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Presence of two eddies in close proximity drives large spatial and temporal heterogeneity in the euphotic zone

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ABSTRACT

Oceanic mesoscale structures, such as eddies, play a fundamental role in ocean circulation, ocean biogeochemical cycles and plankton ecology. They cause lateral and vertical advection, as well as interact with vertical mixing, which is predicted to promote episodic fluxes of macronutrients to the surface ocean. However, the interactions between mesoscale eddies can generate submesoscale fronts and filaments occurring over short temporal and spatial scales and thus their impact on ocean biogeochemistry has been difficult to characterize. During an expedition to the Porcupine Abyssal Plain (PAP) site in the Northeast Atlantic in June 2013, we studied the interface between a cyclonic and an anticyclonic eddy, measuring nutrient and chlorophyll-a concentrations, zooplankton abundance and community structure, and marine snow aggregate abundance and sinking velocities. We observed that eddy rotation and a storm event induced, respectively, lateral stirring and vertical mixing of the two distinct water masses, driving spatial and temporal biogeochemical heterogeneity at the PAP site. Furthermore, we observe that diel and vertical variations in aggregate type and abundance were closely linked to the vertical distribution and abundance of zooplankton, suggesting that zooplankton were the main gatekeepers of carbon flux. Our findings suggest that the interactions between mesoscale structures could significantly modify organic carbon export, as well as provide sustenance for higher trophic levels, processes that have implications for fisheries and global climate.

1. Introduction

Oceanic mesoscale (10–100 km) and submesoscale (1–10 km) processes play a fundamental role in ocean circulation, ocean biogeochemical cycles and plankton ecology (Mahadevan, 2016; McGillicuddy, 2016). These mechanisms are caused by physical instabilities and give rise to complex chemical and biological processes that drive ecosystem structure and function. During the last decades, the improvement of remote sensing technology has substantially increased the spatial resolution of chlorophyll measurements (*e.g.*, 250 m horizontal resolution for the MODIS system on NASA's Aqua satellite). This has led to the realization that meso- and submesoscale turbulent flows cover the majority of the global surface ocean and are the main drivers for phytoplankton patchiness (d'Ovidio et al., 2004; Lévy et al., 2018). Two types of turbulent flow can be identified in relation to phytoplankton distribution and diversity; (i) direct lateral transport (*e.g.*, stirring and trapping of the water masses; d'Ovidio et al., 2004) and (ii) those that indirectly affect phytoplankton *via* regulation of nutrient and/or light availability (Kessouri et al., 2020; Lévy et al., 2001; Mahadevan, 2016).

Lateral and vertical physical forcings of (sub)mesoscale structures modulate primary production and organic matter export out of the photic zone (e.g., Fischer et al., 2016; Stukel et al., 2017; Taylor et al., 2020; von Appen et al., 2018; Waite et al., 2016). In well-stratified regions such as oligotrophic ecosystems, (sub)mesoscale features can generate physical instabilities, releasing nutrients from the mesopelagic to the surface water where they can support phytoplankton growth

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(Mahadevan, 2016). Models estimate that (sub)mesoscale structures such as eddies and elongated filaments could deliver 0.14 and 0.12mol N m⁻² y⁻¹ nutrients via upwelling to the euphotic zone on a global scale, respectively (Lapeyre and Klein, 2006). Paradoxically, submesoscale features can also promote primary production by stabilizing the water column within days in less stratified regions, increasing light exposure of phytoplankton (Mahadevan, 2016). In parallel, vertical velocities induced by submesoscale processes also have consequences for the subduction of surface water together with suspended particulate organic carbon (POC) and phytoplankton cells to the mesopelagic. Eddy-driven subduction has been estimated to equal half of the total springtime POC export in the productive subpolar ocean (Omand et al., 2015; Resplandy et al., 2019). However, our understanding of sub- and mesoscale structures is limited by our capabilities to find them during short research expeditions, since satellite observations only capture surface signatures but cannot measure the complex subsurface processes associated with mesoscale structures. As a result, we only have a very rudimentary understanding of the complex interplay between physical, chemical, biological, and ecological processes that seem to characterize these structures. Furthermore, submesoscale motions cannot be sampled with strategies employed during traditionnal field campaigns and long-term moored instruments. These methodological limitations in detecting sub- and mesoscale structures have caused them to be overlooked in most studies, and, hence, they were considered to only have a negligible role for ecology and biogeochemistry (McGillicuddy et al., 2003).

The recent development of autonomous instruments and sensors mounted on gliders, floats, and moorings has allowed high-resolution spatiotemporal measurements and provided the first insights into how physics shapes oceanic biogeochemistry on both small and large scales (e.g., Picheral et al., 2022). Today, submesoscale features and their impact on chemistry and biology, especially the impact on the oceans' capability to mitigate climate change, constitute one of the biggest challenges for future research. The advent of instruments that increase sample resolution also requires well-designed sampling programs, sophisticated infrastructures, strong coordination and a significant logistical effort. This challenge has been endorsed by the Ocean Surface Mixing, Ocean Submesoscale Interaction Study (OSMOSIS) research consortium, which has helped to bridge the gap between observations and models (Buckingham et al., 2019). Their efforts have improved our understanding of submesoscale processes in the North Atlantic region through the deployment of several autonomous instruments with highfrequency data acquisition (Thompson et al., 2016). The North Atlantic OSMOSIS site was located at the transition between the mesotrophic subpolar gyre and the oligotrophic subtropical gyre, where eddies play a crucial role in shaping oceanic processes and nutrient dynamics (Hartman et al., 2010; Painter et al., 2010a; Robinson et al., 1993). The region also has a strong seasonality with phytoplankton blooms occurring both in spring and summer (Lampitt et al., 2001). Additionally, a substantial amount of carbon is exported from the surface to the deep sea in the region, accounting for 5–18 % of the annual global ocean carbon export (Sanders et al., 2014). Moreover, the OSMOSIS study was close to the Porcupine Abyssal Plain sustained observatory (PAP), which is a heavily instrumented observatory recording physical, biological, and chemical data continuously in the water column and on the seabed (Lampitt et al., 2010a).

Here, we take advantage of a multitude of data to study how (sub) mesoscale physics impact nutrient availability, phytoplankton distribution, zooplankton behavior, and carbon export at the OSMOSIS and the PAP sites. We show that presence of two eddies in close proximity and a storm event drive large spatial and temporal heterogeneity of biological, biogeochemical and ecological processes in the euphotic zone via lateral advection and vertical mixing of subpolar and sub-tropical water masses.

2. Material & methods

The data were obtained using three different approaches; i) shipbased measurements providing high spatial resolution (section 2.1), ii) moorings, gliders and satellites providing long-term observations (section 2.2), and iii) a Lagrangian model to couple the two data sets (section 2.3). All the analyses and figures presented in this manuscript were performed and created using Python and R software.

2.1. Observations from ship

The sampling campaign was carried out at the Porcupine Abyssal Plain sustained observatory (PAP-SO; Lampitt et al., 2010a) (Fig. 1a) aboard the RSS *James Cook* (JC087) from 3rd to 14th June 2013. During this period, twenty-four vertical profiles were made with the CTD-Rosette to determine temperature, salinity, density, fluorescence, and turbidity through the water column (Table 1).

Nutrient and chlorophyll measurements. Vertical profiles of nutrients and chlorophyll-a concentrations were determined from water collected using Niskin bottles. In addition, water was sampled from 5 m depth every 4 h using the ship's underway system. Phosphate (PO_4^{3-}), silicate (Si(OH)₄) and ammonia, nitrate and nitrite (NH_4^+ , NO_3^- , and NO_2^-) concentrations were measured using a SEAL system (Analytical UK Ltd, AA3 segmented flow autoanalyzer) following methods described by Kirkwood (1996). A total of 571 samples were analyzed (502 CTD, 69 underway). Chlorophyll-a concentrations were measured from 250 ml samples filtered onto 25 mm GF/F Whatman filters (nominal pore size ~0.7 µm). The pigment extraction was done by placing the filter in 90 % acetone in 8 ml glass vials in the dark at 4 °C for 18–20 h. The extracted pigments were quantified on a Turner Designs TD700 fluorometer equipped with filters and calibrated against a pure chlorophyll-a standard (Sigma, UK).

Zooplankton abundance. Zooplankton distribution and abundance were measured 10 times during the cruise using a Multinet Midi (Hydrobios) equipped with five nets with a mesh size of 335 μ m and a mouth opening of 0.25 m². Both day and night deployments were carried out, sampling 5 discrete depth layers: 1000–500 m, 500–300 m, 300–100 m, 100–50 m, and 50–0 m. The nets were hauled vertically from the deepest sampling depth to the surface at a speed of 0.5 m.s⁻¹. Each sample was preserved in 4 % buffered formalin before the zooplankton were taxonomically identified and counted using a dissecting microscope.

Video Plankton Recorder. The Video Plankton Recorder (VPR) was used in complement to the plankton nets to provide optically-derived data on the mesozooplankton and particles. The VPR was equipped with a CTD sensor (Seabird SBE49), and a combined chlorophyll-*a* fluorescence sensor and turbidity sensor (Wetlabs Ecopuck). The VPR imaged a water volume of 26.3 ml per image and recorded with a frame rate of ca. 20 images.s⁻¹. The VPR was deployed vertically during both day and night from the surface to 500 or 1000 m at a mean wire speed of 0.83 m.s⁻¹. Recorded images from both the up- and downcasts were downloaded to the shipboard computer and extracted using the Auto-Deck software (Seascan, Inc., USA). Automatic classification of the images was done using the software package 'Visual Plankton' (WHOI-USA, Davis et al., 2005) and the classification was manually verified to extract the vertical distribution of marine snow aggregates. The optical resolution was 1.4 Mpixel, with 10 bits per pixel (*i.e.*, 320 grey levels).

Echosounder. Hull-mounted SIMRAD EK60 echosounders operating at 18, 38, 70, 120 and 200 kHz were used for recording acoustic data. Due to the transducer draft and to prevent near-field effects (Simmonds and MacLennan, 2008), the upper 20 m of the water column was excluded from the analyses of the hydroacoustic data. While the SIM-RAD EK60 was recording during the entire duration of the campaign, we focussed on composite echograms that were recorded simultaneously with the VPR deployments. The observation range (high frequencies attenuate faster) and organism scattering (scatter responses differ as a



Fig. 1. (a) Sampling area location during the JC087 cruise combined with (b) physical structure and the chlorophyll-a concentration obtained by remote sensing on the 31th May 2013. Contour lines and arrows show the sea level anomaly (SLA; m) and the current velocity $(m.s^{-1})$, respectively. The small black and red squares represent the locations of the moorings deployed during the OSMOSIS program and at the PAP site, respectively. The red line refers to a transect by glider SG510 performed between 3rd and 5th June 2013. The letters CE and AE represent the core of the cyclonic and anticyclonic eddy, respectively. (c) Vertical profiles of temperature, salinity, and chlorophyll-a as a transect across the front between the two eddies measured by the SG510 glider. The T-S diagram (d) was used to identify the water masses. Blue dots indicate profiles with maximum salinity < 35.66, characteristic of subpolar Eastern North Atlantic Central Water (ENACWp), while red dots represent salinities > 35.66, associated with subtropical Eastern North Atlantic Central Water (ENACWt). The vertical and horizontal red lines show the references estimated by Harvey (1982) to distinguish between ENACWt and ENACWp.

function of size and body properties) are frequency dependent (Benoit-Bird and Lawson, 2016) making the multi-frequency echosounder system able to differentiate between marine organisms through the water column. Given the high density differences between the surrounding water and different types of organisms, we can use scatter frequencies to identify gas-bearing marine organisms (*e.g.*, fish or siphonophores) from 18 kHz, while fluid-like organisms (*e.g.*, crustacea) and elastic-shelled (*e. g.*, pteropods) scatter from 38 kHz. Additionally, the differences between the two frequencies (Δ 38 kHz – 18 kHz) are useful to represent the scatter from larger fluid-like organisms (*e.g.*, large crustacea). For that reason, echograms are shown for 18 kHz and 38 kHz, as well as for the difference between the two frequencies (Δ 38 kHz – 18 kHz; Madureira et al., 1993). All acoustic data was processed using the Python opensource "echopype" package.

2.2. Gliders and mooring observations

The NERC-funded UK OSMOSIS program combined autonomous sampling strategies (*i.e.*, gliders, moorings) with traditional cruise measurements (*i.e.*, JC087) during the period from September 2012 to September 2013. Nine Moorings were deployed close to the PAP site (four outers, four inners, and a central mooring; square symbol Fig. 1b).

Each mooring consisted of a series of paired CTD (Seabird MicroCAT) and acoustic ocean current sensors (Nortek Aquadopp) fixed at different depths from 30 m to 530 m. For additional information about available mooring data, see Yu et al. (2019). In addition, five gliders (SG579, SG501, SG533, SG566 and SG510) were deployed in three rotation periods of 3 to 5 months each between September 2012 and September 2013. A full dive (to 1000 m depth) was completed in ~4 h. Each glider measured salinity, temperature, depth, chlorophyll-a fluorescence, optical backscatter and dissolved organic matter (performed by CTDs and Wetlabs Triplet ECOpuck sensors, respectively). In addition, Mixed Layer Depth (MLD) was defined as a change in temperature of 0.2 °C relative to the value at 10 m depth. For more details about the glider deployments, see Damerell et al. (2016), Bol et al. (2018) and Rumyantseva et al. (2015). All the OSMOSIS data are available from the British Oceanographic Data Center (https://www.bodc.ac.uk/data/).

2.3. Satellite-based measurements and modeling

In addition to *in situ* measurements, the mesoscale physical dynamics in the surface ocean of the PAP region were determined from satellite measurements during the campaign period. The satellite measurements included sea level anomalies (SLA) and current velocities from the

Table 1

Station, cast, date, time, position (latitude and longitude), depth of CTD.

Station	Cast	Date (dd/ mm/yy)	Start Time (UTC)	Latitude	Longitude	Max Depth (m)
5	1	03/06/ 13	12:31	48°41.969 N	$16^{\circ}2.015W$	4787
7	2	03/06/ 13	20:35	48° 38.898 N	16°8.573 W	200
31	3	05/06/ 13	04:10	48°38.916 N	16°8.577 W	200
37	4	05/06/ 13	07:56	48°39.012 N	16°8.325 W	200
40	5	05/06/ 13	10:24	48°38.919 N	16°8.576 W	200
42	6	05/06/ 13	13:22	48°38.915 N	16°8.578 W	4800
51	7	06/06/ 13	03:50	48°38.929 N	16°8.597 W	200
55	8	06/06/ 13	08:23	48°38.917 N	16°8.569 W	200
60	9	06/06/ 13	19:47	48°38.907 N	16°8.569 W	200
67	10	07/06/ 13	08:36	48°38.915 N	16°8.568 W	200
74	11	08/06/ 13	03:43	48°38.914 N	16°8.574 W	200
75	12	08/06/ 13	10:27	48°29.984 N	16°29.315 W	200
88	13	09/06/ 13	07:18	48°38.919 N	16°8.572 W	500
94	14	09/06/ 13	15:08	48°38.907 N	16°8.468 W	200
90	15	13	19:08	48° 38.401 N	10°8.380 W	200
97	10	13	02:47	48 39.020 N	10 10.805 W	200
101	17	13	08.31	N 48°38 916	10 8.374 W	200
117	10	13	08:55	N 48°38 953	16°8 597 W	200
126	20	13 13/06/	04.42	N 48°38 918	16°8 574 W	200
130	21	13 13/06/	08:32	N 48°38.899	16°8.559 W	200
141	22	13 14/06/	04:11	N 48°38.917	16°8.573 W	200
149	23	13 14/06/	08:42	N 48°38.912	16°8.579 W	200
151	24	13 14/06/ 13	11:42	N 48°38.912 N	16°8.579 W	4800

AVISO weekly averages (Archiving, Validation and Interpretation of Satellite Oceanographic; data resolution of 0.25°). Sea surface wind data in the region (6 h and 0.25° data resolution) were downloaded from the ERDAP server (https://coastwatch.pfeg.noaa.gov/erddap/index.html) and surface chlorophyll-a concentrations were extracted during the period from May to July 2013 based on an analysis of merged sensor data from MODIS and VIIRS satellite (Ocean Colour Climate Change Initiative dataset, Version 4.0, European Space Agency, available online at http://www.esa-oceancolour-cci.org). These analyses were based on 3-days to 5-days averages with a 4 km resolution. However, the region often had dense cloud cover which, at times, affected the averaged composite.

We used the backward finite-size Lyapunov exponent (FSLE) products obtained from AVISO to evaluate the impact of horizontal stirring on the spatial distribution of surface ocean tracers. Following d'Ovidio et al. (2004), the FSLEs highlighted regions of surface frontogenesis (*i.e.*, rapid dispersion and stirring) from simulations of the exponential rate of separation of particle trajectories that were initialized *in silico* in the vicinity of the study region and allowed to advect according to altimetry velocities. Coupled with FSLE data, the Lagrangian OceanParcels-v2 pipeline (Lange and Sebille, 2017) was used to run backward particle tracking simulations, with a time step of 1 h. Four virtual particles were released at the outer OSMOSIS mooring locations on June 5 and then tracked backwards in time for 15 days.

3. Results

3.1. Ocean dynamics: Water masses identification and spatial variabilities

During the JC087 cruise, the analysis of the sea level anomaly at the PAP site showed a clear dipole in the sea surface topography, which suggested a cyclonic and an anticyclonic eddy in the southern and northern regions of the study area, respectively (Fig. 1b). The sea surface height anomaly reached 14 cm in the northern anticyclonic eddy compared to the minimum sea surface height anomaly of -9 cm in the cyclonic eddy in the southern region. The narrow frontal zone between the two eddies was characterized by the highest current velocities in the area, with a maximum of 0.31 m s^{-1} . Additionally, the satellite chlorophyll-a (fluorescence) concentrations and SLA showed considerable variability between the two eddies. The highest chlorophyll-a concentrations were observed in the southern cyclonic eddy reaching more than 1.0 mg m⁻³. Between 3rd June and 5th June 2013, the glider SG510 crossed the frontal zone by traveling from the cyclonic to the anticyclonic eddy in a northeastern direction, albeit at a slant angle (red lines in Fig. 1b). The 15 km transect across the front showed strong variability in temperature, salinity, and chlorophyll-a in the upper 400 m of the water column (Fig. 1c). Glider and satellite observations show that highest temperature, salinity, and chlorophyll-a concentrations occurred in the surface waters of the cyclonic eddy (Fig. 1c, 0-6 km on the x-axis). Temperature and salinity profiles (Fig. 1d) suggested two different water masses: Eastern North Atlantic Central Subtropical Water (ENACWt; in red Fig. 1d) and Eastern North Atlantic Central Subpolar Water (ENACWp; in blue Fig. 1d) (Harvey, 1982).

3.2. Temporal changes and advection of distinct water masses

3.2.1. Water masses advection

Time-series at and close to the southeast OSMOSIS mooring sites from 3rd June to 15th June 2013 showed different phases of water masses dominance (Fig. 2). (i) Prior to the 5th June, we observed the signature of ENACWt water mass in the euphotic layer (salty water and temperature around 13 °C) with stable nutrient concentrations (NO₃, PO_4^{3-} and Si(OH)₄) and a high chlorophyll concentration (>0.5 mg. m^{-3}). (ii) From 5th to 6th June, we observed subpolar water (ENACWp, i.e., cold and less salty water) at the mooring site, which had higher nutrient concentrations but lower chlorophyll-a concentrations. (iii) From 6th to 11th June, the subtropical ENACWt dominated the region and was associated with progressively decreasing nutrient concentrations and increasing chlorophyll-a concentrations. (iv) At the end of the cruise (i.e., from 12th to 15th June), the wind speed was high (i.e., storm event $>10 \text{ m s}^{-1}$), which seems to have induced instability of the water column, resulting in a vertical mixing event and causing an increase in nutrient concentrations and a subsequent increase in chlorophyll-a concentrations (Fig. 2a-e). Despite being unable to obtain an accurate estimate of the MLD from the OSMOSIS mooring data, available measurements suggest that the MLD did not exceed 60 m depth from the 3rd to 15th June.

The backtracking Lagrangian simulations suggested that lateral advection was responsible for the chlorophyll-a and nutrient distributions between 15th May and 5th June 2013 in the study region. Before 22nd May, a clear physical boundary was visible and chlorophyll was organized as a front (Fig. 3). Based on the water mass properties (chlorophyll, temperature, and salinity; Fig. 1), the highest finite-size Lyapunov exponent (FSLE) values were observed along the southern boundaries that separated the subpolar and subtropical water masses



Fig. 2. Temporal evolution of the (a) wind speed recorded by satellite, (b) temperature, and (c) salinity measured in the upper 400 m of the water column at the southeast OSMOSIS mooring, and (d) nutrient (nitrate + nitrite, silicate and phosphate) and (e) chlorophyll-a concentration obtained by the ship's underway system at 5 m depth.

and matched the chlorophyll boundaries in the region. From 22nd to 31st May, the southern subtropical water mass with a high chlorophyll concentration progressively moved to the east, which entrapped the northern subpolar water mass with a low chlorophyll concentration (Fig. 3). This lateral movement explained the signature of the warm and salty water mass (ENACWt) measured by the southeastern OSMOSIS mooring before 5th June (Fig. 2bc). The entrapped subpolar water mass followed the cyclonic rotation and passed over the mooring station on 5th June (Fig. 3), explaining the ENACWp signature observed by the mooring time-series (cold, less salty, low chlorophyll and high nutrient; Fig. 2).

At the end of the cruise, from 12th June and continuing until 25th June, a storm passed through the study area with wind speeds reaching more than 10 m s⁻¹. Two autonomous instruments (glider_533 and PAP_mooring sensors) deployed in the area recorded the biophysical changes in the epipelagic zone. Based on temperatures recorded by the glider, the Mixed Layer Depth (MLD) was stable prior to 12th June and reached down to 20 m depth in the water column (Fig. 4e). The brief variations in temperature, salinity, and chlorophyll through the time series are due to the glider's trajectory between both the ENACW subpolar and subtropical water masses. During the passage of the storm, the MLD increased to 60 m depth. At the northern station, the sensors fixed

on the mooring measured the same temperature at 1 m and 30 m depth (Fig. 4f), reflecting the homogeneous upper layer. During the atmospheric storm event, surface nitrate, silicate, and phosphate concentration increased, reaching 5, 0.5, and 0.34 μ M respectively (Fig. 2d). Towards the end of the time series, the combination of decreasing wind speed and rising temperatures induced water column stratification, enhancing nutrient retention in the euphotic layer and driving an increase in chlorophyll concentrations over 2 mg m⁻³ (Fig. 2e; Fig. 4g and h).

3.2.2. Nutrient measurements

We observed a clear and distinct positive regression between the concentration of different nutrients in the upper 200 m of the two water masses (ENACWp and ENACWt) that represented the two eddy types (Fig. 5). We observed a NO₃⁻:Si(OH)₄ ratio of 2:1 at depths between 30 and 200 m (*i.e.*, below MLD) in ENACWt and from the surface and down to 200 m in ENACWp water mass. From the surface to 25 m in ENACWt (*i.e.*, MLD), we observed a NO₃⁻Si(OH)₄ ratio of 10:1, which indicated that the Si(OH)₄ availability in the ENACWt euphotic zone was low (Fig. 5a) and that the diatoms were silicate limited. Painter et al. (2010a) suggested that NO₃⁻ and Si(OH)₄ ratios between 2:1 and 10:1 are linked to the presence of non-siliceous phytoplankton, since diatoms



Fig. 3. Overview of water mass movements over the Porcupine Abyssal Plain in 2013 from May 23 to June 5, based on (a) Finite-Size Lyapunov Exponent (FSLE), (b) Sea Surface Temperature (SST), (c) satellite-measured Chlorophyll concentration (Chl-a), and (d) a schematic. Red lines represent particles released at the four outer OSMOSIS moorings on June 5, 2013, and tracked backward using OceanParcels. The black and red rectangles represent the location of the OSMOSIS and PAP moorings, respectively. The cyclonic eddy (CE) was dominated by Eastern North Atlantic Central subtropical Water (ENACWt) and the anticyclonic eddy (AE) was dominated by Eastern North Atlantic subpolar Water (ENACWp). The numbers 1 and 2 represent, respectively, the ENACWp trapped by the ENACWt inducing the chlorophyll horizontal stirring and a strong variability at our study site.



Fig. 4. Biophysical data collected by the (a) OSMOSIS glider_533 and (b) PAP mooring instruments coupled with wind measurements estimated from remote sensing. Temporal evolution of the wind speed, temperature and chlorophyll-a concentration obtained from (c & d) remote sensing, (e & g) glider_533 and (f & h) PAP mooring sensors. The black solid lines represent the Mixed Layer Depth defined as a temperature differential of 0.2 °C from the temperatures measured at 10 m depth. The letters AE and CE represent the core of the cyclonic and anticyclonic eddy, respectively.



Fig. 5. Nutrient (nitrate, silicate, phosphate) relationships from surface to 200 m depth in both subpolar (blue gradient) and subtropical (red gradient) water masses. The labeled ratios represent the slope of the linear regressions performed on data recorded from the surface to the MLD (dotted line) or below the MLD (solid line).

require NO₃ and Si(OH)₄ in equal proportions (Brzezinski, 1985) when iron is not a limiting factor (Moore et al., 2007). NO₃ and PO₄³⁻ ratios were consistent (*i.e.*, 15:1) throughout the upper 200 m in both water masses, suggesting that both nutrients were used according to the Redfield ratio (Fig. 5b). At depths below 25 m in the ENACWt and from the surface to 200 m depth for ENACWp the Si(OH)₄:PO₄³⁻ ratio was 10:1. However, for the upper 25 m in the ENACWt, the Si(OH)₄:PO₄³⁻ ratio was only 4:1, which indicated a depletion of PO₄³⁻ relative to Si (OH)₄ (Fig. 5c). This suggests that there was a dominance of nonsiliceous organisms in the plankton community (*i.e.*, not diatoms) and that phytoplankton other than diatoms contributed to the majority of the nutrient drawdown.

3.3. Zooplankton behaviour

3.3.1. Acoustic measurements

Mesopelagic acoustic backscattering at 18 kHz is typically considered to be signals from nekton, micronekton, and squid while the backscattering signal at 38 kHz is considered to be crustaceans (Benoit-Bird and Lawson, 2016). The differences between the two frequencies can be used to discriminate between swim-bladder-bearing fish and fluid-like scattering from large crustaceans such as euphausiids and amphipods. Here, we distinguished between different migrator communities by relating the depth of migration with diel rhythm.

The backscattering from the epipelagic zone (0-100 m depth) was

higher during the night than during the day, which suggested that a high number of organisms migrated from deeper layers to the surface ocean during the night (Fig. 6a). Three different migration layers were observed in the mesopelagic zone (100-1000 m depth) based on distinct layers of high backscatter during the day. Two migrant groups (M1/M2) were observed with the 18 kHz signal and these performed a strong vertical migration from the surface to 550 m (M1) or 400 m (M2) during the day and vice versa during the night. The 38 kHz signal showed a third group (M3), that migrated from the surface to a shallow depth of 150 m during the day and back to the surface during the night. At sunset, the shallow, intermediate and deep migrators moved upwards with velocities of 0.6 \pm 0.2, 3.9 \pm 0.9 and 7.4 \pm 1.4 cm.s^{-1}, respectively. Conversely, at sunrise, the shallow, intermediate and deep migrators moved downwards with velocities of 0.5 \pm 0.2, 3.0 \pm 0.7 and 5.1 \pm 1.4 $cm.s^{-1}$, respectively (Fig. 6a). Finally, a deep non-migrant backscattering layer was also observed in a layer between 550 and 650 m depth both during day and night, presumably consisting of non-migrating organisms (Fig. 6a).

3.3.2. Multinet observations & swimmers collected by neutrally buoyant sediment traps

A total of 10 Multinet deployments were done throughout day and night during the cruise (*i.e.*, 6 during the night defined as 19 h to 8 h and 4 during the day). The organisms collected with the Multinets were sorted into 54 groups and genera of zooplankton (living/moults), phytoplankton, terrestrial matter and non-organic particles (glass/ plastic debris). The groups of fish (larvae/juvenile), *Themisto* spp., Euphausiids and *Pleuromamma* spp. showed a diel vertical migration (Fig. 6b). Faster swimming organisms such as fish, amphipods, and Euphausiids can avoid collection by Multinet, which may have caused an underestimate of their abundance from the net tows. Thus, the abundance of each of these groups was considered as a percentage of the median day and night. Interestingly, the neutrally buoyant sediment trap (PELAGRA) collection cups were full of swimmers, mainly dominated by copepods, *Themisto compressa* and euphausiids that were collected at 200 m depth (Fig. 6c). These unusually high numbers of swimmers prevented us from estimating organic matter flux from the PELAGRA sediment traps. The sediment traps were deployed at a fixed depth for two days and the swimmers were likely collected during their daily migrations.

The combined results from hydroacoustic and multinet collections suggested that the two migration groups observed with the 18 kHz (M1 and M2) were composed of fish and large crustacea (Euphausiacea and amphipods). The third migrating community (M3) was observed with the 38 kHz hydroacoustic back-scattering and seemed to be primarily composed of large crustacea (*e.g.*, amphipod). Given that the smaller copepods are also fluid-like scatterers and are primarily observed at frequencies around 120 kHz (Benoit-Bird and Lawson, 2016), we concluded that our use of 18 and 38 kHz did not include copepods such as *Pleuromanma* spp. and smaller species, and we do not consider those to be included in our backscattering signal.

3.3.3. Interactions between mesozooplankton and settling aggregates

Vertical profiles of marine snow concentrations were recorded by the Video Plankton Recorder (VPR). These results showed only low concentrations of marine snow (aggregates with equivalent spherical diameters larger than 500 μ m) during the ENACWp intrusion on 5th June (Fig. 7a). The low marine snow concentrations correlated well with the low chlorophyll-a concentration observed from satellites and *in situ* measurements for the ENACWp. Cross-comparison between acoustic data and the VPR suggests a relationship between the third migrating community (M3) and particle type and abundance. Five of the nine



Fig. 6. (a) Echograms at the frequencies 18 kHz (upper) and 38 kHz (lower) coupled with (b) the percentage of organisms collected *via* multinets performed during the cruise (start and end sampling time of the individual multinets are represented on subpanel a by the solid and dashed red lines, respectively) showing a diurnal vertical migration pattern (fish, *Themisto* spp., Euphausiacea and *Pleuromamma* sp.; Gray and yellow colors represent night and day samples) and (c) swimmers that were collected in the sedimentation cups at 200 m using the neutrally buoyant sediment traps PELAGRA (mainly small copepods, Euphausiacea and *Themisto compressa*). The subpanel to the right of the time-series (a) represents the daily behavior of the deep (M1), intermediate (M2) and shallow (M3) migrator communities identified in our study.



Fig. 7. Δ 38 kHz – 18 kHz echogram (white-black gradient) combined with the (a) abundance, (b) size (equivalent spherical radius) and (c) volume of particles measured during the Video Plankton recorder vertical tows (blue to red colour overlays). (d) Examples of large particles (*i.e.*, volume over 3 mm³) recorded at depth. The * indicates a significant correlation between Δ 38 kHz – 18 kHz and the volume of the particles.

vertical VPR profiles showed a significant positive correlation between Δ 38 kHz – 18 kHz echogram and the size (volume and equivalent spherical radius (ESR)) of both large and small particles (Fig. 7b/c; Spearman test, *p*-value < 0.05). All the VPR profiles that did not show a significant correlation with the echograms were deployed at the beginning of the night while the migrating organisms still performed their upward migration. We extracted vignettes of the large particles that were imaged by the VPR and sorted the marine snow according to shape and composition (Fig. 7d). The majority of the marine snow was irregular, seemingly formed from discarded appendicularian houses mixed with phytodetritus. We consider it unlikely that marine snow and faecal pellets were detected by the 38 kHz echograms and suggest that the third migrating community (M3) comprised Themisto compressa populations. M3, or T. compressa, were positively correlated to the abundance of marine snow, suggesting that marine snow may be an important food source for T. compressa, as also previously suggested by Lampitt et al. (1993b).

4. Discussion

The North Atlantic region is a complex system impacted by strong physical mechanisms at different temporal and spatial scales. The eddy kinetic energy in this region is normally considered to be moderate with low levels of advective input (Damerell et al., 2016; Lampitt et al., 2010a). Nevertheless, (sub-)mesoscale processes can affect the epi- and mesopelagic zone and complicate data interpretation (Painter et al., 2010b). It is challenging to study the impact of submesoscale structures with *in situ* sampling data sets. Here, we gathered measurements from multidisciplinary instruments to understand how the physical submesoscale features shaped biology, biogeochemistry and ecology at the PAP site. While the field data collected by moorings, gliders and cruise

sampling was at a high temporal resolution, we were limited by spatial coverage. To overcome that issue, we combined satellite measurements with model simulations, accepting the uncertainties associated with these methodological approaches. One should keep in mind that the spatial resolution of some satellite products used to constrain the Lagrangian simulation could be too low for resolving submesoscale structures. In addition, the uncertainties caused by the distance between satellite ground tracks can be large but remain an inherent bias to the instrument.

The sequential appearance of subtropical and subpolar water masses in our study area was caused by lateral motion and vertical mixing led by the anticyclonic-cyclonic dipole and the storm event. Despite the combination of numerous high-frequency autonomous instruments and models that helped us to track lateral movements of the water masses, it is unclear if the frontogenesis dynamics caused by the two counterrotating eddies were strong enough to upwell nutrients from the deep waters, such as described by Lapeyre and Klein (2006). Nevertheless, the nutrient concentrations at the frontal zone in the cyclonic eddy were depleted during the majority of our study, except during the periods when subpolar water intruded on 5th June 2013 and at the end of the cruise during the storm event (from 12th to 15th June). Due to the abrupt changes in the water mass properties and the shallow MLD, we suggest that the increased nutrient concentration on 5th June 2013 was caused by lateral advection of nutrient-rich subpolar water (Fig. 3) and not caused by frontogenesis or upward mixing of deep water. However, due to the methodological uncertainties and limits mentioned previously, we do not exclude the possibility that the subpolar signal observed on the 5th June was due to a latitudinal shift of the frontal boundaries. Nevertheless, the environmental observations, satellite measurements and model output seem to confirm our suggestion of an entrapped subpolar water mass by a subtropical ENACW variant, especially due to the presence of a cold and low chlorophyll-a concentration filament in the cyclonic eddy which corresponds to the backward trajectories simulations (Fig. 3). In contrast, the high nutrient concentration at the end of the cruise was associated with the storm event and a deepening of the MLD, suggesting an upward mixing of nutrient-rich deep water to the euphotic zone. Therefore, we suggest that nutrient concentrations during our study were determined by lateral advection of nutrient-rich subpolar water and upward mixing of deep water to the surface water during a storm event. Rumyantseva et al. (2015) estimated that storm events during late summer at the PAP site provide upwelled nitrate accounting for up to 30 % of the total nitrate supply during winter mixing. Hence, a substantial nutrient input to the surface ocean can occur via mesoscale dynamics during summer.

The good alignment between the finite-size Lyapunov exponent (FSLE) and the remotely sensed chlorophyll-a distribution observed in the southern region suggests that the phytoplankton biomass was controlled by horizontal stirring FSLE patterns (Calil et al., 2011; d'Ovidio et al., 2010). In addition, the stirring caused an expansion of chlorophyll-a that was faster than could be explained by local biologically driven rates of cell division. This is a typical pattern observed during the passive deformation of phytoplankton patches into submesoscale filaments (Lévy et al., 2018). This rapid effect of water mass stirring agrees with our observations and with the observations by Abraham (1998), showing that stirring alone should have no consequences on the productivity or diversity of marine ecosystems but implies a redistribution of the biological constituents by the water motions of the (sub-)mesoscale. d'Ovidio et al. (2010) highlighted the important role played by this horizontal stirring for regionalization of phytoplankton types, delimiting niches supported by water masses of similar history, creating contrasted physiochemical conditions and favouring the emergence of complex community distributions.

Nutrient ratios in the subtropical water masses suggested a dominance of small non-siliceous phytoplankton in the upper 25 m of the water column, based on the high depletion of NO_3^- and PO_4^{3-} relative to Si(OH)₄. Size-fractionated measurements and phytoplankton pigment analysis performed during the cruise and published by Gašparović et al. (2018), confirm our conclusions. Nanophytoplankton (<10 um) made up 82 % of the total chlorophyll-a and was dominated by prymnesiophytes (19HF), while only 18 % of the total chlorophyll-a concentration was contributed by microphytoplankton (>10 um), which was dominated by diatoms (identified by Fucoxanthin-content) (Gašparović et al., 2018). The time-series of chlorophyll-a satellite images confirmed the post and pre-bloom phase of the cyclonic and anticyclonic eddies during our sampling period (Fig. 8). A large phytoplankton bloom occurred in the anticyclonic eddy one month after the JC087 cruise (Fig. 8d) and was triggered by an increasing stratification in the upper water column (Fig. S1). The phytoplankton biomass was shaped following a spiral flow showing high meso/submesoscale variability in the PAP region.

While upwelling and downwelling associated with eddies can influence nutrient levels and chlorophyll concentrations, these effects may be higher-order phenomena, becoming relevant only when other factors are similar. In our case, the primary difference between the anticyclonic eddy in the north and the cyclonic eddy in the south lies in their respective pre- and post-bloom states. The northern anticyclonic eddy likely originated further north in the subpolar gyre and experienced recent, more extreme atmospheric forcing, including lower light availability and deeper winter mixing. These conditions contributed to a persistently deeper mixed layer and delayed phytoplankton bloom onset despite high winter nutrient concentrations, resulting in a high-nutrient, low-chlorophyll phenomenon in the northern ENACWp waters. In



Fig. 8. Evolution of the chlorophyll-a concentration and eddy dynamic from the (a) beginning of the cruise JC087 to (d) one month later. Contour lines, arrows and the dark and white squares show the sea level anomaly (SLA; meters), the current velocity, and the outer and central mooring location, respectively. The letters CE represent the core of the cyclonic eddy and AE indicate the core of the anticyclonic eddy.

contrast, the cyclonic eddy, which originated further south in the subtropical gyre, was in the post-bloom phase. Shallower winter mixing brought nutrients into the mixed layer from a smaller vertical range, supporting an earlier bloom but resulting in a generally more oligotrophic environment. These differences, rooted in the distinct physical and environmental dynamics of the subpolar and subtropical gyres, appear to be the primary drivers of the observed nutrient and chlorophyll distributions rather than direct effects of eddy-specific upwelling or downwelling.

Passive water motions, such as mixing of two water masses within a frontal zone, have been shown to directly impact the phytoplankton community composition (Lévy et al., 2018). However, it is still unclear how this impacts higher trophic levels since they are difficult to study on the relatively short timescale of submesoscale processes. During our cruise, Microsetella norvegica total biomass was highest on 5th June 2013 (Koski et al., 2020) when the subpolar water signal crossed the station. Interestingly, both the abundance of *M. norvegica* and *Oncaea/Triconia* spp. were dominated by adults on 5th June 2013, but this shifted to a higher proportion of nauplii, copepodites and eggs after 5th June (Koski et al., 2020) when the region was strongly influenced by subtropical water. Thus, it is possible that temperature and food availability regulated zooplankton phenology (e.g., spawning frequency), as suggested by Koski et al. (2020). However, an alternative explanation could be that the temporal changes in zooplankton abundance observed at the PAP site were caused by lateral advection of different water masses with differing zooplankton abundance to the observation site. Still, both our study and that of Koski et al. (2020) confirm that submesoscale mechanisms impact zooplankton dynamics and modulate planktonic distribution on small spatial scales. In addition, the time-series of the chlorophyll-a ingestion by M. norvegica (Koski et al., 2020), showed less ingestion per individual during the storm event, suggesting a strong dilution of phytoplankton and weak feeding activity.

Phytodetritus aggregates have previously been observed to dominate the particle flux at the PAP site (Belcher et al., 2016; Cavan et al., 2017). Unfortunately, we were not able to determine particle flux from the PELAGRA neutrally buoyant sediment trap deployments due to the unusually high collection of swimmers in the collection cups. We, therefore, estimated POC flux from direct measurements of size-specific settling velocities and POC content. Sinking velocities have been measured on aggregates collected in situ using Marine Snow Catchers and following the method of Belcher et al. (2016). We observed a significant relationship (p-value < 0.01, $R^2 = 0.2$) between aggregate ESD and sinking velocity (Fig. S2a). However, the low R² suggests that particle size is not the main parameter determining sinking velocity, which confirms previous observations at the PAP site (Iversen and Lampitt, 2020). The carbon content of each individual particle was estimated using the power law function $\mu g \ C = 0.99 \ V^{0.52}$, with V representing the volume aggregates (mm3; Alldredge, 1998). Using the size-specific settling velocities and POC content, the calculated POC flux showed large daily variations at the OSMOSIS site in the upper water column. POC fluxes were extremely low in the subpolar water as was observed on 5th June 2013 and during the storm event (i.e., due to low aggregate concentration), but this shifted to a higher POC flux after 5th June, when the region was strongly influenced by subtropical water (Fig. S2b). This showed that the nutrient rich, but chlorophyll-a poor subpolar water had low POC flux, while the chlorophyll-a rich, but nutrient poor subtropical water had high POC flux.

We observed strong vertical variabilities in particle abundance and size-distribution for the high POC flux in subtropical waters, while the subpolar water with low POC flux showed little to no variation in particle abundance with increasing depth. Interestingly, variations in daily total volume of all particles were also observed by a moored camera system deployed by Lampitt et al. (1993a) at 270 m depth for the same period of the year (*i.e.*, May/June) and location as during our expedition. Several suggestions can be made to explain such changes in particle dynamics. For instance, several studies have demonstrated the importance of coagulation for the aggregate formation and increasing aggregate size (Jackson, 1990; Kiørboe et al., 1990), production of faecal pellets and feeding nets can transform and produce aggregates both in the surface ocean and at depth (Wilson et al., 2013), active carbon transport by vertically migrating zooplankton may contribute with an input of particles at depths in the mesopelagic (Steinberg et al., 2000), and differences in particle density may enhance the vertical flux of specific aggregate compositions and sizes (Iversen and Ploug, 2010). At the PAP site, Lampitt et al. (1993b) suggested that a substantial amount of the marine snow was formed from discarded appendicularian houses and they concluded that the daily variability of marine snow is probably intimately related to the activity of the migrating plankton and nekton. In our study, the good alignment of the Δ 38 kHz –18 kHz echograms to the large aggregates identified from the VPR profiles provides evidence for the direct interaction between large particles and *T. compressa*. It has been suggested that, due to its highly developed optical sensory apparatus, T. compressa can capture a variety of prey, including marine snow aggregates in the dimly lit deep ocean (Lampitt et al., 1993a; Pakhomov and Perissinotto, 1996). The shape and composition of the marine snow were irregular but it seemed to primarily be formed from a mixture of discarded appendicularian houses and phytodetritus. The daily changes in appendicularian abundance within the upper 100 m were determined from multinet deployments and showed significantly higher abundance during the day (2.7 \pm 1.4 ind m⁻³) compared to the abundance during the night (0.6 \pm 0.5 ind.m⁻³) (Wilcoxon test; p-value < 0.01). This pelagic tunicate may produce 2-40 houses per day (Sato et al., 2003). However, due to the fragile nature of the gelatinous structures, it is likely that their abundances are underestimated when they are sampled with standard techniques such as plankton nets. Discarded appendicularian houses represent an important food source for many zooplankton grazers and nekton species, including copepods, euphausiids or fishes (Alldredge, 1972; Gorsky and Fenaux, 1998; Koski et al., 2007). Based on the high contribution from appendicularian houses to marine snow and the correlations between vertical distributions of amphipods and marine snow, we suggest that amphipods feed on the large aggregates and appendicularian houses, impacting the daily vertical distribution of large marine snow in the water column. This supports previous observations of marine particle signatures in amphipod faecal pellets at the PAP, suggesting that amphipods feeding on marine snow may be an important controller for the efficiency of the biological carbon pump at the PAP site (Lampitt et al., 1993b).

Previous studies at the PAP site have shown that the export flux to 50 and 100 m typically varies between 64 and 207 mg $C.m^{-2}.d^{-1}$ (Belcher et al., 2016; Giering et al., 2017; Lampitt et al., 2008; Riley et al., 2012) and that this flux is equivalent to 15 % of the net primary production in the surface ocean (Frigstad et al., 2015). This suggests that there is high flux attenuation in the upper water column at the PAP site, with flux attenuation coefficients ranging from 0.5 to 0.7 (Belcher et al., 2016; Lampitt et al., 2010a; Lampitt et al., 2010b). However, it has generally proven difficult to match the variation in flux collected in the deep sea to upper ocean processes (Giering et al., 2017; Lampitt et al., 2010b). This is not surprising, especially for the PAP site which has a very dynamic oceanography. During our short study alone, we observed transitions from subpolar to subtropical water masses with marked physical, chemical and biological differences. It is therefore important not only to consider phytoplankton biomass and export flux when determining the efficiency of the biological carbon pump, but also to consider the presence of (sub-) mesoscale structures and ocean dynamics in the study region. These will impact both biologically driven export (e.g., via upwelling of nutrient and/or lateral dispersion of nutrient and organisms; this study, von Appen et al., 2020; von Appen et al., 2018) and physical downward transport of organic matter via subduction (e.g., Fischer et al., 2016; Stukel et al., 2017; von Appen et al., 2018; Waite et al., 2016).

5. Conclusion

Our multidisciplinary research confirms and emphasizes the effect of meso- and sub-mesoscale activity in the North Atlantic area as effective mechanisms to modulate biogeochemistry as well as the planktonic community composition. Besides the large spatial and temporal heterogeneity in the euphotic zone due to the presence of two eddies in close proximity, we also highlighted that vertical turbulence after a storm event in the area delivered a high amount of nutrients from the deep to the surface ocean and likely induced changes in planktonic biomass and composition. The relationship between the flux attenuation (i.e., loss of marine snow aggregates with increasing depth) and the presence of the amphipod Themisto compressa distribution underline the importance of understanding and quantifying the role of zooplankton and nekton for the efficiency and magnitude of the biological carbon pump. Together, these processes decouple surface ocean biomass from the export of organic matter to the deep ocean and highlight the importance of taking high resolution measurements of physical, chemical and biological processes in order to understand the driving mechanisms for biological production, organic matter export, and oceanic carbon sequestration.

CRediT authorship contribution statement

Simon Ramondenc: Writing – review & editing, Writing – original draft, Visualization, Supervision, Formal analysis, Conceptualization. Richard S. Lampitt: Writing – review & editing, Supervision, Resources, Funding acquisition. Maria Fredrika Norrbin: Writing – review & editing, Validation, Supervision, Resources, Methodology, Data curation. Anna Belcher: Writing – review & editing, Supervision, Resources. Wilken-Jon von Appen: Supervision, Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2025.103476.

Data availability

Data will be made available on request.

References

- Abraham, E.R., 1998. The generation of plankton patchiness by turbulent stirring. *Nature* 391, 577–580.
- Alldredge, A., 1998. The carbon, nitrogen and mass content of marine snow as a function of aggregate size. *Deep-Sea Research Part I-Oceanographic Research Papers* 45, 529–541.
- Alldredge, A.L., 1972. Abandoned larvacean houses: a unique food source in the pelagic environment. *Science* 177, 885–887.
- Belcher, A., Iversen, M., Giering, S., Riou, V., Henson, S.A., Berline, L., Guilloux, L., Sanders, R., 2016. Depth-resolved particle-associated microbial respiration in the northeast Atlantic. *Biogeosciences* 13, 4927–4943.
- Benoit-Bird, K.J., Lawson, G.L., 2016. Ecological insights from pelagic habitats acquired using active acoustic techniques. Ann. Rev. Mar. Sci. 8, 463–490.
- Bol, R., Henson, S.A., Rumyantseva, A., Briggs, N., 2018. High-frequency variability of small-particle carbon export flux in the Northeast Atlantic. *Global Biogeochem. Cycles* 32, 1803–1814.
- Brzezinski, M.A., 1985. The Si: C: N ratio of marine diatoms: interspecific variability and the effect of some environmental variables 1. J. Phycol. 21, 347–357.
- Buckingham, C.E., Lucas, N.S., Belcher, S.E., Rippeth, T.P., Grant, A.L., Le Sommer, J., Ajayi, A.O., Naveira Garabato, A.C., 2019. The contribution of surface and submesoscale processes to turbulence in the open ocean surface boundary layer. J. Adv. Model. Earth Syst. 11, 4066–4094.
- Calil, P.H., Doney, S.C., Yumimoto, K., Eguchi, K., Takemura, T., 2011. Episodic upwelling and dust deposition as bloom triggers in low-nutrient, low-chlorophyll regions. J. Geophys. Res. Oceans 116.
- Cavan, E.L., Henson, S.A., Belcher, A., Sanders, R., 2017. Role of zooplankton in determining the efficiency of the biological carbon pump. *Biogeosciences* 14, 177–186.
- d'Ovidio, F., Fernández, V., Hernández-García, E., López, C., 2004. Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents. *Geophys. Res. Lett.* 31.
- d'Ovidio, F., De Monte, S., Alvain, S., Dandonneau, Y., Lévy, M., 2010. Fluid dynamical niches of phytoplankton types. Proc. Natl. Acad. Sci. 107, 18366–18370.
- Damerell, G.M., Heywood, K.J., Thompson, A.F., Binetti, U., Kaiser, J., 2016. The vertical structure of upper ocean variability at the Porcupine Abyssal Plain during 2012–2013. J. Geophys. Res. Oceans 121, 3075–3089.
- Davis, C.S., Thwaites, F.T., Gallager, S.M., Hu, Q., 2005. A three-axis fast-tow digital Video Plankton Recorder for rapid surveys of plankton taxa and hydrography. *Limnol. Oceanogr. Methods* 3, 59–74.
- Fischer, G., Karstensen, J., Romero, O., Baumann, K.-H., Donner, B., Hefter, J., Mollenhauer, G., Iversen, M., Fiedler, B., Monteiro, I., 2016. Bathypelagic particle flux signatures from a suboxic eddy in the oligotrophic tropical North Atlantic: production, sedimentation and preservation. *Biogeosciences* 13, 3203–3223.
- Frigstad, H., Henson, S., Hartman, S., Omar, A., Jeansson, E., Cole, H., Pebody, C., Lampitt, R., 2015. Links between surface productivity and deep ocean particle flux at the Porcupine Abyssal Plain sustained observatory. *Biogeosciences* 12, 5885–5897.
- Gašparović, B., Penezić, A., Lampitt, R.S., Sudasinghe, N., Schaub, T., 2018. Phospholipids as a component of the oceanic phosphorus cycle. *Mar. Chem.* 205, 70–80.
- Giering, S.L., Sanders, R., Martin, A.P., Henson, S.A., Riley, J.S., Marsay, C.M., Johns, D. G., 2017. Particle flux in the oceans: Challenging the steady state assumption. *Global Biogeochem. Cycles* 31, 159–171.
- Gorsky, G., Fenaux, R., 1998. The role of Appendicularia in marine food webs. *The Biology of Pelagic Tunicates* 161–169.
- Hartman, S., Larkin, K., Lampitt, R., Lankhorst, M., Hydes, D., 2010. Seasonal and interannual biogeochemical variations in the Porcupine Abyssal Plain 2003–2005 associated with winter mixing and surface circulation. *Deep Sea Res. Part II* 57, 1303–1312.
- Harvey, J., 1982. 0-S relationships and water masses in the eastern North Atlantic. Deep Sea Research Part A. Oceanographic Research Papers 29, 1021–1033.
- Iversen, M.H., Lampitt, R.S., 2020. Size does not matter after all: no evidence for a sizesinking relationship for marine snow. Prog. Oceanogr. 189, 102445.
- Iversen, M.H., Ploug, H., 2010. 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.
- Jackson, G.A., 1990. A model of the formation of marine algal flocs by physical coagulation processes. *Deep Sea Research Part A. Oceanographic Research Papers* 37, 1197–1211.
- Kessouri, F., Bianchi, D., Renault, L., McWilliams, J.C., Frenzel, H., Deutsch, C.A., 2020. Submesoscale currents modulate the seasonal cycle of nutrients and productivity in the California Current System. *Global Biogeochem. Cycles* 34, e2020GB006578.
- Kiørboe, T., Andersen, K., Dam, H., 1990. Coagulation efficiency and aggregate formation in marine phytoplankton. *Mar. Biol.* 107, 235–245.
- Kirkwood, D., 1996. Nutrients: Practical notes on their determination in sea water. Koski, M., Møller, E.F., Maar, M., Visser, A.W., 2007. The fate of discarded
- appendicularian houses: degradation by the copepod, Microsetella norvegica, and other agents. J. Plankton Res. 29, 641-654.
- Koski, M., Valencia, B., Newstead, R., Thiele, C., 2020. The missing piece of the upper mesopelagic carbon budget? Biomass, vertical distribution and feeding of aggregateassociated copepods at the PAP site. *Prog. Oceanogr.* 181, 102243.

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Lampitt, R., Bett, B., Kiriakoulakis, K., Popova, E., Ragueneau, O., Vangriesheim, A., Wolff, G., 2001. Material supply to the abyssal seafloor in the Northeast Atlantic. *Prog. Oceanogr.* 50, 27–63.

Lampitt, R., Billett, D., Martin, A., 2010a. The sustained observatory over the Porcupine Abyssal Plain (PAP): Insights from time series observations and process studies. Vol. 57 (pp. 1267-1271): Elsevier.

Lampitt, R., Hillier, W., Challenor, P., 1993a. Seasonal and diel variation in the open ocean concentration of marine snow aggregates. *Nature* 362, 737–739.

Lampitt, R., Salter, I., de Cuevas, B., Hartman, S., Larkin, K., Pebody, C., 2010. Long-term variability of downward particle flux in the deep northeast Atlantic: Causes and trends. *Deep Sea Res. Part II* 57, 1346–1361.

Lampitt, R., Wishner, K., Turley, C., Angel, M., 1993b. Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. *Mar. Biol.* 116, 689–702.

Lampitt, R.S., Boorman, B., Brown, L., Lucas, M., Salter, I., Sanders, R., Saw, K., Seeyave, S., Thomalla, S.J., Turnewitsch, R., 2008. Particle export from the euphotic zone: Estimates using a novel drifting sediment trap, 234Th and new production. *Deep Sea Res. Part I* 55, 1484–1502.

Lange, M., Sebille, E.V., 2017. Parcels v0. 9: prototyping a Lagrangian ocean analysis framework for the petascale age. *Geosci. Model Dev.* 10, 4175–4186.

Lapeyre, G., Klein, P., 2006. Impact of the small-scale elongated filaments on the oceanic vertical pump. J. Mar. Res. 64, 835–851.

Lévy, M., Franks, P.J., Smith, K.S., 2018. The role of submesoscale currents in structuring marine ecosystems. Nat. Commun. 9, 1–16.

Lévy, M., Klein, P., Treguier, A.-M., 2001. Impact of sub-mesoscale physics on production and subduction of phytoplankton in an oligotrophic regime. J. Mar. Res. 59, 535–565.

Madureira, L.S., Everson, I., Murphy, E.J., 1993. Interpretation of acoustic data at two frequencies to discriminate between Antarctic krill (Euphausia superba Dana) and other scatterers. J. Plankton Res. 15, 787–802.

Mahadevan, A., 2016. The impact of submesoscale physics on primary productivity of plankton. Ann. Rev. Mar. Sci. 8, 161–184.

McGillicuddy Jr, D., Anderson, L., Doney, S., Maltrud, M., 2003. Eddy-driven sources and sinks of nutrients in the upper ocean: Results from a 0.1 resolution model of the North Atlantic. *Global Biogeochem. Cycles* 17.

McGillicuddy Jr, D.J., 2016. Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale. Ann. Rev. Mar. Sci. 8, 125–159.

Moore, C.M., Seeyave, S., Hickman, A.E., Allen, J.T., Lucas, M.I., Planquette, H., Pollard, R.T., Poulton, A.J., 2007. Iron–light interactions during the CROZet natural iron bloom and EXport experiment (CROZEX) I: Phytoplankton growth and photophysiology. *Deep Sea Res. Part II* 54, 2045–2065.

Omand, M.M., D'Asaro, E.A., Lee, C.M., Perry, M.J., Briggs, N., Cetinić, I., Mahadevan, A., 2015. Eddy-driven subduction exports particulate organic carbon from the spring bloom. *Science* 348, 222–225.

Painter, S.C., Lucas, M.I., Stinchcombe, M.C., Bibby, T.S., Poulton, A.J., 2010a. Summertime trends in pelagic biogeochemistry at the Porcupine Abyssal Plain study site in the northeast Atlantic. *Deep Sea Res. Part II* 57, 1313–1323.

Painter, S.C., Pidcock, R.E., Allen, J.T., 2010b. A mesoscale eddy driving spatial and temporal heterogeneity in the productivity of the euphotic zone of the northeast Atlantic. *Deep Sea Res. Part II* 57, 1281–1292. Pakhomov, E., Perissinotto, R., 1996. Trophodynamics of the hyperiid amphipod Themisto gaudichaudi in the South Georgia region during late austral summer. *Mar. Ecol. Prog. Ser.* 134, 91–100.

Picheral, M., Catalano, C., Brousseau, D., Claustre, H., Coppola, L., Leymarie, E., Coindat, J., Dias, F., Fevre, S., Guidi, L., 2022. The Underwater Vision Profiler 6: an imaging sensor of particle size spectra and plankton, for autonomous and cabled platforms. *Limnol. Oceanogr. Methods* 20, 115–129.

Resplandy, L., Lévy, M., McGillicuddy Jr, D.J., 2019. Effects of eddy-driven subduction on ocean biological carbon pump. *Global Biogeochem. Cycles* 33, 1071–1084.

Riley, J., Sanders, R., Marsay, C., Le Moigne, F.A., Achterberg, E.P., Poulton, A.J., 2012. The relative contribution of fast and slow sinking particles to ocean carbon export. *Global Biogeochem. Cycles* 26.

Robinson, A., McGillicuddy, D., Calman, J., Ducklow, H., Fasham, M., Hoge, F., Leslie, W., McCarthy, J., Podewski, S., Porter, D., 1993. Mesoscale and upper ocean variabilities during the 1989 JGOFS bloom study. *Deep Sea Res. Part II* 40, 9–35.

Rumyantseva, A., Lucas, N., Rippeth, T., Martin, A., Painter, S.C., Boyd, T.J., Henson, S., 2015. Ocean nutrient pathways associated with the passage of a storm. *Global Biogeochem. Cycles* 29, 1179–1189.

Sanders, R., Henson, S.A., Koski, M., Christina, L., Painter, S.C., Poulton, A.J., Riley, J., Salihoglu, B., Visser, A., Yool, A., 2014. The biological carbon pump in the North Atlantic. Prog. Oceanogr. 129, 200–218.

Sato, R., Tanaka, Y., Ishimaru, T., 2003. Species-specific house productivity of appendicularians. Mar. Ecol. Prog. Ser. 259, 163–172.

Simmonds, J., MacLennan, D.N., 2008. Fisheries acoustics: theory and practice. John Wiley & Sons.

Steinberg, D.K., Carlson, C.A., Bates, N.R., Goldthwait, S.A., Madin, L.P., Michaels, A.F., 2000. Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep Sea Res. Part I* 47, 137–158.

Stukel, M.R., Aluwihare, L.I., Barbeau, K.A., Chekalyuk, A.M., Goericke, R., Miller, A.J., Ohman, M.D., Ruacho, A., Song, H., Stephens, B.M., 2017. Mesoscale ocean fronts enhance carbon export due to gravitational sinking and subduction. *Proc. Natl. Acad. Sci.* 114, 1252–1257.

Taylor, J.R., Smith, K.M., Vreugdenhil, C.A., 2020. The influence of submesoscales and vertical mixing on the export of sinking tracers in large-eddy simulations. J. Phys. Oceanogr. 50, 1319–1339.

Thompson, A.F., Lazar, A., Buckingham, C., Garabato, A.C.N., Damerell, G.M., Heywood, K.J., 2016. Open-ocean submesoscale motions: A full seasonal cycle of mixed layer instabilities from gliders. J. Phys. Oceanogr. 46, 1285–1307.

von Appen, W.-J., Strass, V.H., Bracher, A., Xi, H., Hörstmann, C., Iversen, M.H., Waite, A.M., 2020. High-resolution physical-biogeochemical structure of a filament and an eddy of upwelled water off northwest Africa. *Ocean Sci.* 16, 253–270.

von Appen, W.J., Wekerle, C., Hehemann, L., Schourup-Kristensen, V., Konrad, C., Iversen, M.H., 2018. Observations of a submesoscale cyclonic filament in the marginal ice zone. *Geophys. Res. Lett.* 45, 6141–6149.

Waite, A.M., Stemmann, L., Guidi, L., Calil, P.H., Hogg, A.M.C., Feng, M., Thompson, P. A., Picheral, M., Gorsky, G., 2016. The wineglass effect shapes particle export to the deep ocean in mesoscale eddies. *Geophys. Res. Lett.* 43, 9791–9800.

Wilson, S.E., Ruhl, H., Smith, J., Kl., 2013. Zooplankton fecal pellet flux in the abyssal northeast Pacific: A 15 year time-series study. *Limnol. Oceanogr.* 58, 881–892.

Yu, X., Naveira Garabato, A.C., Martin, A.P., Buckingham, C.E., Brannigan, L., Su, Z., 2019. An annual cycle of submesoscale vertical flow and restratification in the upper ocean. J. Phys. Oceanogr. 49, 1439–1461.