The influence of zooplankton and oxygen on the particulate organic carbon flux in the Benguela Upwelling System

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Abstract. We conducted extensive sediment trap experiments in the Benguela Upwelling System (BUS) in the south-eastern Atlantic Ocean to study the influence of zooplankton on the flux of particulate organic carbon (POC) through the water column and its sedimentation. Two long-term moored and sixteen short term free-floating sediment trap systems were deployed. The mooring experiments were conducted for several years and the sixteen drifters were deployed on three different research cruises between 2019 and 2021. Zooplankton was separated from the trapped material and divided into 8 different zooplankton groups. In contrast to zooplankton which actively carries POC into the traps in the form of biomass (active POC flux), the remaining fraction of the trapped material was assumed to fall passively into the traps along with sinking particles (passive POC flux). The results show, in line with other studies, that copepods dominate the active POC flux, with the active POC flux in the southern BUS (sBUS) being about three times higher than in the northern BUS (nBUS). In contrast, the differences between the passive POC fluxes in the nBUS and sBUS were small. Despite large variations, which reflected the variability within the two subsystems, the mean passive POC fluxes from the drifters and the moored traps could be described using a common POC flux attenuation equation. However, the almost equal passive POC flux, on the one hand, and large variations in the POC concentration in the surface sediments between the nBUS and sBUS, on the other hand, imply that factors others than the POC supply exert the main control on POC sedimentation in the BUS. The varying intensity of the near-bottom oxygen minimum zone (OMZ), which is more pronounced in the nBUS than in the sBUS, could in turn explain the differences in the sediments, as the lack of oxygen reduces the POC degradation. Hence, globally expanding OMZs might favour POC sedimentation in regions formerly exposed to oxygenated bottom water but bear the risk of increasing the frequency of anoxic events in the oxygen-poor upwelling systems. Apart from associated release of CH_4, which is a much more potent greenhouse gas than CO_2, such events pose a major threat to the pelagic ecosystem and fisheries.

Introduction

Carbon storage by pelagic marine ecosystems, known as the biological carbon pump, exerts a strong control over atmospheric CO_2 concentrations by influencing CO_2 storage in the ocean and underlying sediments. Although scientific studies have widely shown that the biological pump responds to climate change (e.g., Devries and

Deutsch, 2014; Duce et al., 2008;; Laufkötter et al., 2017; Riebesell et al., 2007) and is affected by fisheries (Bianchi et al., 2021), it is not yet possible to predict the extent of the changes or its direction of development (Laufkötter and Gruber, 2018; Passow and Carlson, 2012; Rixen et al., 2024). These uncertainties reduce confidence in climate predictions (Passow and Carlson, 2012), call into question sustainability criteria related to

45   the growing blue economy (Jouffray et al., 2020) and assessments of the state of the ocean such as the Ocean Health Index (Halpern et al., 2012). In addition, pelagic ecosystems, which fuel the biological carbon pump and enable the transfer of POC to the sediment, are not considered as blue carbon ecosystems (e.g. Lovelock and Duarte, 2019; Macreadie et al., 2019), which means that their response to human perturbation is largely ignored in national reports to the UNFCC (United Nations Framework Convention on Climate Change) in the framework

50   of the Paris Agreement. As shelves located in the 200-mile exclusive economic zone (EEZ) are of great relevance for the global carbon cycle (Rixen et al., 2024), lately efforts are being made to include sediments in the blue carbon concept (European Marine Board, 2023; von Maltitz et al., 2024). To emphasize the relevance of this effort, it should be noted that the carbon storage in the EEZs with 1092 - 1166 PgC (Atwood et al., 2020) by far exceed those in the classic blue carbon ecosystems (salt marshes, mangroves and seagrasses: ~7.3 - 22.7 Pg C (Pendleton

55   et al., 2012).

One of the difficulties in studying pelagic ecosystems is that they develop in a moving medium, the ocean. The residence time of ocean water on the shelf is on average around 12 to 17 months (Lacroix et al., 2021), so that it falls only temporarily under the jurisdiction of an individual state. Although processes that control the delivery of POC to the sediment are known in general, there are also a number of unknown and difficult to determine processes

60   as well as methodological problems in determining POC fluxes to the sediment. Accordingly, global estimates of the amount of POC exported from the sunlit surface ocean (export production) vary between 1.8 - 27.5 10^{15} g C yr^{-1} (Del Giorgio and Duarte, 2002; Honjo et al., 2008; Lutz et al., 2007).

The delivery of POC to the sediment begins with primary production, which converts dissolved inorganic carbon into POC. Incorporated into particles and following gravity, these particles sink through the water column onto

65   the sediment. Three different types of particles are generally distinguished, namely fecal pellets from zooplankton and fish, amorphous aggregates (marine snow) and remains of dead marine organisms (Turner, 2015). Global modelling studies conclude that fecal pellets are on average responsible for 16 - 85 % of gravitational POC export (Archibald et al., 2019; Nowicki et al., 2022), which is consistent with sediment trap results. In sediment traps, the proportion of fecal pellets in the POC flux can vary between 1 and 100 %, but many experiments show that the

70   proportion of fecal pellets in the POC flux is around 40 % (Turner, 2015).

On their way through the water column, bacteria and zooplankton degrade the sinking organic material. The decrease in sinking POC with depth has been described by a whole series of relatively simple attenuation equations, of which the so-called Martin equation is probably the best known (Martin et al., 1987). The Martin equation (Eq. 1) is based on the POC flux at the base of the mixed layer (F_{MLD} ~ export production) and requires a regionally

75   varying attenuation rate (b) in addition to the water depth (z).

$$F_z = F_{MLD} * \left(\frac{z}{MLD}\right)^b \qquad\qquad (1)$$

A comparison of some of these equations shows that they all represent the measured data well but differ significantly in their implications, e.g. with regard to the calculation of the POC degradation rates inherent in them (Cael and Bisson, 2018). In addition, these equations have also been criticized because they do not consider the

80   role of zooplankton. The diurnal vertical migration of zooplankton is one of the largest known mass movements in the animal kingdom, extending from the surface to water depths of 200 to 650 m (Bianchi et al., 2013). However,

model calculations show that zooplankton degrade approximately 15 % and 43 % of the exported POC (Bianchi et al., 2013; Archibald et al., 2019). On average, this would be around 30 %, which is consistent with the results of a comprehensive field study from Giering et al. (2014) in the Atlantic Ocean. This study found that 70 - 92 %

85   of the sinking POC at depths between 100 and 1000 m was degraded by bacteria, which conversely means that up to 30 % of the POC is decomposed by zooplankton (Giering et al., 2014). To investigate the influence of zooplankton on POC flux and sedimentation, we conducted extensive sediment trap experiments in the BUS, where the accumulation of POC in the sediment can become so high that in some places 'mud belts' are formed, characterized by POC concentrations >12 % and high POC storage in the sediments (Fig. 1, van der Plas et al.,

90   2007; Monteiro et al., 2005; Emeis et al., 2017; Atwood et al., 2020).
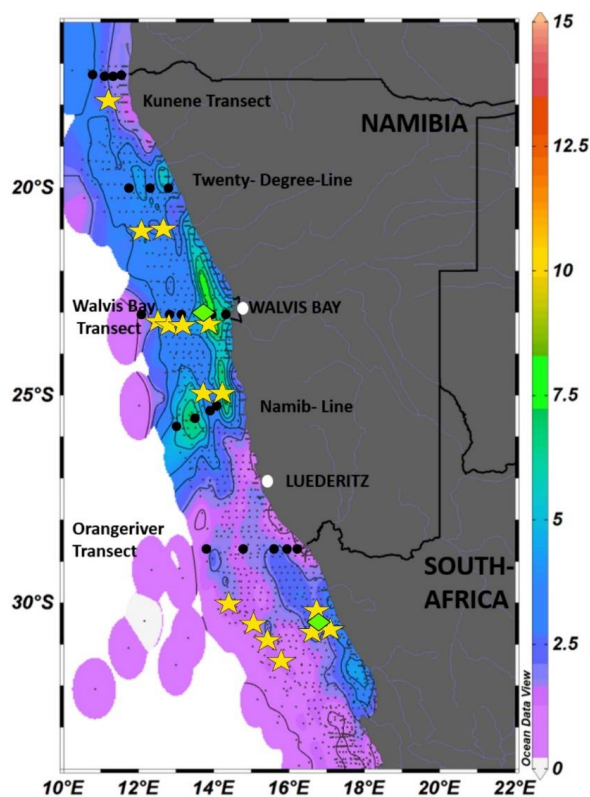

Figure 1 POC concentration in the BUS from various research expeditions published in Emeis et al. (2018). Yellow stars with numbers show deployment drifter positions. Green diamonds show long term mooring locations. Black dots indicate main sampling transects in the nBUS.

95   **Working area**

The BUS is one of the four major Eastern Boundary Upwelling Systems, which are among the most productive marine ecosystems in the world (Chavez and Messié, 2009; Carr, 2001). Although they cover only 2 % of the global ocean surface, they provide more than 20 % of the total global marine fishery yields (Pauly and Christensen, 1995; Sydeman et al., 2014) and contribute about 11 % to global export production (Chavez and Toggweiler,

100   1995). In almost all Eastern Boundary Upwelling Systems, distinct OMZ have been formed below the euphotic zone at depths between approximately 100 and 1000 m (e.g. Monteiro et al., 2011). They are the product of high

oxygen consumption, caused by the degradation of the exported POC, compared to the ventilation of the OMZ (Rixen et al., 2020 and references therein). Their expansion due to global warming is considered one of the greatest threats to marine life (Stramma et al., 2008; Stramma et al., 2012), alongside global warming and ocean

105 acidification (https://www.globalgoals.org/goals/14-life-below-water/).

The BUS extends from the Kunene river (~17°S) in the north to Cape Agulhas (~35°S) in the south. It is driven by the southeast trade winds that result from the pressure difference between the South Atlantic high and the continental low over southern Africa, which leads to the formation of individual, particularly prominent upwelling cells along the shoreline (e.g. Kämpf and Chapman, 2016; Sell et al., 2024; Shannon and Nelson, 1996; Veitch et

110 al., 2009). The strongest is the Lüderitz Cell, which divides the BUS at about 27°S into a northern (nBUS) and a southern subsystem (sBUS) (Hutchings et al., 2009; Shannon and O'tool, 2003). The two subsystems are influenced by two different source water masses, namely the South Atlantic Central Water (SACW) in the north and the Eastern South Atlantic Central Water (ESACW) in the south (McCartney, 1977; Shillington et al., 2006) which differ in their biogeochemical properties (Mohrholz et al., 2008; Flohr et al., 2014). Compared to the

115 ESACW, the SACW is low in oxygen and enriched in dissolved nutrients, which differentiates the dynamics of the OMZ in the nBUS and sBUS. In the nBUS, the OMZ is essentially controlled by the seasonally varying inflow of SACW (Monteiro et al., 2006; Mohrholz et al., 2008), whereas the sBUS OMZ is assumed to be influenced to a much greater extent by the seasonally varying productivity (Bailey, 1991; Pitcher and Probyn, 2011; Pitcher et al., 2014; Lamont et al., 2015). The consequences are that the sBUS OMZ develops predominantly in the bottom

120 waters on the shelf while the nBUS OMZ also extends along the continental slope (Fig. 2). Even if seasonal mass extinctions of some benthic organisms indicate that anoxic events occur in the sBUS in the shadow of oceanic fronts (Cockcroft, 2001; Cockcroft et al., 2008; Hutchings et al., 2009), the oxygen concentrations in the sBUS OMZ are generally higher than in the nBUS OMZ. Accordingly, anoxic processes such as anammox and denitrification have a significant effect on the nitrogen cycle in the nBUS (Kalvelage et al., 2011; Nagel et al.,

125 2013). Anoxic events, during which reduced gases such as CH_4 and H_2S are released from the sediment, often occur in connection with an increased influx of SACW in summer (Ohde and Dadou, 2018; Ohde et al., 2007).
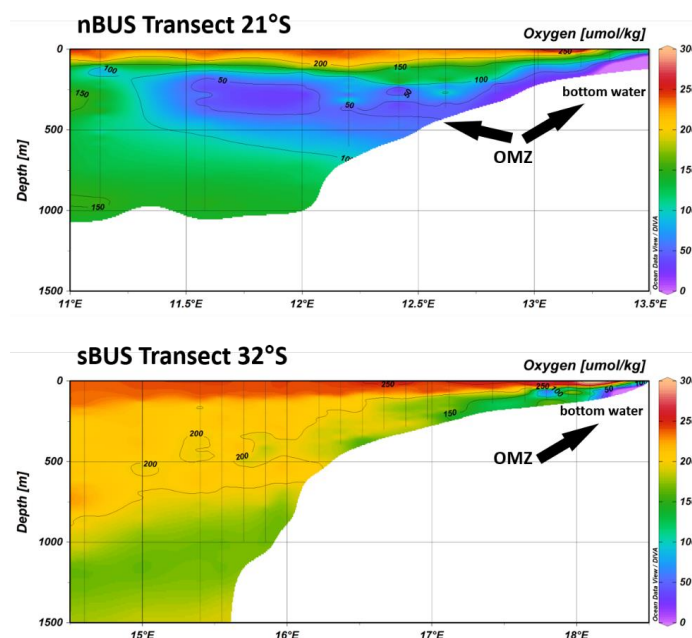
Figure 2 Oxygen concentrations along a transect in the nBUS and sBUS during cruise SO285, showing the near-bottom OMZ in the nBUS and sBUS, and the OMZ on the continental slope in the nBUS.

130   Calculations of the upwelling velocities from wind fields in comparison with model results show that strong spatial variations occur within the two subsystems due to the interaction of wind stress and the geometry of the coast. The upwelling at the coast and in the adjacent ocean (open ocean upwelling) can even be in opposite directions, meaning that strong coastal upwelling can be accompanied by weak upwelling in the adjacent ocean (Bordbar et al., 2021). In addition, mesoscale and sub-mesoscale processes such as eddies, filaments, the formation of oceanic

135   fronts and vertical mixing influence the vertical water mass transport (Rixen et al., 2021b; Flynn et al., 2020; Bakun, 2017; Rubio et al., 2009). As a result, localised upwelling can exhibit a pronounced seasonality, such as off Walvis Bay in the nBUS, but the seasonality is only weakly evident overall in the two subsystems (Bordbar et al., 2021).

    In contrast, sea surface temperatures (SST) in both subsystems show a pronounced seasonality with lower

140   temperatures in winter and higher temperatures in summer (Fig. 3). Off Walvis Bay, stronger upwelling develops in phase with the winter cooling whereas off Cape Columbine in the sBUS, the winter cooling is accompanied by weaker upwelling (Bordbar et al., 2021).
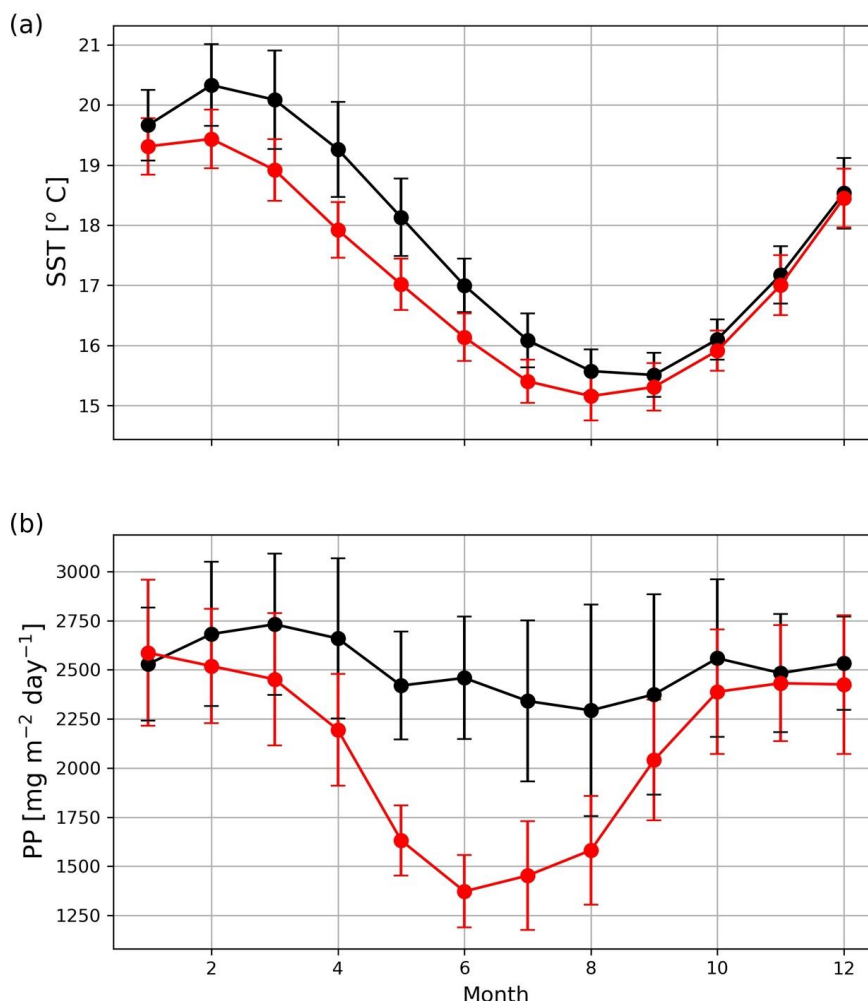
(a)

(b)

Figure 3 Mean annual cycles of sea surface temperatures (SST, a) and primary production rates (PP, b).

145   In line with satellite data, observations along the Namibian monitoring line off Walvis Bay showed that, favoured by the weak upwelling and summer warming, a relatively strong stratification develops in the surface water at the beginning of the summer. It dissipates at the end of the summer with the onset of winter cooling and the strengthening of the upwelling (Louw et al., 2016). The highest concentrations of chlorophyll were found in these transitional phases, with clear maxima at the beginning and end of the summer between November and January,

150   and March and April, respectively. Averaged over the two subsystems, the primary production derived from satellite data follows the seasonal pattern of chlorophyll concentration off Walvis Bay in both subsystems in so far as that primary production is lower on average in winter than in summer. In the sBUS, however, the seasonality is much more pronounced than in the nBUS, which, as already mentioned, also affects the sBUS OMZ, which expands in summer due to the increased production and stronger stratification in surface waters (Bailey, 1991;

155   Pitcher and Probyn, 2011; Pitcher et al., 2014; Lamont et al., 2015).

Methods

To investigate the seasonality and the influence of zooplankton on the POC, we moored a sediment trap system off Walvis Bay in the nBUS and off Hondeklip Bay in the sBUS (Table 1) and deployed a total of sixteen free-floating sediment trap arrays (drifters) on three research cruises (Table 2, Fig. 1). The sediment trap mooring off Walvis Bay was part of a long-term sediment trap experiment (Rixen et al., 2021a; Vorrath et al., 2018) that was conducted intermittently between April 2010 and August 2022 (Table 1, Fig. 4a). The long-term mooring experiment in Hondeklip Bay was carried out intermittently between October 2019 and April 2022. Both locations are close to the coast in water depths between 100 and 200 m. Hydrobios MST-12 sediment traps were anchored at both stations in water depths of ca. 60 and 95 m respectively. The Hydrobios MST-12 sediment traps were equipped with twelve sample bottles (250 ml Nalgene) that rotated under the trap at fixed programmed intervals. The collection intervals of the individual sample bottles were on average between 9 and 40 days. In order to prevent biological activity in the sample cups and to reduce the exchange with the ambient water, the water in the sample cups was poisoned with $HgCl_2$ (3.3 g/l) and enriched with salt (NaCl 70 g/l) before trap deployment.
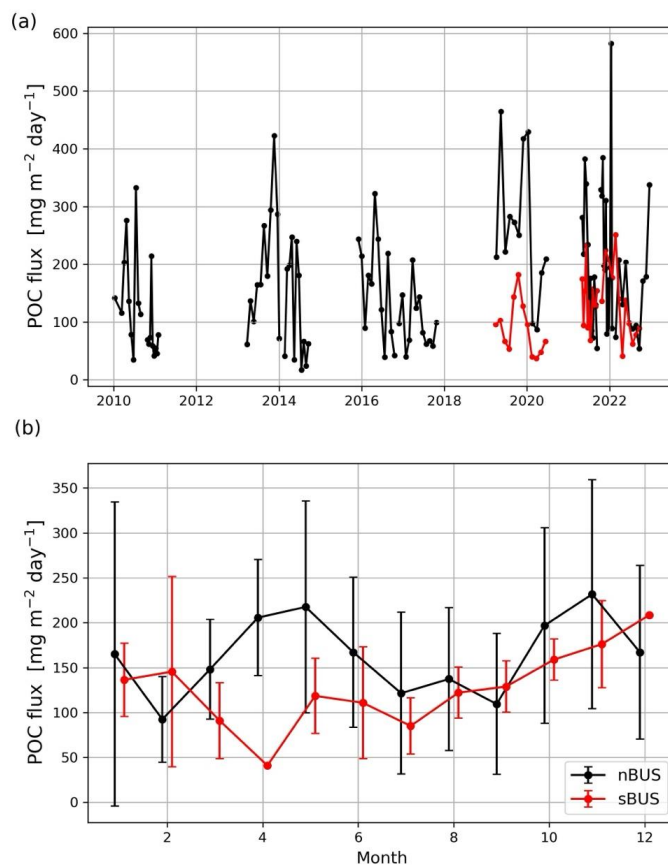
Figure 4 POC flux rates measured off Walvis Bay in the nBUS and Hondeklip Bay in the sBUS(a) and the mean annual cycle (b) derived from the data shown in (a).

Table 1 Overview of moored sediment trap deployments.

Station	Mooring No	Latitude [°S]	Longitude [°E]	Water Depth [m]	Trap Depth [m]	Start	End	Sampling Interval [days]
nBUS	1	-23.0000	14.0800	140	70	2009-12-15	2010-08-26	21
nBUS	2	-22.6000	14.2000	127	60	2010-11-27	2010-12-09	12
nBUS	3	-23.0225	14.0277	130	75	2013-07-04	2013-07-31	30
nBUS	4	-23.0248	14.0370	130	75	2014-05-14	2014-06-03	21
nBUS	6	-23.0165	14.0368	130	75	2016-04-25	2016-05-24	29
nBUS	7	-23.0173	14.0368	130	75	2017-04-26	2017-05-25	29
nBUS	8	-23.0231	14.2185	110	65	2019-10-21	2019-11-30	40
nBUS	9	-23.0229	14.0370	130	75	2021-07-01	2021-07-13	12
nBUS	10	-23.0232	14.0370	130	75	2021-11-29	2021-12-08	9
nBUS	11	-23.0233	14.0371	130	75	2022-07-22	2022-08-21	30
sBUS	1	-30.6367	17.0158	170	95	2019-10-21	2019-11-20	30
sBUS	2	-30.6374	17.0172	170	95	2021-07-02	2021-07-14	12
sBUS	3	-30.6378	17.0175	170	95	2022-03-24	2022-04-23	30

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Table 2 Overview of drifter deployments.

Region	Cruise ID	Drifter	Water depth (m)	Deployment [UTC]	Recovery [UTC]	Dep. Lat [°S]	Dep. Lon [°E]	Rec. Lat [°S]	Rec. Lon [°E]	Drift Distance [km]	Number of Traps	Trap Depth [m]
nBUS	M153	1	2050	2019-03-03 22:36	2019-03-05 16:33	22.9996	12.2489	22.9358	12.1475	15.4	5	50, 100, 200, 300, 500
nBUS	M153	2	1000	2019-03-06 22:18	2019-03-10 10:30	20.9999	11.9992	20.8942	11.9064	29.7	5	30, 50, 100, 150, 200
sBUS	M153	3	1300	2019-02-22 18:51	2019-02-25 12:13	31.0440	15.2280	30.9683	15.095	20.5	5	50, 100, 200, 300, 500
sBUS	M153	4	160	2019-02-18 11:07	2019-02-20 08:27	30.6417	17.0226	30.5275	16.8453	24.4	4	20, 30, 50, 75
sBUS	SO283	5	997	2021-04-15 19:58	2021-04-17 12:33	31.4987	15.4980	31.4802	15.4353	8.5	6	50, 100, 200, 300, 400, 500
sBUS	SO283	6	192	2021-04-16 09:15	2021-04-18 05:52	30.9998	16.9998	31.0366	16.9735	11.4	5	20, 30, 50, 75, 100
nBUS	SO283	7	1155	2021-04-21 09:16	2021-04-23 14:26	23.0001	12.7496	22.9750	12.6905	9.4	5	50, 100, 300, 400, 500
nBUS	SO283	8	248	2021-04-21 05:49	2021-04-23 10:19	23.0001	13.5833	22.9887	13.4818	15.6	5	20, 30, 50, 75, 100
nBUS	SO283	9	732	2021-04-24 14:41	2021-04-25 15:07	17.9998	11.3001	17.9641	11.3210	5.6	7	10, 50, 100, 200, 300, 400, 500
nBUS	SO283	10	360	2021-04-27 10:57	2021-04-29 11:19	25.0004	13.9151	24.868	13.6998	22.1	5	20, 30, 50, 75, 100
nBUS	SO283	11	1045	2021-04-27 04:59	2021-04-29 06:00	25.0002	13.3333	24.8684	13.2678	18.1	4	50, 100, 300, 400
sBUS	SO285	12	1097	2021-09-19 02:50	2021-09-19 15:48	31.9298	15.7738	31.9298	15.7738	1.91	5	20, 50, 100, 150, 200
sBUS	SO285	13	155	2021-09-21 01:22	2021-09-21 14:44	30.9962	17.3493	30.9180	17.3133	9.95	5	20, 30, 50, 75, 100
sBUS	SO285	14	1047	2021-09-24 07:57	2021-09-25 14:15	30.3525	14.5834	30.3296	14.4208	17.8	6	50, 100, 200, 300, 400.0, 500
nBUS	SO285	15	1888	2021-10-01 19:35	2021-10-02 15:35	22.9981	12.3988	22.8982	12.4168	18.01	6	50, 100, 200, 300, 400, 500
nBUS	SO285	16	517	2021-10-05 07:19	2021-10-07 12:01	21.0223	12.4218	20.7052	12.4466	35.97	5	20, 50, 100, 150, 200

Haake et al. (1993) and Rixen et al. (1996) described the sediment trap sample processing and analysis of sediment

180   trap samples in detail. Initially the samples were divided into > 1 and < 1 mm fractions following the international protocol from (Honjo et al., 2008). The > 1 mm fraction contains active swimmers, i.e. zooplankton (Lee et al., 1988). The < 1 mm fraction represents the passive flux whose main components (POC, carbonate, biogenic opal and lithogenic material) were analyzed. The POC flux multiplied by 1.8 gives the flux of organic material (OM) and the flux of lithogenic material is the difference between the total flux and the fluxes of OM, carbonate and

185   biogenic opal.

The sixteen drifters were deployed during the cruises with the German RVs Meteor (M153) and Sonne (SO283, SO285, Rixen et al., 2021b; Lahajnar et al., 2021). During the cruises a total of 83 single sediment traps were deployed along with the sixteen drifters (Table 3). To keep the drifter in an upright position, they were equipped with a buoyancy unit at the upper end and a 30 kg ballast anchor at the lower end. The buoyancy unit also included

190   an Iridium GPS transmitter, in order to track the drifter after the deployment. Between the buoyancy unit and the ballast anchor, 4 - 7 Saarso single sediment traps were attached. The water depth at which the sediment traps were deployed varied with the bottom water depth. At water depths of > 1000 m, the sediment traps were generally deployed at water depths of 50 m, 100 m, 200 m, 300 m, 400 m and 500 m (see Table 2 for further details). The Hydrobios MST-12 and Saarso Single Trap are both manufactured by Hydrobios, Germany, which uses an

195   identical cylinder design for both traps with a funnel collection area of 0.015 m².

Table 3 List of drifter-related cruises.

Cruises	Start	End	Season	Ports of embarkation and arrival
M153	2019-02-15	2019-03-31	Summer 2019	Walvis Bay, Namibia – Mindelo, Cape Verde
SO283	2021-03-19	2021-05-25	Autumn 2021	Emden – Emden, Germany
SO285	2021-08-20	2021-11-02	Spring 2021	Emden – Emden, Germany

After recovery, the drifter samples as well as the samples from the moored traps were stored at 4°C in the laboratory

200   until further processing. In the laboratory in Hamburg, the drifter samples were analyzed macroscopically and microscopically using a Keyence VHX-6000 digital microscope. Identifiable zooplankton, mostly > 1 mm, was removed from the samples and classified according to Tutasi and Escribano (2020), Ekau et al. (2018) and Castellani and Edwards (2017). The zooplankton was divided into 8 groups: amphipoda, copepoda, decapoda, euphausiacea, ostracoda, pteropoda, fish larvae, and gelatinous zooplankton. However, there were also some

205   samples where the zooplankton could not be further identified and were classified as 'zooplankton unknown'.

Subsequently, all samples (the removed zooplankton groups and the remaining < 1mm fraction) were transferred to 0.45 μm polycarbonate filters and rinsed with a sodium tetraborate buffer solution (2 mg $Na_2[B_4O_5(OH)_4]$ $8H_2O$ per 1 liter H_2O) to remove the salt and avoid the dissolution of carbonates. After filtration, the filters were dried and weighed to determine the flux in the individual zooplankton groups and the < 1mm fraction. The dried material

210   was removed from the filters to analyze the main components, as described before.

Due to the lack of sample material, it was often not possible to analyze carbonate and biogenic opal. In addition, the chemical analysis of the zooplankton groups was limited to determine the total carbon and nitrogen concentrations, hence the carbonate carbon concentration was not taken into account. As a larger proportion of carbonate is only to be expected in shell-bearing zooplankton, e.g. from the pteropoda group, we assume that the

215   resulting error is small and negligible. The calculated POC flux of the individual zooplankton groups was added

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to the total zooplankton POC flux, which is referred to as the active POC flux. The active POC and the passive (<1 mm) POC flux together result in the total POC flux.

Satellite-derived monthly mean sea surface temperature (SST, Reynolds et al., 2002) and net primary production rates (Behrenfeld and Falkowski, 1997) were downloaded from the OI-SST web site

220 (http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/. sst/) and the ocean primary production website (http://www.science.oregonstate.edu/ocean.productivity/) in November 2023. The SST data with a spatial resolution of 0.33 * 0.33 degrees covered the period from 1981 to 2023 while the primary production rates with 1x1 degree resolution covered the periods between 2002 and 2023. When calculating the mean values for the BUS and the two subsystems, it was assumed that the BUS covers the

225 area between the coast and approximately 250 km offshore, within the latitudes we have previously specified (15-35°S).

Results

During the research cruises, the primary production rates at the coast reached values of > 9000 mg m^{-2} day^{-1}, which decreased with increasing distance from the coast and fell to values of < 10 mg m^{-2} day^{-1} far offshore (Fig. 5). The

230 primary production rates at the drifter positions varied between 544.6 mg m^{-2} day^{-1} and 5115.4 mg m^{-2} day^{-1} and revealed a mean of 1618.6 ± 1110.6 mg m^{-2} day^{-1}. They thus fell below the average primary production rates, which were 2505.3 mg m^{-2} day^{-1} in the nBUS and 2089.6 mg m^{-2} day^{-1} in the sBUS (Fig. 3b). Overall, the primary production derived from the satellite data largely fell within the range of primary production rates determined during research cruises (140 – 8830 mg m^{-2} day^{-1}) and hardly revealed any difference between the nBUS and sBUS

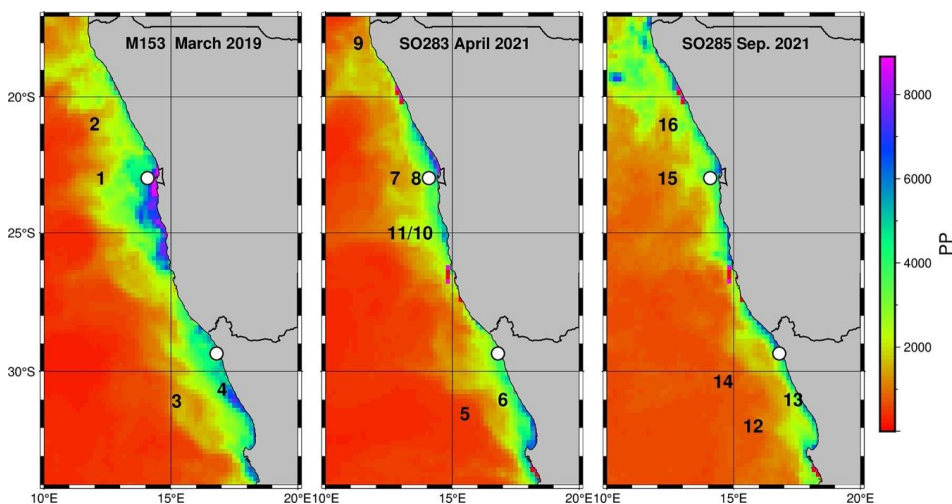235 (Barlow et al., 2009).

Figure 5 Primary production rates (PP) in mg C m^{-2} day^{-1} during the various research cruises as well as the locations of the drifters (black numbers) and long-term sediment trap moorings (white circles).

The drifter results from the 83 traps showed that copepod biomass accounts for the largest proportion of the active

240 POC flux in both subsystems (55.7 % and 46.2 % in the nBUS and sBUS), followed by the biomass of amphipods and euphausiids (Fig. 6). The combined proportion of the three groups (copepods, amphipods and euphausiids) amount to about 77.3 % (nBUS) and 87.4 % (sBUS).
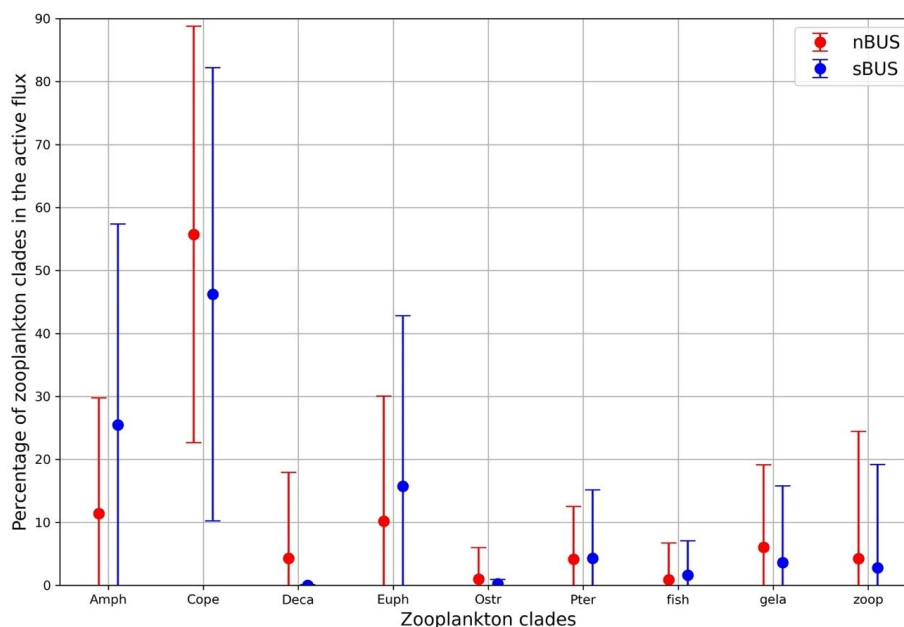
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Figure 6 Proportion of zooplankton groups in the active POC averaged over all traps.

245   The proportion of the active POC flux to the total POC flux was on average higher in the sBUS (72.9 %) than in the nBUS (62.0 %) and varied with depth by ± 14.2 % (nBUS) and ± 9.0 % (sBUS). Averaged over all water depths and drifter deployments, an active POC flux of 944.5 ± 743.6 mg m^{-2} day^{-1} in the sBUS was almost 3 times as high as in the nBUS with 322 ± 231.7 mg m^{-2} day^{-1}. This difference was particularly visible in the upper water column (water depths < 100 m), and decreased in greater water depths where the active POC flux in nBUS could

250   even exceed that in the sBUS (Fig. 7a).

Compared to the active POC flux, the passive POC flux in the sBUS is only slightly higher (293.9 ± 249.0 mg m^{-2} day^{-1}) than in the nBUS (203.1 ± 157.0 mg m^{-2} day^{-1}). The passive POC flux tends to decrease with depth (Fig. 7b) and shows an average POC flux of 135.9 ± 82.3 mg m^{-2} day^{-1} (nBUS) and 365.1 ± 187.3 mg m^{-2} day^{-1} (sBUS) at a water depth of 100 m. In contrast, the POC flux in the moored traps averaged over the entire observation

255   period in the nBUS at a water depth of 64 m and in the sBUS at a water depth of about 100 m was 169.8 ± 128.6 mg m^{-2} day^{-1} and 120.1 ± 55.8 mg m^{-2} day^{-1}, respectively. The data from the moored sediment traps showed no clear seasonal variability, but in the nBUS there was significant interannual variability (Fig. 4). However, our time series is still too short to make statements about interannual variability in the nBUS and sBUS.
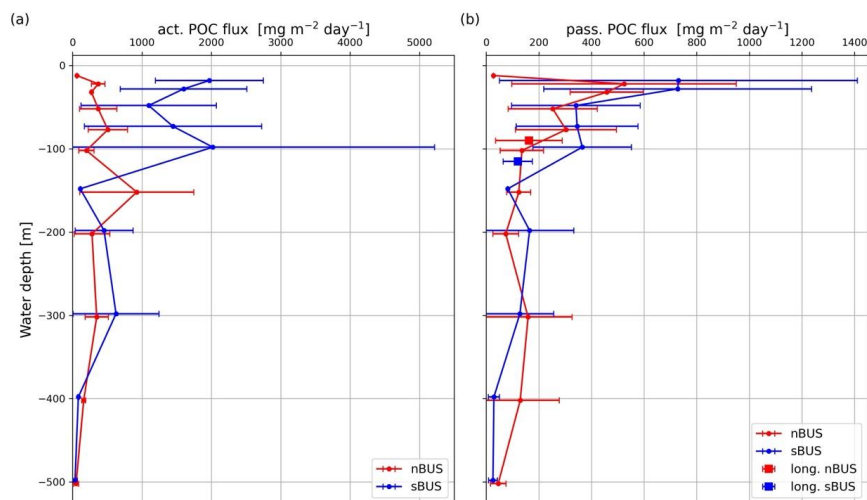
Figure 7 Active (a) and passive POC flux (b) averaged over all traps deployed at the same water depth versus water depth, including mean passive POC flux rates of the long-term moorings in the nBUS and sBUS.

Discussion

The drifters were deployed on the shelf and along the continental slope at the beginning and end of the summer season. However, as mentioned before, the drifters were deployed in areas where the primary production was on average below the mean summer primary production and it ranged between 544.6 and 5114.4 mg m^{-2} day^{-1}. The active and passive POC flux in the upper water column (water-depth < 100 m) varied between 45.3 and 9121.2 mg m^{-2} day^{-1} and 8.8 – 1878 mg m^{-2} day^{-1} respectively. This means that the variability of the active POC flux exceeded that of primary production, and the variability of the passive POC flux, which is comparatively low, still extends over three orders of magnitude. These large variations are the product of the interaction between the oceanographic processes that influence the transport of nutrients into the euphotic zone, their horizontal distribution in the surface water and biological processes that convert the nutrients into biomass and export them as POC. Our data density is not sufficient to disentangle this complex interaction completely, but on average the sediment trap results agree well with the results of other studies. For instance, vertical hauls down to a water depth of 600 m with a Hydro-Bios Multi Plankton Sampler in the Humboldt Upwelling System off northern Chile yielded a mean biomass of migrating zooplankton of 958 mg C m^{-2} day^{-1} (Tutasi and Escribano, 2020), which is quite similar to the mean active POC flux derived from our free-floating trap samples (944.5 ± 743.6 mg m^{-2} day^{-1} in the sBUS and 322 ±- 231.7 mg m^{-2} day^{-1} in nBUS). In the California Upwelling System, the active and passive POC flux at a water depth of 100 m was estimated at 34.8 and 108.0 mg m^{-2} day^{-1}, respectively (Stukel et al., 2023). This active POC flux is below what we have measured in nBUS at a water-depth of 100 m (200 ± 108 mg m^{-2} day^{-1}) but in the range of what we have seen in the sBUS (2022.1 ± 3195 mg m^{-2} day^{-1}, Fig. 7a). The passive flux off California, on the other hand, is in the range of what we have measured with the free-floating sediment traps in the nBUS (135.8 ± 82 mg m^{-2} day^{-1}, Fig. 7b) but falls below what was measured in the sBUS (365.1 ± 187.2 mg m^{-2} day^{-1}, Fig. 7b). Hence, overall our results agree quite well with those derived from other Eastern Boundary Upwelling Systems.

285   Our sediment trap results show furthermore, that copepods dominate the active POC flux, which is consistent with
        biological studies showing that the most commonly found cyclopoida and calanoida copepod orders dominate the
        abundance of mesozooplankton in the nBUS and sBUS (Verheye et al., 2016; Bode et al., 2014). Between 70-85
        %, the average proportion of copepods in the zooplankton abundance is slightly greater than the proportion of
        copepods in the active POC flux in the nBUS (55.7 ± 33.1 %) and sBUS (46.2 ± 36 %, Fig. 6). However, this
290   implies that copepods in the BUS not only play a key role as a food source for the conservation of marine fish
        stocks, but are also of great importance with respect to the active POC flux. Nevertheless, the question now arises
        to what extent this also applies to the POC transport to the sediment.

        Zooplankton influence POC flux to sediment in many ways (Steinberg and Landry, 2017). They reduce it through
        grazing and disaggregation and can increase it by dying and/or excretion, which both increase the passive POC
295   flux. This means that the active POC flux affects the POC supply to the sediment through its influence on the
        passive POC flux which might be underestimated as it is ultimately difficult to decide whether an animal actively
        swam into the trap or died above the trap and fell passively into it. However, in the sBUS the active POC flux is
        almost 3 times higher than in the nBUS, but passive POC flux does not differ greatly between the two subsystems,
        considering the large standard deviations (Fig. 7). This implies that, influence of zooplankton on the passive POC
300   flux during the period of our observations was small or that processes in the nBUS compensate for the influence
   of zooplankton compared to the sBUS.

        On average, the passive POC flux decreases with depth as commonly observed in other studies (Cael and Bisson,
        2018; Martin et al., 1987; Giering et al., 2014). In order to ensure comparability with other regions, we used the
        mean passive POC flux rates to determine the F_{MLD} and the 'b' of the Martin curve by means of a curve fit (Python
305   scipy.optimize/curve fit). This resulted in a F_{MLD} of 1117.2 mg C m^{-2} day^{-1} and a 'b' of -0.74 (Fig. 8). If the 'b' is
        reduced to -0.86, the resulting curve represents the long-term sediment trap data off Walvis Bay in nBUS and
        Hondeklip Bay in sBUS significantly better. 'b' values of -0.74 and -0.86 are in the range of the 'b' values found in
        the Pacific Ocean and the Atlantic Ocean (b = -0.5 to -1.38, (Giering et al., 2014) as well as in the California
        upwelling system (b = -0.72, Stukel et al., 2023). The calculated POC flux rates also agree well with those
310   measured in previous sediment trap studies in the BUS at water depth > 500 m (Fig. 8a, Vorrath et al., 2018).
        Overall, the measured and calculated POC fluxes correlated with each other and showed a Pearson correlation
        coefficient (r) of 0.927 (Fig. 9).
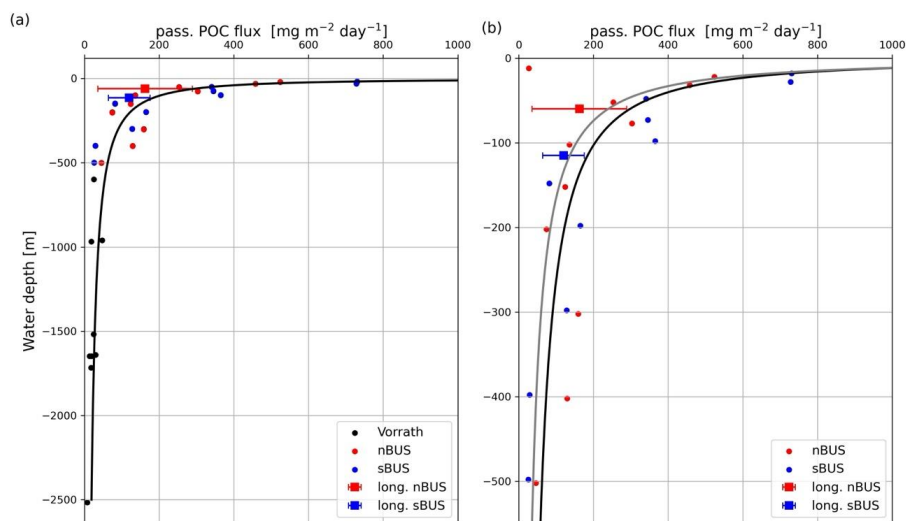
Figure 8 Mean POC flux rates versus water depths of 0 m - 2500 m (a) and 0 m - 500 m (b). The curves are Martin curves with
315 a 'b' of -0.74 (black) and -0.86 (grey). The result of an nBUS trap at 10 m water depth (see b, red circle at 10 m depth) was not
considered in the curve fitting. Vorrath data taken from Vorrath et al. (2018).

When fitting the determined POC fluxes to the curve, we assumed a mixed layer depth (MLD) of 10 m. This
corresponds to the shallowest deployment depth of our traps (see Table 3) and reflects the decrease of the mean
POC flux with depth (Fig. 8). Furthermore, it roughly corresponds to observations of the MLD near the coast, but
320 the MLD also increased further offshore (Louw et al., 2016). Other studies used a MLD of 100 m (Stukel et al.,
2023; Emeis et al., 2017). However, the selected MLD of 10 m results in a F_{MLD} (=export production) of 1117.2
mg C m^{-2} day^{-1}. If the MLD is reduced, the calculated F_{MLD} increases. If the MLD is set to 1 m, it loses its influence
on the calculated F_{MLD}. Theoretically, the F_{MLD} would then correspond to the primary production, assuming that
the equation only applies if the MLD is >= 1 m. By using an MLD of 1 m, the F_{MLD} reaches a value of
325 5994.7 mg C m^{-2} day^{-1} which is more than twice as high as the average primary production rates in the nBUS of
2505.3 mg C m^{-2} day^{-1} (Fig. 3). However, compared with the primary production rates of 2089.75 mg C m^{-2} day^{-1}
(sBUS) and 2505.3 mg C m^{-2} day^{-1} (nBUS), the 10 m export production of 1117.2 mg C m^{-2} day^{-1} suggest an f-
ratio (=export production/primary production) of approximately 0.4 to 0.5, which is characteristic of highly
productive systems (Eppley and Peterson, 1979). The mean passive POC flux in the BUS thus appears to follow
330 the general attenuation equations, which means that we have performed a sufficiently high number of experiments
that allowed us to recognize this general rule despite the large spatial and temporal variability.

Assuming a mean water depth of 150 m, the derived Martin equations (b of -0.74 and -0.86, respectively) suggest
a POC supply to sediments of 108.8 - 152.0 mg C m^{-2} day^{-1}. Compared to the primary production rate this implies
that 4 – 7 % of primary produced POC reaches the sediment. This is consistent with our former result of 5 % based
335 on the long-term sediment trap study off Walvis Bay and contradicts the results of a numerical model, which states
that 49 % of the primary produced POC reaches the sediment surface (Emeis et al., 2017). However, the similar
POC fluxes in nBUS and sBUS are remarkable, especially considering the differences in the active POC flux and
the OMZ intensity.
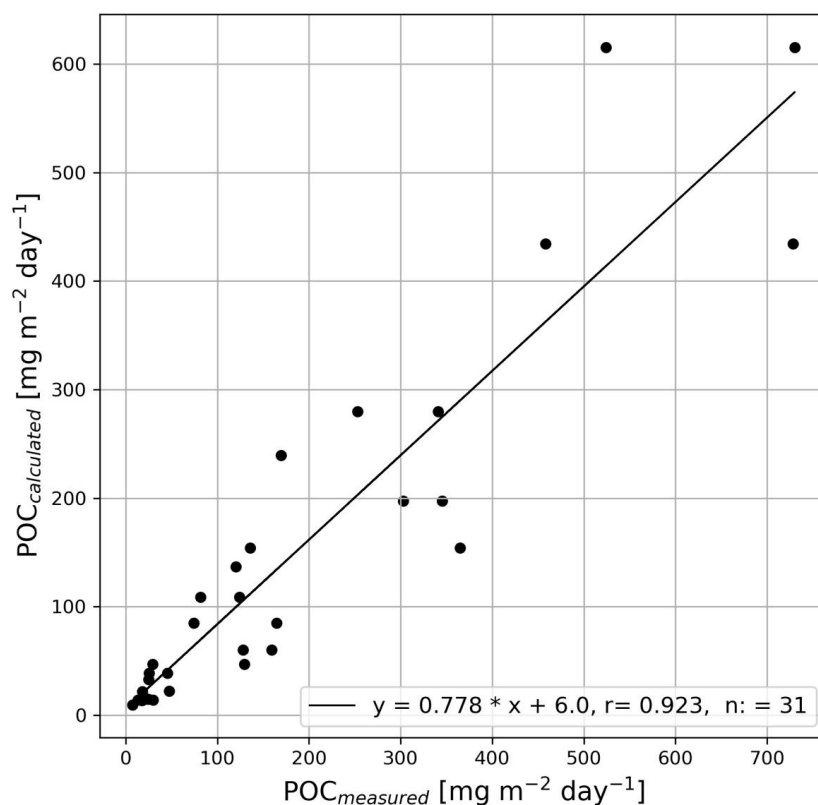
Figure 9 Correlation of measured POC fluxes shown in Fig. 8a versus that calculated POC fluxes derived from the Martin curve with a 'b' of -0.74.

Low oxygen concentrations and the associated transition from oxic to anoxic degradation processes are considered to be a factor that reduces POC degradation in the water column and surface sediments (Paropkari et al., 1993; Laufkötter et al., 2017). In the nBUS it was also shown that oxygen concentration affects the quality of the preserved organic matter (Nagel et al., 2016). If the lower oxygen concentrations in the nBUS have a positive effect on the POC flux, one could also say that this applies to the higher zooplankton abundance in the sBUS. Therefore, bearing in mind that primary production rates and passive POC fluxes differ only slightly in the two systems, zooplankton seem to increase the POC flux in the sBUS in the same way that low oxygen levels do in the nBUS. A more efficient export, e.g. by producing fast sinking fecal pellets, could explain this and it would also be consistent with our observations. They show, as mentioned before, that the difference in the active POC flux between the sBUS and nBUS is essentially limited to water depths of < 100 m (Fig. 7 a), suggesting an increased production of fecal pellets in the surface water of the sBUS.

Nearly equal POC fluxes compared to POC concentrations and POC storage in the sediment in turn indicate that the more intensive OMZ largely caused the formation of the mud belt in the nBUS. Hence an expansion of the OMZ as a result of global warming could therefore increase CO_2 storage in sediments by reducing POC degradation in sediments that are still flushed by oxygenated bottom waters. However, this also increases the risk of anoxic events that threaten fisheries, and the emission of reduced gases such as CH_4 could increase.

Summary

Our results indicate that the large variability of the measured POC fluxes reflect the expected spatial and temporal

360   variability of the BUS. On average, however, and in line with other studies, our results show that copepods

dominate the abundance of zooplankton and the active POC in both subsystems. The active POC flux in the sBUS

was almost 3 times as high as in the nBUS. This difference was particularly evident in the upper 100 m of the

water column. In contrast to the active POC flux, the passive POC flux was nearly equal in both subsystems, and

could be described by common POC flux attenuation equations similar to those used in other regions. A similar

365   productivity and POC supply but large variations in POC concentration and storage in the surface sediments of the

nBUS and sBUS suggest that the oxygen concentration in the bottom water of the OMZ has a decisive influence

on POC sedimentation. Anoxic events as a result of the influx of oxygen-depleted water into the BUS indicated

the sensitivity of the system to decreasing oxygen concentrations as caused by the global intensification of OMZs.

Although this could favour the accumulation of POC in the sediments still flushed by oxygen-rich bottom water,

370   it bears the risk of increasing the frequency of anoxic events in oxygen-poor upwelling systems, with as yet

unknown consequences for the emission of reduced gases such as CH_4 and fatal consequences for the pelagic

ecosystem and fisheries.

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Figure Caption

Figure 1 POC concentration in the BUS from various research expeditions published in Emeis et al. (2018). Yellow stars with numbers show deployment drifter positions. Green diamonds show long term mooring locations. Black dots indicate main sampling transects in the nBUS.

665 **Figure 2** Oxygen concentrations along a transect in the nBUS and sBUS during cruise SO285, showing the near-bottom OMZ in the nBUS and sBUS, and the OMZ on the continental slope in the nBUS.

Figure 3 Mean annual cycles of sea surface temperatures (SST, a) and primary production rates (PP, b).

Figure 4 POC flow rates measured off Walvis Bay in the nBUS and Hondeklip Bay in the sBUS(a) and the mean annual cycle (b) derived from the data shown in (a).

670 **Figure 5** Primary production rates (PP) during the various research cruises as well as the locations of the drifters (black numbers) and long-term sediment trap moorings (white circles).

Figure 6 Proportion of zooplankton groups in the active POC averaged over all traps.

Figure 7 Active (a) and passive POC flux (b) averaged over all traps deployed at the same water depth versus water depth, including mean passive POC flux rates of the long-term moorings in the nBUS and sBUS.

675 **Figure 8** Mean POC flux rates versus water depths of 0 m - 2500 m (a) and 0 m - 500 m (b). The curves are Martin curves with a 'b' of -0.74 (black) and -0.86 (grey). The result of an nBUS trap at 10 m water depth (see b, red circle at 10 m depth) was not considered in the curve fitting.

Figure 9 Correlation of measured POC fluxes shown in Fig. 8a versus that calculated POC fluxes derived from the Martin curve with a 'b' of -0.74.

680 **Table Caption**

Table 1 Overview of moored sediment trap deployments.

Table 2 Overview of drifter deployments.

Table 3 List of drifter-related cruises.