreme winter 2010-ACME, Fischer et al. (2016) obtained mean winter C:N ratios of 13.5 and 15.7 at 1 and 3 km depth, respectively, which is far above the classical Redfield Ratio (Redfield et al., 1963) and typical sediment trap values for degraded phytodetritus in the bathypelagic (Schneider et al., 2003; Martin et al., 1987). The high values suggest that the sedimentation of highly degraded zooplankton fecal pellets or very slowly settling organic matter. However, estimated settling rates of particles during the low oxygen ACME in winter 2010 contradicts this scenario (Fischer et al., 2016).

The C:N ratios during the ACME-2010 (CVOO-3, both depths) provided a best fit with a non-linear function, whereas the 2012 data (CVOO-4, both depths) showed a normal linear relationship with a high correlation coefficient (Fig. 10). Investigating the composition of organic matter during the winter ACME-2010, Fischer et al. (2016) argued that high C:N ratios may be best explained by nitrate limitation in the surface layer of the eddy. Nitrogen limitation and recycling within low oxygen ACMEs are also considered (Karstensen et al. 2017; Löscher et al. 2015). Due to flux focusing, C:N ratios increased with depth to 15.7. Individual collection cups provided C:N ratios around even 25 (deep traps; Fischer et al. 2016). Based on the organic carbon composition, we conclude that the conditions prevailing in the surface layer of the eddies in 2010, 2012 and 2016 were different, despite the fact they were characterized as ACMEs (Schütte et al., 2016a) (Table 2). Indeed, the oxygen anomaly in winter 2010 was lower and of longer duration (the entire February 2010 approaching zero) compared to 2012 (Fig. 3; Schütte et al., 2016a), thus suggesting different biogeochemical conditions. However, a relationship between fluxes (e.g. of organic carbon) and the oxygen drawdown and duration of low oxygen conditions due to eddy passages over site CVOO is not observed.



5. Conclusions and Outlook

- 440 A multiyear monitoring of the biogeochemical particle fluxes of passing eddies north of the Cape Verde Islands (site CVOO, oligotrophic setting) revealed the following major findings:
- during eddy passages in the winters of 2010, 2012 and 2016, particle fluxes showed a consistent sinusoidal flux pattern with increasing fluxes in fall, a decrease at the turn of the year and maxima around February-March,
 - BSi showed a stronger seasonal pattern with distinct peaks compared to organic carbon and the lithogenic
 - 445 component. In addition, BSi flux patterns at 3 km depth revealed a higher seasonality compared to the 1 km depth level which was due to passages of low oxygen eddies,
 - the diatom assemblage during eddy passages in winter was dominated by small species and the flux was not related to the organic carbon or BSi fluxes. Such small species were presumably transported downwards within large fast settling diatom aggregates,
 - 450 - we speculate that BSi and Corg/lithogenics originate from different sources within the eddies and are transported differently to depth. Large BSi-rich ballasted aggregates with diatoms may be formed at the eddy boundaries where high shear occurs and may be actively transported downwards (via the 'eddy subduction pump', Boyd et al., 2019) at the eddy boundaries to constitute distinct flux peaks at depth,
 - deep ocean carbon flux attenuation between ca. 1 and 3 km at CVOO appears to be reduced during eddy passages
 - 455 when compared to the Martin curve (open-ocean composite). This may be due to a combination of a reduced microbial degradation of organic carbon and/or lower zooplankton grazing under low oxygen availability within the eddies,
 - we suggest that low oxygen eddies (ACMEs) sequester more carbon compared to oligotrophic conditions combined with less severe OMZ in the epi- and mesopelagic of the eastern North Atlantic.
 - 460 The study presents particle fluxes over a ca. 7-year long period from the oligotrophic site CVOO characterized by a regular passage of low-oxygen eddies containing elevated phytoplankton biomass. This results in significantly higher organic carbon fluxes than during oligotrophic conditions at CVOO or in the North Atlantic Subtropical Gyre. The study supports other findings, suggesting a positive effect of low-oxygen eddy structures or OMZ on organic carbon export and sequestration (e.g. Weber und Bianchi, 2020). However, it remains unclear why similar
 - 465 eddies (e.g. ACMEs) with comparable oxygen conditions release different flux signals and compositions at bathypelagic depths. One reason could be that the eddies approaching site CVOO directly moved over the mooring site (i.e. flux focusing during winter ACME-2010, Fischer et al., 2016) or could have touched CVOO marginally. Deep ocean sediment traps collect particles from a relative large surface area (100 km² or more; Siegel and Deuser,



1997), therefore we might record flux signals from more remote areas. In contrast, oxygen and salinity are directly
470 measured at the CVOO site and a comparison of both time series (sediment traps and sensors) may be limited.
Surface water conditions such as satellite-measured chlorophyll did not show a statistical significant relationship
to the fluxes, e.g. of organic carbon. Carbon degradation between ca. 1 and 3 km during eddy passages appears to
be smaller than predicted although the reasons remain unclear so far. Organic carbon attenuation may be less due
475 to a shorter residence time of the settling particles (Iversen and Ploug, 2010) within the low-oxygen eddies when
microbial degradation and zooplankton grazing was reduced. A combination of the biological gravitational pump
with the eddy subduction pump (Boyd et al., 2019), leading to high particle settling velocities may have led to a
higher efficiency of the biological pump within the ACMEs in winters 2010, 2012 and 2016.

Data availability. Data are available at www.pangaea.de (data were already submitted, doi will be given upon
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References

- Benitez-Nelson, C.R., and McGillicuddy, D.J.: Mesoscale physical–biological–biogeochemical linkages in the open ocean: An introduction to the results of the E-Flux and EDDIES programs. *Deep Sea Res. II*, 55, 1133–1138, doi: 10.1016/j.dsr2.2008.03.001, 2008.
- 505 Berger, W.H., and Wefer, G.: Export production: seasonality and intermittency, and paleoceanographic implications, *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 89, 245–254, 1990. doi.org/10.1016/0921-8181(90)90020-D, 1990.
- Boyd, P. W., Claustre, H., Levy, M., Siegel, D.A., and Weber, T.: Multi-faceted particle pumps drive carbon sequestration in the ocean, *Nature*, 568, 327–335, 2019.
- 510 Bory, A., Jeandel, C., Leblond, N., Vangriesheim, A., Khripounoff, A., Beaufort, L., Rabouille, C., Nicolas, E., Tachikawa, K., Etcheber, H., and Buat-Menard, P.: Particle flux within different productivity regimes off the Mauritanian upwelling zone (EUMELI program), *Deep-Sea Res. II*, 48, 2251–2282, 2001.
- Buesseler, K.O., Lamborg, C., Cai, P., Escoube, R., Johnson, R., Pike, S., Masque, P., McGillicuddy, D., and Verdeny, E.: Particle fluxes associated with mesoscale eddies in the Sargasso Sea., *Deep Sea Res. II*, 55 (10–13), 1426–1444, <https://doi.org/10.1016/j.dsr2.2008.02.007>, 2008.
- 515 Brandt, P., Bange, H. W., Banyte, D., Dengler, M., Didwischus, S.-H., Fischer, T., Greatbatch, R. J., Hahn, J., Kanzow, T., Karstensen, J., Körtzinger, A., Krahnemann, G., Schmidtke, S., Stramma, L., Tanhua, T., and Visbeck, M.: On the role of circulation and mixing in the ventilation of oxygen minimum zones with a focus on the eastern tropical North Atlantic, *Biogeosciences*, 12, 489–512, <https://doi.org/10.5194/bg-12-489-2015>, 2015.
- 520 Christiansen, S., Hoving, H., Schütte, F., Hauss, H., Karstensen, J., Körtzinger, A., Schröder, S., Stemmann, L., Christiansen, B., Picheral, M., Brandt, P., Robison, B., Koch, R., and Kiko, R.: Particulate matter flux interception in oceanic mesoscale eddies by the polychaete *Poebius* sp. *Limnol. Oceanogr.*, doi:10.1002/lno.10926, 2018.
- 525 Fiedler, B., Grundle, D. S., Schütte, F., Karstensen, J., Löscher, C. R., Hauss, H., Wagner, H., Loginova, A., Kiko, R., Silva, P., Tanhua, T., and Körtzinger, A.: Oxygen utilization and downward carbon flux in an oxygen-depleted eddy in the eastern tropical North Atlantic, *Biogeosciences*, 13, 5633–5647, <https://doi.org/10.5194/bg-13-5633-2016>, 2016.
- 530 Fischer, G., and Wefer, G.: Sampling, preparation and analysis of marine particulate matter, in: *Marine particles: Analysis and Characterization*, edited by: Hurd, D.C. and Spencer, D.W., AGU Monograph Series, 63, Washington, DC, 391–397, 1991.



- Fischer, G., Neuer, S., Davenport, R., Romero, O., Ratmeyer, V., Donner, B., Freudenthal, T., Meggers, H. and Wefer, G.: The Northwest African Margin, in: Carbon and Nutrient Fluxes in Continental Margins: A Global Synthesis, edited by: Liu, K. K., Atkinson, L., Quinones, R., and Talaue-McManaus, L., IGBP Book Series, Springer, Berlin, 77-103, 2010.
- 535 Fischer, G., Karstensen, J., Romero, O., Baumann, K.-H., Donner, B., Hefter, J., Mollenhauer, G., Iversen, M., Fiedler, B., Monteiro, I., and Körtzinger, A.: Bathypelagic particle flux signatures from a suboxic eddy in the oligotrophic tropical North Atlantic: production, sedimentation and preservation, *Biogeosciences*, 13, 3203–3223, <https://doi.org/10.5194/bg-13-3203-2016>, 2016.
- 540 Gama, C., Tchepel, O., Baldasano, J.M., Basart, S., Ferreira, J., Pio, C., Cardoso, J., and Borrego, C.: Seasonal patterns of Saharan dust over the Cape Verde – a combined approach using observations and modelling, *Tellus B*, 67, 24410, <http://dx.doi.org/10.3402/tellusb.v67.24410>, 2015.
- Gaube, P., McGillicuddy, D.J., Chelton, D.B., Behrenfeld, M.J., Strutton, P.G.: Regional variations in the influence of mesoscale eddies on near-surface chlorophyll, *J. Geophys. Res. Oceans*, 119, 8195–8220, 2014.
- 545 Goldthwait, S.A., and Steinberg, D.K.: Elevated biomass of meso-zooplankton and enhanced fecal pellet flux in cyclonic and mode-water eddies in the Sargasso Sea, *Deep Sea Res. II*, 55 (10–13), 1360-1377, doi.org/10.1016/j.dsr2.2008.01.003, 2008.
- Grundle, D., Löscher, C., Krahnmann, G., Altabet, M., Bange, H., Karstensen, J., Körtzinger, A. and Fiedler, B.: Extreme N₂O activity in an oxygenated ocean, *Nature Scientific reports*, 7: 480, [doi:10.1038/s41598-017-04745-y](https://doi.org/10.1038/s41598-017-04745-y), 2017.
- 550 Hahn, J., Brandt, P., Greatbatch, R., Krahnmann, G., and Körtzinger, A.: Oxygen variance and meridional oxygen supply in the Tropical North East Atlantic oxygen minimum zone, *Clim. Dynam.*, 43, 2999–3024, 2014.
- Hauss, H., Christiansen, S., Schütte, F., Kiko, R., Edvam Lima, M., Rodrigues, E., Karstensen, J., Löscher, C. R., Körtzinger, A., and Fiedler, B.: Dead zone or oasis in the open ocean? Zooplankton distribution and migration in low-oxygen modewater eddies, *Biogeosciences*, 13, 1977-1989, [doi:10.5194/bg-13-1977-2016](https://doi.org/10.5194/bg-13-1977-2016), 2016.
- 555 Hedges, J. I., Baldock, J. A., Gelinas, Y., Lee, C., Peterson, M. L., and Wakeham, S. G.: The biochemical and elemental compositions of marine plankton: a NMR perspective. *Mar. Chem.*, 78 (1), 47–63, 2002.
- Iversen, M.H., and Ploug, H.: Ballast minerals and the sinking carbon flux in the ocean: carbon-specific respiration rates and sinking velocity of marine snow aggregates. *Biogeosciences* 7, 2613-2624, 2010.
- 560 Jackson, G.A., and Kiorboe, T.: Maximum phytoplankton concentrations in the sea. *Limnol. Oceanogr.*, 53, 1, 395-399, DOI: 10.4319/lo.2008.53.1.0395, 2008.



- Karstensen, J., Stramma, L., and Visbeck, M.: Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans, *Prog. Oceanogr.*, 77, 4, 331-350, doi.org/10.1016/j.pocean.2007.05.009, 2008.
- 565 Karstensen, J., Fiedler, B., Schütte, F., Brandt, P., Körtzinger, A., Fischer, G., Zantopp, R., Hahn, J. Visbeck, M., and Wallace, D.: Open ocean dead zones in the tropical North Atlantic Ocean, *Biogeosciences*, 12, 2597-2605, 2015.
- Karstensen, J., Schütte, F., Pietri, A., Krahnemann, G., Fiedler, B., Grundle, D., Hauss, H., Körtzinger, A., Löscher, C. R., Testor, P., Vieira, N., and Visbeck, M.: Upwelling and isolation in oxygen-depleted anticyclonic modewater eddies and implications for nitrate cycling, *Biogeosciences*, 14, 2167–2181, <https://doi.org/10.5194/bg-14-2167-2017>, 2017.
- 570
- Korte, L. F., Brummer, G.-J. A., van der Does, M., Guerreiro, C. V., Hennekam, R., van Hateren, J. A., Jong, D., Munday, C. I., Schouten, S., and Stuut, J.-B. W.: Downward particle fluxes of biogenic matter and Saharan dust across the equatorial North Atlantic, *Atmos. Chem. Phys.*, 17, 6023–6040, <https://doi.org/10.5194/acp-17-6023-2017>, 2017.
- 575
- Kremling, K., Lentz, U., Zeitzschell, B., Schulz-Bull, D.E., and Duinker, J.C.: New type of time-series sediment trap for the reliable collection of inorganic and organic trace chemical substances, *Rev. Scient. Instr.*, 67, 4360–4363, 1996.
- Löscher, C. R., Fischer, M. A., Neulinger, S. C., Fiedler, B., Philippi, M., Schütte, F., Singh, A., Hauss, H., Karstensen, J., Körtzinger, A., Künzel, S., and Schmitz, R. A.: Hidden biosphere in an oxygen-deficient Atlantic open-ocean eddy: future implications of ocean deoxygenation on primary production in the eastern tropical North Atlantic, *Biogeosciences*, 12, 7467-7482, doi:10.5194/bg-12-7467-2015, 2015.
- 580
- Maiti, K., Benitez-Nelson, C.R., Rii, Y., and Bidigare, R.: The influence of a mature cyclonic eddy on particle export in the lee of Hawaii, *Deep Sea Res. II*, 55 (10–13), 1445-1460, doi.org/10.1016/j.dsr2.2008.02.008, 2008.
- 585
- Martin, J. H., Knauer, G.A., Karl, D., and Broenkow, W.W.: VERTEX: Carbon cycling in the northeast Pacific, *Deep Sea Res. I*, 34, 267–285, 1987.
- McCave, I.N.: Size spectra and aggregation of suspended particles in the deep ocean. *Deep-Sea Res. I*, 31, 329–352, 1984.
- 590
- McGillicuddy, D. J., Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., Ewart, C., Falkowski, P. G., Goldthwait, S. A., Hansell, D. A., Jenkins, W. J., Johnson, R., Kosnyrev, V. K., Ledwell, J. R., Li, Q. P., Siegel, D. A., and Steinberg, D. K.: Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms, *Science*, 316, 1021–1026, doi:10.1126/science.1136256, 2007.



- Mittelstaedt, E.: The ocean boundary along the northwest African coast: Circulation and oceanographic properties
595 at the sea surface. *Prog. Oceanogr.*, 26, 307–355, 1991.
- Müller, P.J., and Schneider, R.: An automated leaching method for the determination of opal in sediments and
particulate matter. *Deep Sea Res. I*, 40 (3), 425–444, 1993.
- Oschlies, A., Garçon, V.: Eddy-induced enhancement of primary production in a model of the North Atlantic
Ocean, *Nature* 394, 266–269, 1998.
- 600 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, 6231, 222–225, DOI:
10.1126/science.1260062, 2015.
- Pietri, A., and Karstensen, J.: Dynamical characterization of a low oxygen submesoscale coherent vortex in the
Eastern North Atlantic Ocean. *J. Geophys. Res., Oceans*, 123, 2049– 2065.
605 <https://doi.org/10.1002/2017JC013177>, 2018.
- Ploug, H., Iversen, M.H., and Fischer, G.: Ballast, sinking velocity, and apparent diffusivity within marine snow
and fecal pellets: Implications for substrate turnover by attached bacteria. *Limnol. Oceanogr.*, 53 (5), 1878–
1886, 2008.
- Rasse, R., and Dall’Olmo, G.: Do Oceanic Hypoxic Regions Act as Barriers for Sinking Particles? A Case Study
610 in the Eastern Tropical North Atlantic. *Global Biogeochem. Cycles*, 33, 1611– 1630.
<https://doi.org/10.1029/2019GB006305>, 2019.
- Redfield, A. C., Ketchum, B.H., and Richards, F.A.: The influence of organisms on the composition of seawater,
in: *The Sea*, edited by: Hill, M.N., Vol. 2, Wiley and Sons, Chichester, 26–77, 1963.
- Rii, Y.M., S Brown, F Nencioli et al.: The transient oasis: Nutrient-phytoplankton dynamics and particle export in
615 Hawaiian lee cyclones, *Deep-Sea Res II*, 55, 1275–1290, 2008.
- Romero, O.E., Lange, C.B., Fischer, G., Treppke, U.F., Wefer, G.: Variability in export production documented
by downward fluxes and species composition of marine planktonic diatoms: Observations from the tropical
and equatorial Atlantic, in: *Use of Proxies in Paleooceanography, Examples from the South Atlantic*, edited
by: Fischer, G., Wefer, G., Springer Verlag, Berlin, Heidelberg, 365–392, 1999.
- 620 Romero, O. E., Fischer, G., Karstensen, J., and Cermeño, P.: Eddies as trigger for diatom productivity in the open-
ocean Northeast Atlantic. *Prog. Oceanogr.*, 147, 38–48, 2016.
- Romero, O. E., and Fischer, G.: Shift in the species composition of the diatom community in the eutrophic
Mauritanian coastal upwelling: Results from a multi-year sediment trap experiment (2003–2010), *Prog.*
Oceanogr., 159, 31–44, 2017.

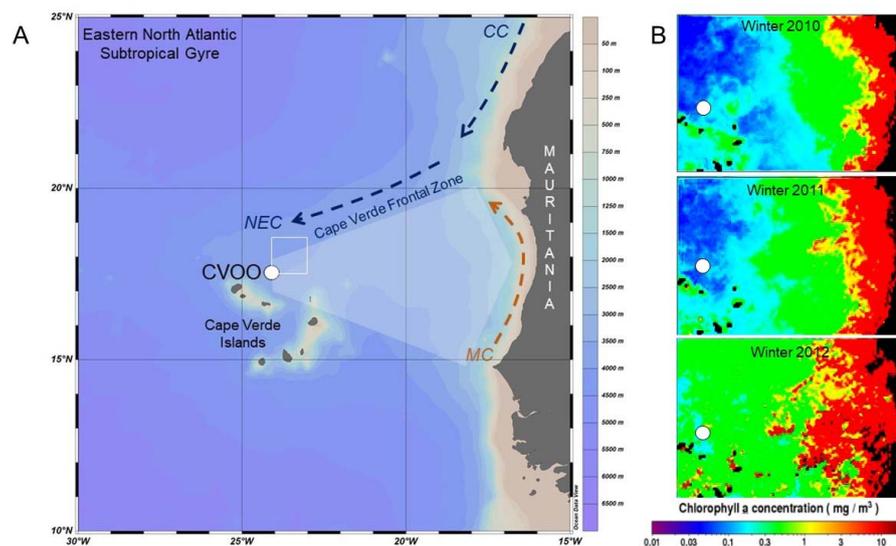


- 625 Romero, O. E., Baumann, K.-H., Zonneveld, K. A. F., Donner, B., Hefter, J., Hamady, B., Pospelova, V., and Fischer, G.: Flux variability of phyto- and zooplankton communities in the Mauritanian coastal upwelling between 2003 and 2008, *Biogeosciences*, 17, 187–214, <https://doi.org/10.5194/bg-17-187-2020>, 2020.
- Sancetta, C., Calvert, S.E.: The annual cycle of sedimentation in Saanich Inlet, British Columbia: implications for the interpretation of diatom fossil assemblages. *Deep-Sea Res. I*, 35, 71-90, 1988.
- 630 Schneider, B., Schlitzer, R., Fischer, G., and Noethig, E.-M.: Depth-dependent elemental compositions of particulate organic matter (POM) in the ocean. *Global Biogeochem. Cycles*, 17 (2), 1032, doi:10.029/2002GB001871, 2003.
- Schrader, H.-J., Gersonde, R.: Diatoms and silicoflagellates, in: *Micropaleontological counting methods and techniques - an exercise on an eight meter section of the Lower Pliocene of Capo Rosello, Sicily*. edited by: Zachariasse, W.J., Riedel, W.R., Sanfilippo, A., Schmidt, R.R., Broolsma, M.J., Schrader, H., Gersonde, R., Drooger, M.M., and Broekman, J.A., *Utrecht Micropal. Bull.*, 17, 129-176, 1978.
- 635 Schütte, F., Brandt, P., and Karstensen, J.: Occurrence and characteristics of mesoscale eddies in the tropical northeast Atlantic Ocean, *Ocean Sci.* 12, 663–685, 2016, doi:10.5194/os-12-663-2016, 2016a.
- Schütte, F., Karstensen, J., Krahnemann, G., Hauss, H., Fiedler, B., Brandt, P., Visbeck, M., and Körtzinger, A.: Characterization of “dead-zone” eddies in the tropical Northeast Atlantic Ocean, *Biogeosciences*, 13, 5865–5881, doi:10.5194/bg-13-5865-2016, 2016b.
- Shih, Y.-Y., Hung, C.-C., Gong, G.-C., Chung, W.-C., Wang, Y.-H., Lee, I.-H., et al.: Enhanced Particulate Organic Carbon Export at Eddy Edges in the Oligotrophic Western North Pacific Ocean. *PLoS ONE* 10(7): e0131538, <https://doi.org/10.1371/journal.pone.0131538>, 2015.
- 645 Siegel, D.A., and Deuser, W.G.: Trajectories of sinking particles in the Sargasso Sea: Modeling of statistical funnels above deep-ocean sediment traps. *Deep Sea Res. I*, 44 (9–10), 1519–1541, [https://doi.org/10.1016/S0967-0637\(97\)00028-9](https://doi.org/10.1016/S0967-0637(97)00028-9), 1997.
- Smetacek, V.: Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.*, 84, 239-251, 1985.
- 650 Verdeny, E., Masqué, P., Maiti, K., Garcia-Orellana, J., Bruach, J.M., Mahaffey, C., and Benitez-Nelson, C.R.: Particle export within cyclonic Hawaiian lee eddies derived from 210Pb–210Po disequilibrium *Deep Sea Res. II*, 55 (10–13), 1461-1472, doi.org/10.1016/j.dsr2.2008.02.009, 2008.
- Weber, T., and Bianchi D.: Efficient Particle Transfer to Depth in Oxygen Minimum Zones of the Pacific and Indian Oceans, *Front. Earth Sci.*, 8, 376, DOI=10.3389/feart.2020.00376, 2020.

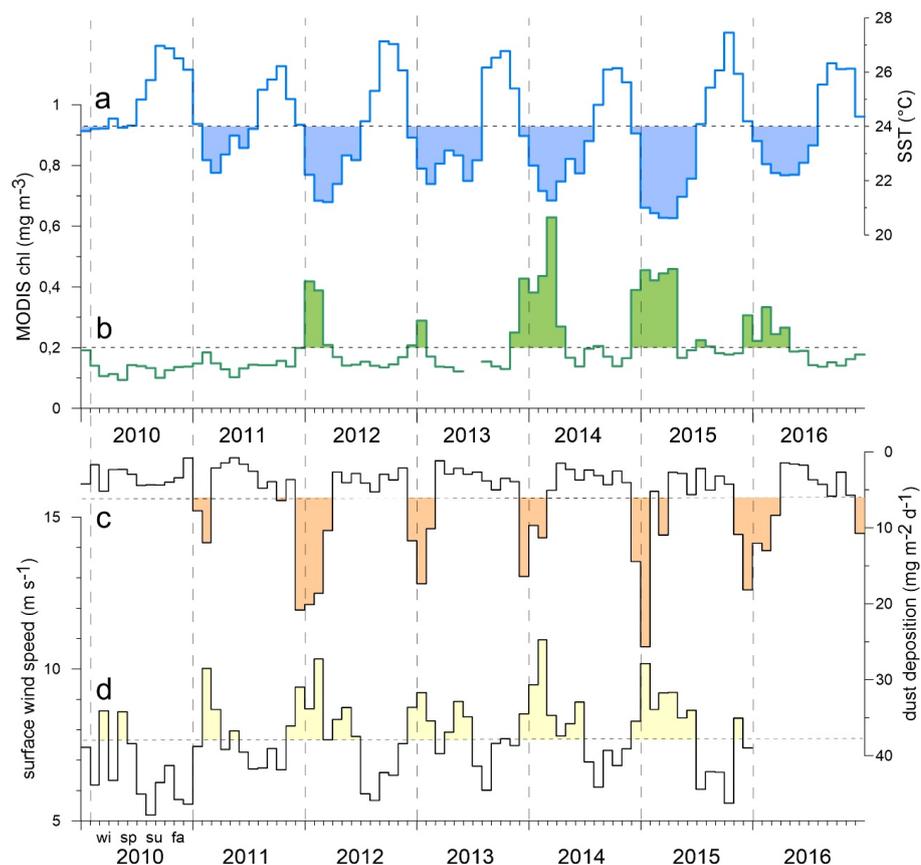
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FIGURES



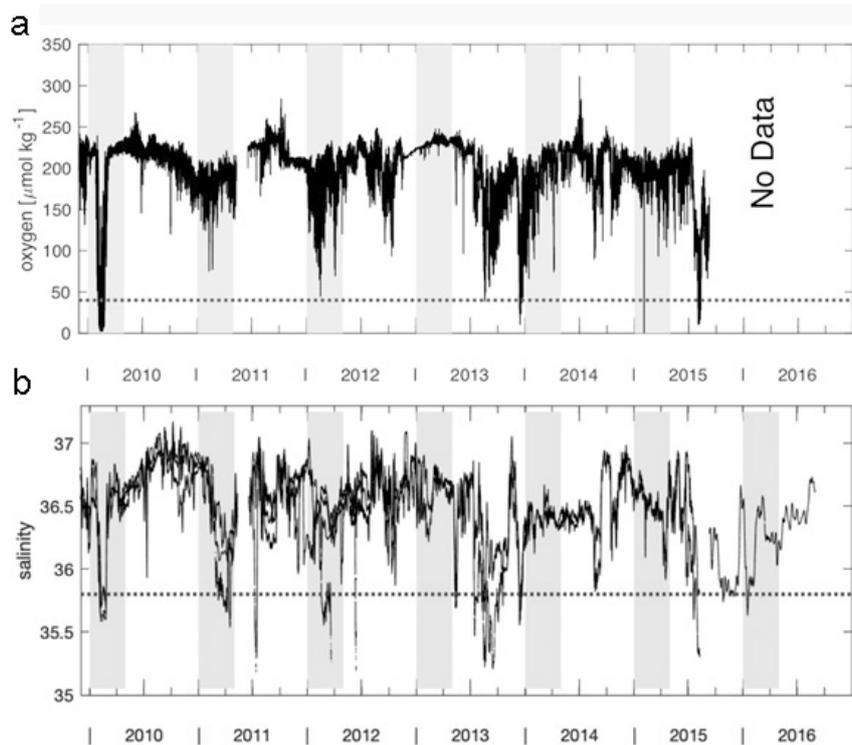
660 Fig. 1. (a) Location of the CVOO site in the eastern tropical North Atlantic with the major currents systems of the
Canary Current (CC), the North Equatorial Current (NEC) and the Mauritanian Current (MC) (ODV map:
Schlitzer, Reiner, Ocean Data View, odv.awi.de, 2021). Note the corridor of eddy passages from the African coast
to CVOO schematically indicated as a light polygon. A white box with the environmental data from GIOVANNI
is shown NE of CVOO. (b) Winter MODIS satellite chlorophyll between the African coast and the Cape Verde
665 Islands (site CVOO = white dot) for winters 2010, 2011 and 2012 (2016 is comparable to 2012, not shown)
showing the increasing extensions of the high chlorophyll area ($> 1 \text{ mg m}^{-3}$) from the coast to the open ocean,
approaching site CVOO.



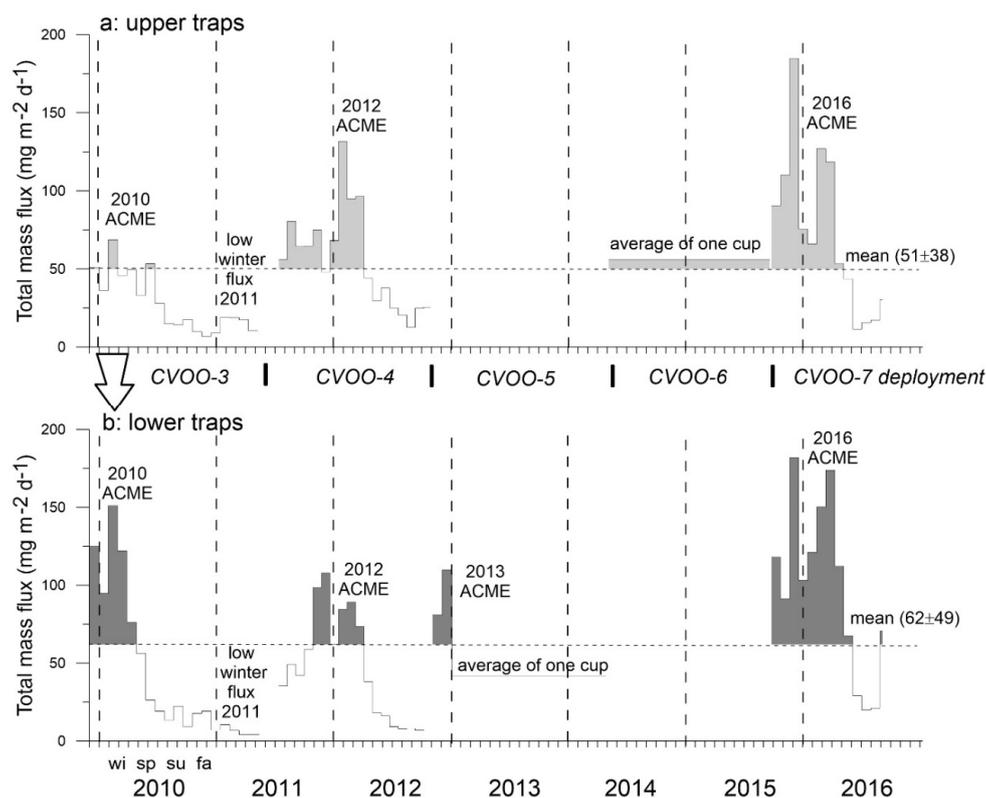
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Fig. 2. Monthly SSTs (a), chlorophyll (b), modelled (MERRA) dry dust deposition (c) and surface wind speed (d) recorded in the study box northeast (17.5-18.5° N / 23-24° W) of CVOO between 2010 and 2016 (satellite-derived, from GIOVANNI, <https://giovanni.gsfc.nasa.gov/giovanni/#service=TmAvMp&starttime=&endtime=>). Note that during the extreme ACME in winter 2010, chlorophyll, surface wind and dust deposition were all low, combined with relatively high SSTs. Thereafter, surface biomass, winds and dust increased during winter and early spring. Horizontal dashed lines indicate mean values, peaks above or below are marked as filled bars. Vertical dashed lines mark years, wi sp su fa indicate the seasons.

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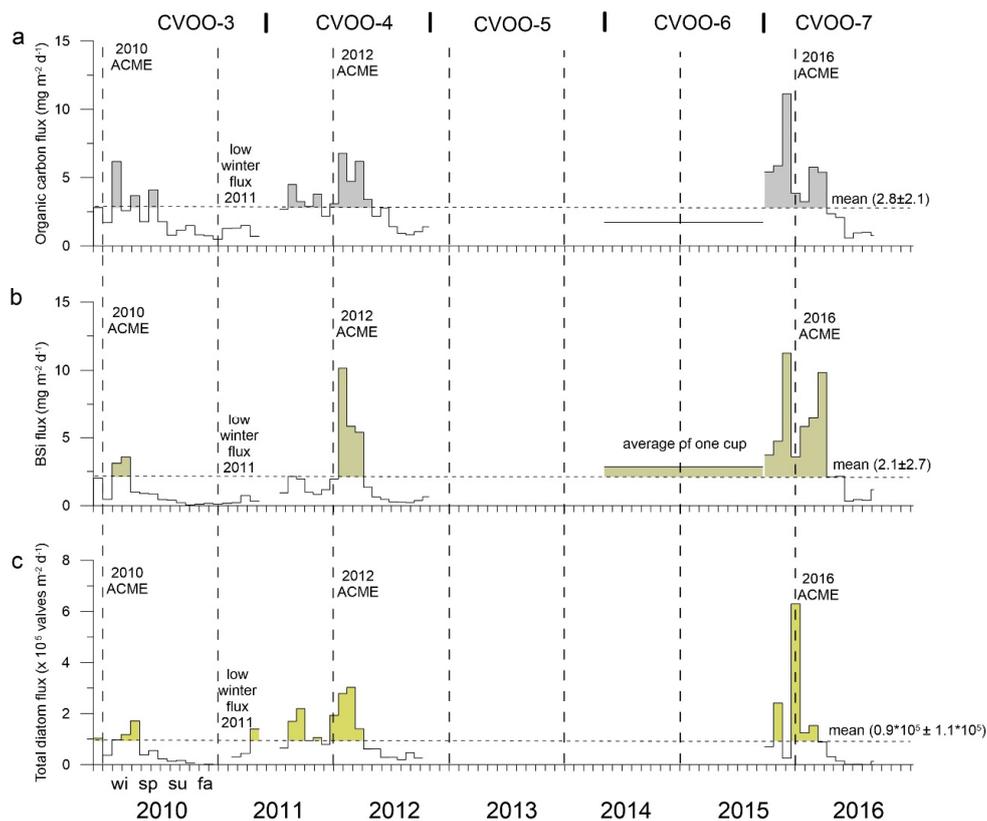


680 Fig. 3. CVOO time series of 12h lowpass oxygen (a, $\mu\text{mol kg}^{-1}$) and salinity (b, in PSS-78). Dotted lines are considered thresholds that indicate the passage of low oxygen eddies. Grey shaded areas indicate the periods January to April for reference. For instrument depth see text.



685

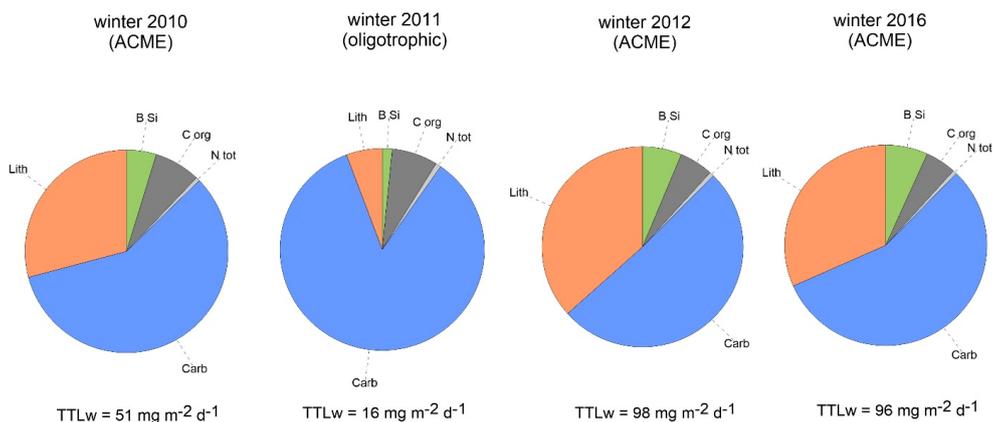
Fig. 4. Total mass fluxes between 2009 and 2016 for the upper (a) and the lower traps (b). Means (horizontal
stippled lines) were only slightly above typical oligotrophic flux values (ca. $50 \text{ mg m}^{-2} \text{ d}^{-1}$; Bory et al., 2001;
Fischer et al., 2010; Korte et al., 2017). Peak fluxes (above the means) are grey-shaded to indicate maxima in late
fall and winter. Arrow indicates flux focusing during the winter ACME 2010 (Fischer et al., 2016). Note the low
690 (= oligotrophic) fluxes in winter 2011 far below the means. Horizontal dashed lines indicate mean fluxes, vertical
lines separate years, wi sp su fa indicate the seasons.



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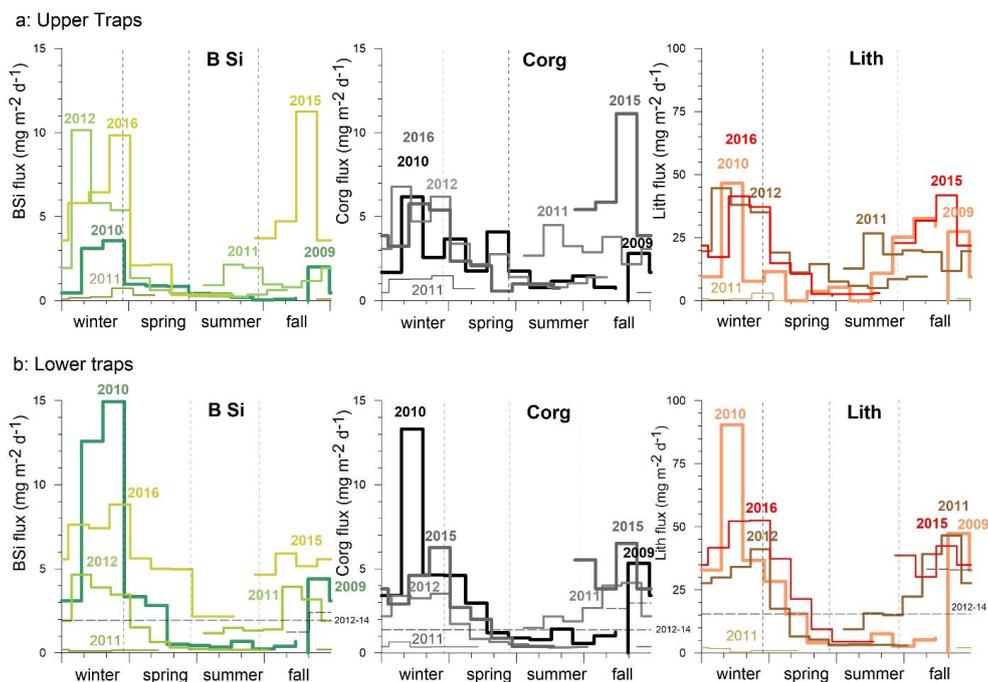
Fig. 5. Organic carbon (a), BSi (b) and diatom fluxes (c) of the upper traps at site CVOO. Flux peaks are highlighted (grey, olive and green) when above the mean values (horizontal dashed lines). Note that the peaks of diatom valves (largely composed of small species) only partly matched the BSi fluxes. Vertical dashed lines separate years, wi sp su fa indicate seasons.

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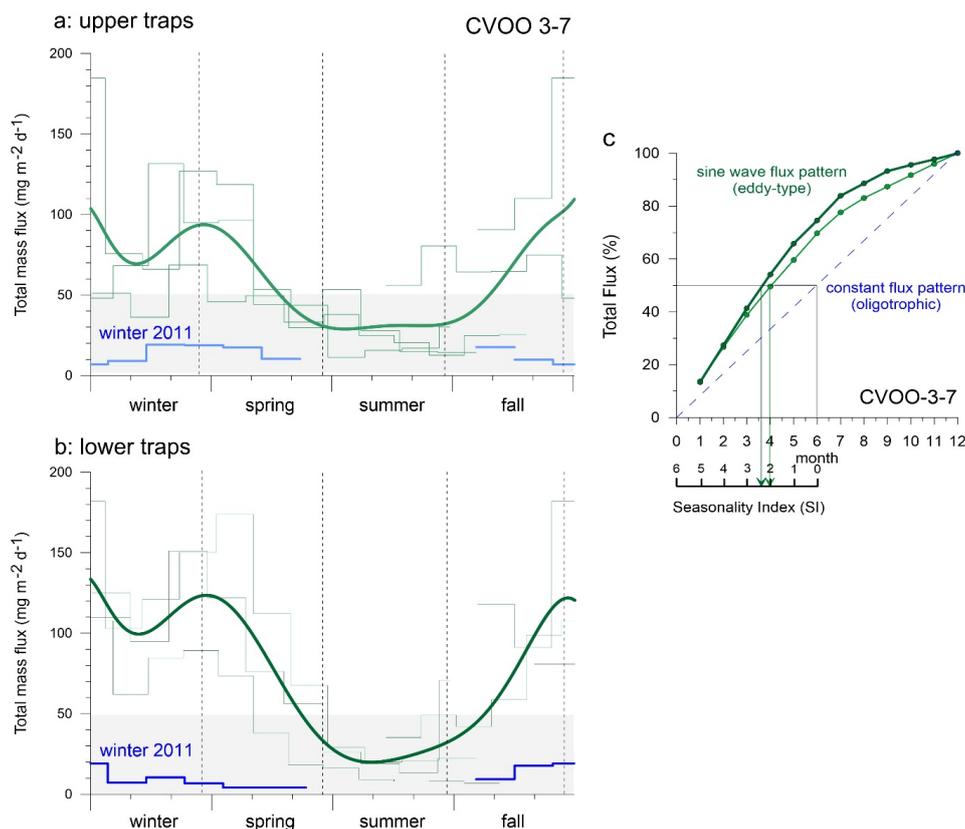


705 Fig. 6. Flux compositions in winter (% of total winter mass flux = TTL_w) from the upper traps during the low-oxygen ACME 2010 (Fischer et al., 2016), the low flux (oligotrophic) conditions in winter 2011 and during the following ACMEs in winter 2012 and 2016 (high and almost equal total fluxes). Lithogenic components constitute approx. 1/3 of the total flux, except during oligotrophic conditions in winter 2011. Note that organic carbon content is almost constant among the winter seasons despite variable total fluxes.

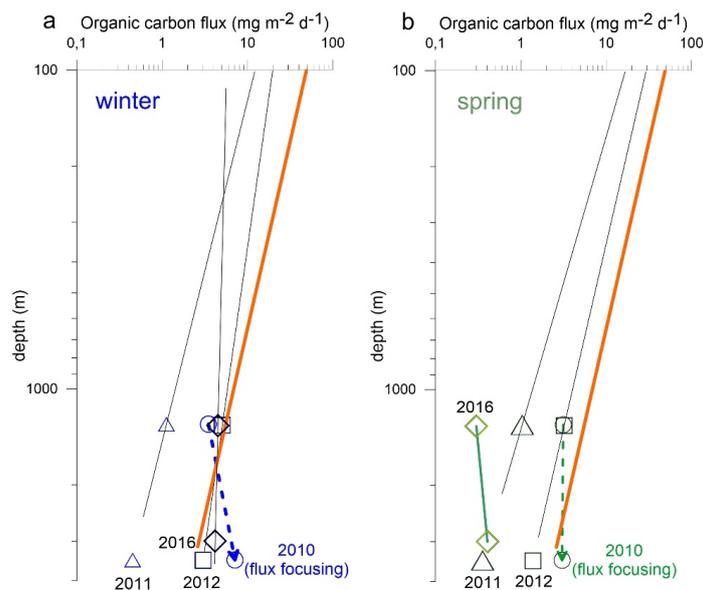
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715 Fig. 7. Upper (a) and lower trap (b) seasonal flux patterns of BSi, organic carbon, and lithogenics on a Julian day scale. In 2013, only one sampling cup was available which collected all the material (Table 1). Note the overall higher seasonality recorded in the lower traps (B) and for BSi in both trap depth levels. During the oligotrophic winter-spring 2011, fluxes remained very low compared to the other years, revealing almost no seasonality.



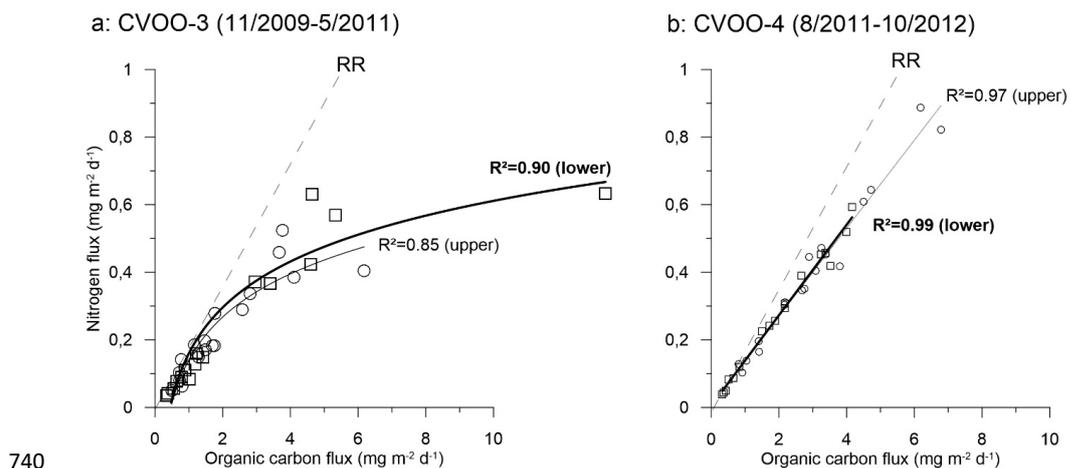
720 Fig. 8. Seasonal total flux patterns for the upper (a) and lower traps (b) characteristic for different types of eddies
 (light and dark green (9-order polynomial fit) vs oligotrophic conditions in winter 2011 (blue: oligotrophic
 background with more or less constant flux/productivity pattern and low seasonality (SI-Index of 0-1 in c) at
 CVOO. Grey-shaded: typical oligotrophic background fluxes in the North Atlantic Gyre. (c) Sum of total particle
 fluxes and Seasonality Index (Berger and Wefer, 1990) for the upper (light green) and lower traps (dark green)
 725 taken from the means in a/b. Note the overall higher seasonality (sine wave production) in the lower (SI = ca. 2.4)
 compared to the upper traps (SI = ca. 2.0) during eddy passages (2010, 2012, 2016). For comparison, a constant
 flux pattern, typical for oligotrophic settings is shown schematically in b.



730

Fig. 9. Carbon flux attenuation (log-log plot) in the water column in winter (a) and spring (b) for 2010 (extreme low oxygen ACME), 2011 (oligotrophic situation), 2012 and 2016 (ACME). Attenuation according to Martin et al. (1987; with $b=-0.858$, orange line) is shown. Note a reduced carbon flux attenuation than predicted by the Martin curve in the winters 2010, 2012 and 2016 when low-oxygen eddies passed. During the extreme winter ACME 2010, deep ocean fluxes increased strongly with depth (also in spring) due to flux focusing (arrows, Fischer et al., 2016). Fluxes more typical for oligotrophic conditions and carbon flux attenuation occurred in winter and spring 2011.

735



745 Fig. 10. Different C:N flux relationships (best fits) during the 2010 and 2012 ACME passages in fall-winter (2011 oligotrophic fluxes are included in a); RR=Redfield Ratio (Redfield et al. 1963). Note the non-linear changes during the extreme 2010-ACME (a), pointing to nitrogen limitation and, for comparison, the linear relationship later in 2012 (b).



TABLES

Trap deployment	Location		Trap depth m	Start	End	Days sampled d	Number of samples x days	Remarks/References
	LAT N	LONG W						
CVOO-3	ca. 17°35.	ca. 24°15.	1290	2009-12-01	2011-05-11	522	18 x 29 d	Fischer et al. (2016); Romero et al. (2016)
			3439	2009-12-01	2011-05-11	555.5	17 x 29d; 1 x 62.5	Fischer et al. (2016)
CVOO-4	ca. 17°35.	ca. 24°15.	1300	2011-07-12	2012-10-24	471	17 x 26.5; 1 x 20.5	Romero et al. (2016)
			3449	2011-07-12	2012-10-24	450.5	17 x 26.5	
CVOO-5	ca. 17°35.	ca. 24°15.	2993	2012-12-01	2014-04-24	539	2 x 30.5; 1 x 478d	3 samples only
CVOO-6	ca. 17°35.	ca. 24°15.	1304	2014-05-01	2015-09-07	500	1 x 500d	1 sample only
CVOO-7	ca. 17°35.	ca. 24°15.	1304	2015-09-20	2016-08-29	344	12 x 28; 1 x 8d	
			3002	2015-09-20	2015-09-20	344	12 x 28; 1 x 8d	

750

Table 1. Data of sampling with sediment particle traps at site CVOO



Corg-R ²		N=	B Si	carb	lith	structure
winter 2010	upper	4	0.31	-0.72	0.92	ACME
	lower	4	0.22	-0.83	0.99	(S and O ₂)
winter 2011	upper	4	0.42	0.48	0.22	ACME
	lower	3	0.17	0.70	0.20	(S and O ₂)
winter 2012	upper	4	0.77	0.53	0.78	ACME
	lower	4	0.74	0.04	0.50	(S and O ₂)
winter 2016	upper	4	0.37	0.99	0.99	ACME
	lower	4	0.66	0.76	0.51	(S, no O ₂)

755 **bold: 99% c.l.**

Table 2. Flux relationships with correlation coefficients (R²) for winter ACMEs 2010, 2012 and 2016 and under oligotrophic conditions. Values at the 99 % c.l. are in bold and were found only during the ACME in winter 2010. The case of the structure is estimated from the salinity (S) and oxygen (O₂) recordings from the CVOO site (Fig. 3). With respect to the slopes of the relationships, ACME 2012 and 2016 largely match.

760



Season	Trap	days in winter	Chl- <i>a</i> MODIS	oxygen (eddy)	eddy type	References (eddy)	FLUXES					RATIOS	
							B Si	Corg	Ntot	CaCO ₃	Lith	C:N	Corg:Lith
			mg m ⁻³				mg m ⁻² d ⁻¹	molar					
winter 2010	upper	89	0.15	hypoxic- suboxic	ACME	Karstensen et al. 2015 Fischer et al. 2016	2.25	3.49	0.30	27.60	13.83	13.7	0.25
	lower	89				Schütte et al. 2016a	9.25	7.13	0.54	45.32	54.04	15.5	0.13
winter 2011	upper	90	0.15	hypoxic	ACME	Karstensen et al. 2015	0.24	1.12	0.13	13.09	0.88	10.0	1.27
	lower	90				Fischer et al. 2016 Schütte et al. 2016a	0.13	0.45	0.05	5.46	1.25	10.4	0.36
winter 2012	upper	94	0.30	hypoxic	ACME	Romero et al. 2016	5.88	5.07	0.66	47.66	34.22	8.9	0.15
	lower	94				Schütte et al. 2016a	3.47	3.02	0.41	36.13	32.18	8.7	0.09
winter 2013	upper		0.20	hypoxic	CE	Schütte et al. 2016a	-	-	-	-	-	-	-
	lower	90					1.99	1.57	0.21	27.10	17.57	8.9	0.09
winter 2014	upper		0.47	hypoxic		Schütte et al. 2016a	-	-	-	-	-	-	-
	lower	90					1.93	1.38	0.18	22.01	15.43	9.0	0.09
winter 2015	upper	90	0.43	hypoxic	ACME	Schütte et al. 2016a	2.84	1.70	0.21	34.95	14.67	9.37	0.12
	lower						-	-	-	-	-	-	-
winter 2016	upper	90	0.28	hypoxic	ACME	-	6.18	4.51	0.58	51.33	28.99	9.08	0.16
	lower	91					10.05	4.18	0.69	71.13	45.23	7.06	0.09

765 Table 3. Biogeochemical characterization of the different eddies passing CVOO in the winter seasons between 2010 and 2016 with respect to deep ocean fluxes and compositions. Flux characteristics are also shown for winter 2011 with oligotrophic background conditions. ACME=Anticyclonic Modewater Eddy, CE=Cyclonic Eddy.