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Low Contribution of the Fast-Sinking Particle Fraction to Total Plankton Metabolism in a Temperate Shelf Sea

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Key Points:

- Higher microbial respiration and bacterial production rates estimated in slow-sinking compared to fast-sinking fractions in shelf waters
- Due to the low number of particles in the fast-sinking fraction, their contribution to water column metabolism was low
- Slow-sinking fraction made the greatest contribution to the potential export of particulate organic carbon to sediments or off-shelf

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Temperate shelf seas are productive areas with the potential to export high quantities of particulate organic carbon (POC), as sinking particles, to the sediments or off-shelf to the open ocean. The amount of carbon which can be exported depends partly on the amount of POC produced and on the remineralization processes occurring on the sinking material. Here, we assessed the relative seasonal importance of microbial respiration and bacterial production associated with suspended, slow- and fast-sinking particle fractions. The three fractions were collected in the Celtic Sea above and below the seasonal thermocline in November 2014, April and July 2015 using Marine Snow Catchers. The slow-sinking fraction had higher microbial respiration and bacterial production rates than the fast-sinking fractions, and these two fractions sustained rates of microbial respiration and bacterial production between 1 and 3 orders of magnitude lower than the suspended fraction. This low contribution of the slow- and fast-sinking fractions was consistent with their low contribution to the POC concentration at the two depths sampled. The POC-specific respiration rates associated with the slow- and fast-sinking fractions were low (median 0.17 and 0.08 d^{-1}, respectively), indicating low-sinking particle degradation. Our results indicate that ~5% of the POC in surface waters can be exported below the thermocline.

1. Introduction

Temperate shelf seas are important areas due to their role in the uptake of atmospheric carbon dioxide (Frankignoulle & Borges, 2001; Kitidis et al., 2019), their high productivity (Behrenfeld et al., 2005; Wollast, 1998), and therefore the existence of abundant particulate organic carbon (POC) (Dunne et al., 2007). In global terms, shelf seas can export more POC produced by primary production from the euphotic zone than open ocean areas (Dunne et al., 2007), which together with the shallower water depth implies that large amounts of POC potentially can be exported off the shelf or deposited in sediments through sinking particles. The POC export flux depends on the amount of sinking POC, particle sinking velocity, and the degradation rates that microorganisms and zooplankton exert on the particles. All these rates vary over time, depending on the transformation of the particles during sinking, such as through aggregation or fragmentation by turbulence, or through the activity of the organisms (bacteria, phytoplankton, and zooplankton) (Alldredge & Gotschalk, 1989; Briggs et al., 2020; Dilling & Alldredge, 2000; Goldthwait et al., 2004; Smith et al., 1992; Steinberg et al., 2008). Temperature can also have an effect on the biological activity of the attached microorganisms, and therefore, on the remineralization rates. However, in situ studies have reported higher carbon-specific respiration rates in the Southern Ocean (Cavan & Boyd, 2018) than in warmer areas of the North East Atlantic (Bach et al., 2019) indicating that factors other than temperature, such as the microbial community and particle composition, play an important role (Bach et al., 2019; Fontanez et al., 2015; Johnson et al., 2020; Kiørboe, 2001). This is consistent with the wide range in estimates of the percentage of sinking carbon that is respired in the surface layer. Several studies proposed that more than 80% of surface sinking POC is respired through the euphotic zone (Buesseler, 1998; Hedges, 1992; Lampitt et al., 2008; Riley et al., 2012). However, other studies reported high POC export from the euphotic zone. Results from a study in the North Atlantic during the spring bloom showed ~45% of the net primary production was exported out of the euphotic zone as POC (Buesseler & Boyd, 2009). In the Southern Ocean,

Belcher et al. (2016) indicated low particle respiration associated with high sinking velocities, and therefore low POC remineralization of sinking particles in surface waters and high export.

Characterizing particles by their sinking velocity into slow- (<20 m d^{-1}) and fast-sinking (>20 m d^{-1}) (Riley et al., 2012) helped to discern their different contributions to POC fluxes. Thus, data from the North Atlantic indicated that slow-sinking particles tend to have a relatively higher contribution to particulate POC fluxes in the euphotic zone than fast-sinking particles (Baker et al., 2017; Riley et al., 2012; Villa-Alfageme et al., 2016). Despite the importance of the particle degradation rates and the sinking velocity to the determination of POC fluxes, only two studies, both in the Southern Ocean, have reported respiration rates for the two sinking fractions in natural conditions (Baker et al., 2017; Cavan et al., 2017). Cavan et al. (2017) showed greater respiration rates in slow-sinking particles than fast-sinking particles in post-bloom conditions, whereas, Baker et al. (2017) reported different remineralization rates depending on the bloom conditions, with faster POC remineralization rates in slow-sinking particles in non-bloom conditions, and slower POC remineralization rates in slow-sinking particles in bloom conditions. A common challenge related to the studies reporting particle remineralization (Bach et al., 2019; Baker et al., 2017; Belcher et al., 2016; Cavan & Boyd, 2018; Cavan et al., 2017; Ploug et al., 1999) is that they tend to be performed at a specific time of the year, and therefore, it is difficult to infer the seasonal variability of particle remineralization.

The main objectives of this study were to quantify the microbial respiration (R) and bacterial production (BP) associated with suspended, slow-sinking, and fast-sinking fractions, to investigate their relative contribution to water column metabolism, and to study their seasonality in a temperate shelf sea. Based on the low microbial respiration of fast-sinking particles observed in the Southern Ocean (Baker et al., 2017; Cavan et al., 2017), we hypothesize that the fast-sinking fraction sustains lower respiration rates compared to the slow-sinking fraction, and that remineralization rates are seasonally dependent. As part of the UK NERC Shelf Sea Biogeochemistry programme, we collected particles above and below the seasonal thermocline, corresponding to the euphotic and aphotic zones, using Marine Snow Catchers (MSCs). These are sampling devices that divide "bulk" waters into suspended, slow-sinking, and fast-sinking fractions depending on their sinking rates (Riley et al., 2012).

2. Material and Methods

2.1. Marine Snow Catcher Deployments and Particle Collection

Measurements were made in the Celtic Sea at two stations (Central Celtic Sea, 49.39°N, 8.58°W, maximum depth 150 m; and Shelf Edge, 48.57°N, 9.5°W, maximum depth 200 m) and at three sampling times: November 2014 (18th and 25th), April 2015 (12th, 16th, and 21st), and July 2015 (15th, 20th, 25th, and 30th). One to four hours prior to the deployment of the MSC, we deployed a conductivity-temperature-depth (CTD) unit to characterize the physical properties of the full water column. The base of the seasonal thermocline was identified by the depth at which the temperature was >0.05°C warmer than the deepest recorded temperature in the profile. This seasonal thermocline (~96 m, ~50, and ~55 m in November, April, and July, respectively) was used to identify two layers: the upper mixed layer (UML), which corresponds to the layer from the surface to above the seasonal thermocline, extending across the euphotic layer (considered as the layer between the surface and the depth at which incident irradiance is 1% of surface irradiance) and the bottom mixed layer (BML), which corresponds to the layer below the seasonal thermocline and therefore, in the aphotic layer (Davis et al., 2019).

MSCs are routinely used for collecting sinking particles (Baker et al., 2017; Belcher et al., 2016; Cavan et al., 2017; Giering et al., 2016; Riley et al., 2012). A full description of the MSC methodology, schematic diagrams, and explanations of the working mechanisms are reported in Riley et al. (2012) and Giering et al. (2016). Briefly, an MSC is a large cylindrical sampling bottle with a removable base section that contains a particle tray. MSCs are used to collect a large volume of water (~95–300 L) that is left to settle for a specific time on deck; thus, particles are segregated based on their sinking rates. Typically, three fractions are defined: suspended (SU), which corresponds to the water sample in the upper part of the MSC; slow-sinking (SS), which corresponds to water plus particles above the fast-sinking tray; and fast-sinking (FS), which corresponds to the water sample plus particles that reached the particle tray at the bottom of the MSC (Giering et al., 2016; Riley et al., 2012). Water samples for the suspended and slow-sinking fractions are

collected from taps located on the top and lower section of the MSC, and the fast-sinking fraction is sampled directly from the sinking tray. Collecting sinking particles with MSCs implies differentiating them depending on their position in the MSC, which in turn is influenced by the initial position of the particles and their sinking velocity. Thus, the suspended fraction contains organisms attached to suspended particles plus free-living organisms, the slow-sinking fraction contains organisms attached to both slow-sinking and suspended particles plus free-living organisms and the fast-sinking fraction contains organisms attached to the fast-sinking, slow-sinking and suspended particles plus free-living organisms.

In this study, we used MSCs of two sizes: 300 L (large) MSCs in November and 95 L (small) MSCs in April and July. MSCs were deployed after dusk at two depths: two MSCs were deployed at 10–15 m (corresponding to the UML) and two MSCs at 10–20 m below the base of the seasonal thermocline (70–110 m), which corresponds to the BML. The two MSCs which sampled the same depth, were deployed consecutively within ∼10 min. From each depth, the first MSC was sampled for the estimation of metabolic rates (R and BP) and the second one was sampled for particulate organic carbon and nitrogen (POC and PON). After the deployment and collection of the water sample, the MSCs were left on deck to settle for 1.33 h (small) or 2 h (large) before sampling. The different settling times are proportional to the height of the small and large MSC, thus maintaining similar sinking velocities for the slow- and fast-sinking fractions (sinking velocity <24 m d^{-1} and >24 m d^{-1}, respectively). The suspended fraction is assumed to be of non-sinking material.

2.2. Microbial Metabolic Rates

For the estimation of the metabolic rates, six liters of the suspended fraction were collected by siphoning the water sample from the top tap of the MSC and two liters of the slow-sinking fraction were collected from the lower tap into 10 and 2 L carboys, respectively, and transported in darkness to a controlled-temperature room for subsequent subsampling and analysis. The fast-sinking fraction was collected from the particle tray at the bottom of the MSC and transported to a temperature-controlled room (set to in situ surface temperature). This fraction was transferred to a 0.5–1 L plastic beaker from where a specific volume (see below) was subsampled for the analysis of microbial respiration and bacterial production. The relatively small volume (≤0.5–≤1 L, small and large MSC, respectively) of the fast-sinking fraction required the dilution of the sample to create sufficient volume to undertake our multiple analyses with suitable replication. Thus, we performed six experiments where we quantified the effect of the dilution procedure on microbial respiration and bacterial production, two for each sampling cruise (see Section 2.3).

2.2.1. Dissolved Oxygen Consumption

The rate of microbial respiration, for each fraction, was determined by measuring the decrease in dissolved oxygen after a 24 h incubation in the dark. Dissolved oxygen concentration was measured by automated Winkler titration performed with a Metrohm 765 burette to a photometric end-point. Ten gravimetrically calibrated 60 mL borosilicate glass bottles were carefully filled with samples from the suspended fraction and another 10 with samples from the slow-sinking fraction. For the fast-sinking fraction microbial respiration rates, 10×15 mL samples of the fast-sinking fraction containing particles were collected with a pipette and placed into 10 gravimetrically calibrated 30 mL borosilicate glass bottles, which were then topped up with 15 mL of the suspended fraction (dilution 1:1). Prior to the subsampling, the plastic beaker containing the fast-sinking fraction was gently swirled to ensure that particles did not settle at the bottom of the beaker.

Five bottles from each of the three fractions (suspended, slow-sinking, and diluted fast-sinking) were fixed at the start of the incubation ("zero") with 3 M manganese sulfate (0.5 mL for the 60 mL bottles and 0.25 mL for the 30 mL bottles) and 4 M sodium iodide/8 M sodium hydroxide solution (0.5 mL for the 60 mL bottles and 0.25 mL for the 30 mL bottles). The other five bottles from each fraction were placed underwater in darkened temperature-controlled incubators located in a temperature-controlled room for 24 h ("dark"). The incubation temperature was within ±0.5°C of the in situ temperatures. "Dark" bottles were removed from the incubators after 24 h, and the samples were fixed as described for the "zero" bottles above. All bottles were analyzed together within 24 h. Microbial respiration for each fraction was calculated from the difference in oxygen concentration between the mean of the "zero" replicates and the mean of the "dark" replicates, and reported with a propagated standard error.

Table 1
Diluted (Fast-Sinking Fraction: Suspended Fraction, 1:1) to Undiluted (1:0) Ratios for Microbial Respiration (R) and Bacterial Production (BP) Rates for the Six Experiments Performed in November 2014, April 2015, and July 2015 in the Upper Mixed Layer (UML) and Bottom Mixed Layer (BML)

Month	Mixed layer	Depth (m)	R	BP
November 2014	UML	15	0.48 ± 0.1	0.58 ± 0.09
April 2015		10	0.67 ± 0.1	1.74 ± 0.73
July 2015		10	0.52 ± 0.1	1.17 ± 0.07
November 2014	BML	100	0.51 ± 0.18	1.19 ± 0.16
April 2015		70	0.50 ± 0.09	1.24 ± 0.89
July 2015		70	0.50 ± 0.06	1.19 ± 0.08

Note. Ratios are reported with their associated standard error.

2.2.2. Bacterial Production

Samples of the suspended, slow- and fast-sinking fractions were collected from the same carboys and plastic beaker as for the microbial respiration measurements. Rates of the bacterial production were estimated from the uptake of ^{14}C leucine (GE Healthcare UK Ltd). Two stock solutions of ^{14}C leucine (GE Healthcare UK Ltd) were used: 11.8 GBq/mmol, 318 mCi/mmol and 11.3 GBq/mmol, 306 mCi/mmol. Aliquots of 10 μL ^{14}C leucine working solution (0.04 MBq mL^{-1}) were pipetted into 2 mL sterile centrifuge tubes with 1.6 mL of sample (suspended and slow-sinking) and into 2 mL sterile centrifuge tubes with 0.8 mL of fast-sinking plus 0.8 mL of suspended fractions (diluted fast-sinking, see above) and mixed. Duplicate samples from each fraction were incubated at in situ temperature for 0, 1, 2, and 3 h in the dark. At the end of each incubation time, these samples were fixed with 80 μL of 20% paraformaldehyde (final concentration of 1%) and filtered onto 0.2 μm polycarbonate filters presoaked in 1 mM non-labeled leucine on top of a 25 mm GF/F filter as a backing filter. Each 0.2 μm polycarbonate filter was placed into a scintillation vial, dried overnight in a fume hood at room temperature and mixed with 4 mL of Optiphase Hi-Safe II scintillation fluid. Radioactivity in the samples was measured using a Beckman Coulter LS6500 liquid scintillation counter. Bacterial population growth (cells m^{-3} d^{-1}) was calculated from ^{14}C leucine incorporation using a theoretical approach assuming no isotope dilution (Kirchman, 2001).

2.3. Dilution Experiments and Theoretical Considerations

In order to quantify the effect of diluting the fast-sinking fraction, six dilution experiments were undertaken, two during each cruise (November 24th, 2014, April 25th, 2015, and July 22nd, 2015) with water collected at the two sampling depths (UML and BML). Details and explanations of the methods used to test for a dilution effect are reported in the Supporting Information S1 (Figures S1 and S2). The ratios of the diluted rates to the undiluted rates (Table 1) were used to correct the diluted rates (see Section 2.4).

2.4. Calculation of the Metabolic Rates

Microbial respiration and bacterial production rates reported for the fast-sinking fraction were corrected for the dilution effect, multiplying the measured rates (R and BP) at each experiment by the corresponding factor obtained in the dilution experiments for each cruise and depth (Table 1).

Microbial respiration and bacterial production rates in the slow- and fast-sinking fractions were scaled to the volume of sample in which they originally occurred by multiplying the rates by the ratio of the volume associated to each fraction relative to the volume of the MSC (7/95 and 10/300 for the small and large MSC, respectively, for the slow-sinking fraction and 0.5/95 and 1/300 for the small and large MSC, respectively, for the fast-sinking fraction). These scaled rates provide information on the contribution of these fractions to water column metabolism.

2.5. Particulate Organic Carbon and Nitrogen

POC and PON values (reported in full in Davis et al., 2019) were used to calculate POC-specific respiration in the three fractions (suspended, slow-, and fast-sinking), and to derive relationships between the composition of the organic material (POC:PON ratio) and the metabolic rates. The specific POC and PON data used in this study are given in the supporting material (Figure S3).

In brief, samples for the analysis of particulate organic carbon and nitrogen (POC and PON) in the suspended, slow- and fast-sinking fractions were collected from MSCs deployed ∼10 min after those used for R and BP samples. Two liters of the suspended and slow-sinking fractions and the contents of the whole fast-sinking tray were filtered through Whatman glass fiber filters (GF/F, 25 mm diameter, 0.7 μm pore size,

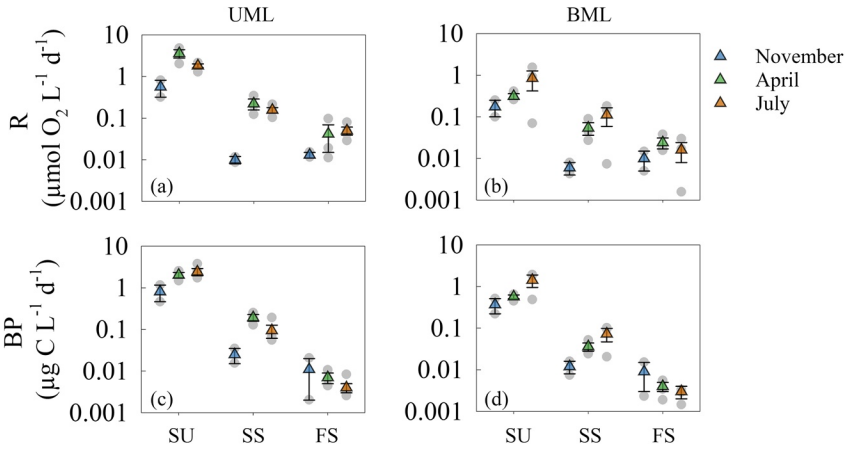

Figure 1. (a and b) Microbial respiration (R) and (c and d) bacterial production (BP) for the suspended, slow-sinking and fast-sinking fractions (SU, SS, and FS, respectively) measured in the (a and c) upper mixed layer and (b and d) bottom mixed layer. Individual data points are in gray circles and the average in colored triangles for November 2014 (blue), April 2015 (green), and July 2017 (brown). Error bars represent the standard error. Note the logarithmic scale of the *y*-axes.

and pre-combusted for 4 h at 450°C). Filters were vapor-phase decarbonated and analyzed using a Carlo Erba Instruments NC2500 elemental analyzer (Yamamuro & Kayanne, 1995).

Rates of microbial respiration (measured as the consumption of dissolved oxygen) were converted to carbon respiration rates assuming a respiratory quotient (RQ) of 1. We acknowledge the variability in this respiratory quotient (0.7–1.2) depending on the substrate being respired (from carbohydrates to lipids) (Berggren et al., 2012). However, due to the lack of information on the composition of the particles, we adopted the most common respiratory quotient used in laboratory and ocean studies reporting respiration on particles (RQ = 1) (Bach et al., 2019; Belcher et al., 2016; Iversen & Ploug, 2013; Ploug & Grossart, 2000). Therefore, the POC-specific respiration associated with the different fractions was calculated as the carbon respiration rates in the suspended, slow-, or fast-sinking fractions divided by their associated POC.

2.6. Comparison of Rates Collected With MSC and With Niskin Bottles

In order to confirm that the rates measured in samples collected with the MSC were representative of the rates in the natural environment, we performed a comparison between the sum of the volume scaled R and BP rates of the three fractions (suspended + slow-sinking + fast-sinking) with the R and BP rates measured in bulk waters collected with Niskin bottles at the same station on the day prior to the deployment of the MSCs (García-Martín, Aranguren-Gassis et al., 2019; García-Martín, Daniels et al., 2019).

2.7. Statistical Analysis

The relationship between R and BP rates measured in water samples collected with the MSC and in water samples collected with Niskin bottles, as well as the relationship between R and BP in the different fractions were determined with a type II least squares model regression using the package lmodel2 (Legendre, 2013) in R (R Core Team, 2020). Spearman nonparametric correlation tests were used to study the relationship between microbial respiration, bacterial production, and POC concentration.

3. Results

3.1. Microbial Respiration and Bacterial Production in the Three Fractions

The slow- and fast-sinking fractions sustained between 1 and 2 orders of magnitude lower microbial respiration rates than the R associated with the suspended fraction at the two depths (Figures 1a and 1b). The BP showed a similar pattern, with rates in the slow- and fast-sinking fractions between 1 and 3 orders of magnitude lower than in the suspended fraction (Figures 1c and 1d).

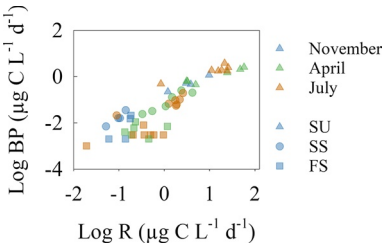

Figure 2. Log-log relationship between microbial respiration and bacterial production for the suspended (triangles), slow-sinking (circles), and fast-sinking fractions (squares) in November 2014 (blue), April 2015 (green), and July 2015 (brown).

There were seasonal differences in the R rates in the three fractions in the UML, with lower rates in November (average 0.57 ± 0.25, 0.01 ± 0.001, and 0.014 ± 0.002 µmol O_2 L^{-1} d^{-1} for the suspended, slow-, and fast-sinking fractions, respectively) compared to April (average 3.58 ± 0.82, 0.22 ± 0.07, and 0.04 ± 0.02 µmol O_2 L^{-1} d^{-1} for the suspended, slow-, and fast-sinking fractions, respectively) and July (average 1.81 ± 0.19, 0.16 ± 0.02, and 0.05 ± 0.01 µmol O_2 L^{-1} d^{-1} for the suspended, slow-, and fast-sinking fractions, respectively) (Figure 1a). In the BML, there was a similar variability to the UML for the suspended and slow-sinking fractions, but the seasonality was not clear for the fast-sinking fraction due to the high variability measured in July (Figure 1b). Likewise, bacterial production only showed seasonal differences in the suspended and slow-sinking fractions in both layers, with lower BP rates measured in November (average 0.81 ± 0.35 and 0.03 ± 0.01 µmol C L^{-1} d^{-1} for the suspended, slow-sinking fractions in the UML, respectively) than April (average 2.02 ± 0.31 and 0.19 ± 0.04 µmol C L^{-1} d^{-1} for the suspended, slow-sinking fractions in the UML, respectively) and July (average 2.43 ± 0.48 and 0.09 ± 0.03 µmol C L^{-1} d^{-1} for the suspended, slow-sinking fractions in the UML, respectively) (Figures 1c and 1d).

Assuming that bacteria were responsible for 50% of the R in our study, our average estimates of bacterial growth efficiencies (the balance between the biomass produced per unit of substrate assimilated, BGE = BP/(BP + bacterial respiration)) would be 0.21 ± 0.03, 0.15 ± 0.02, and 0.06 ± 0.01 for the suspended, slow- and fast-sinking fractions, respectively.

3.2. Relationship Between Respiration and Bacterial Production in the Different Fractions

In general, monthly average microbial respiration and bacterial production rates were greater in the UML compared to the BML for all fraction types. Taking the two layers together, there was a significant positive relationship between the R and BP for the suspended and slow-sinking fractions, but not for the fast-sinking fraction (Figure 2). The slopes of the log-log linear regressions for the suspended (slope = 0.64, R^2 = 0.80, and n = 17) and slow-sinking (slope = 0.68, R^2 = 0.74, and n = 17) fractions were not significantly different (df = 69, t = 0.36, and p = 0.71).

3.3. POC-Specific Respiration Rates

The largest POC pool was associated with the suspended fraction, followed by the slow-sinking fraction and the smallest pool measured in the fast-sinking fraction (Figure S3; Davis et al., 2019). Taking all depths and seasons together, the average contribution of the suspended fraction was 91 ± 4% of the total POC, whereas the slow-sinking and fast-sinking fractions contributed 5 ± 2% and 4 ± 3%, respectively.

Microbial respiration rates were proportional to POC concentration for the suspended and slow-sinking fractions (nonparametric correlation, $p < 0.05$), but not for the fast-sinking fraction (Table 2). Whereas, bacterial production showed a positive significant correlation to POC only in the slow-sinking fraction.

Table 2
Correlation Coefficients Between Particulate Organic Carbon Concentration and Microbial Respiration and Bacterial Production in the Three Fractions

	Microbial respiration			Bacterial production		
Fraction	r	p	N	r	p	N
Suspended	**0.75**	<0.001	17	0.48	0.05	17
Slow-sinking	**0.55**	0.02	17	**0.65**	<0.01	17
Fast-sinking	−0.04	0.90	12	0.34	0.26	12

Note. Significant correlations are indicated in bold.

In the UML, the POC-specific respiration rate varied from 0.06 to 0.22 d^{-1} for the suspended fraction, 0.053 to 0.31 d^{-1} for the slow-sinking fraction, and between 0.01 and 0.5 d^{-1} for the fast-sinking fraction (Figure 3a). However, this latter single high value could be considered an outlier due to the high respiration rate measured in a sample associated with very low values of POC. In the BML, the POC-specific respiration rate varied from 0.01 to 0.29 d^{-1} for the suspended fraction, 0.04 to 0.8 d^{-1} for the slow-sinking fraction, and between 0.01 and 0.1 d^{-1} for the fast-sinking fraction (Figure 3b). There was a seasonal pattern in the suspended and slow-sinking fractions with lower POC-specific respiration in November, which was not observed in the fast-sinking fraction.

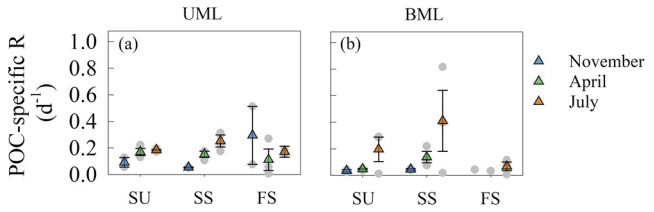

Figure 3. POC-specific respiration rates for the suspended, slow-, and fast-sinking fractions (SU, SS, and FS, respectively) in (a) the upper mixed layer and (b) the bottom mixed layer (BML). Individual data points are in gray circles and the average is in colored triangles for November 2014 (blue), April 2015 (green), and July 2017 (brown). Error bars represent the standard error. There is only one data point for the FS fraction in November and in April for the BML and therefore, there is no average available for this fraction in these months.

3.4. Microbial Rates Measured in Samples Collected With the Marine Snow Catcher Versus Niskin Bottles

There was no significant difference between the R rate measured in waters collected with Niskin bottles and with the sum of the R rates in the three fractions collected with the MSCs (paired t-test, $t = 0.305$, df = 12, and $p = 0.76$, Figure S4a). The slope of the relationship was 1.08 (Type II linear regression) and was not significantly different from unity (Clarke test, $t = 0.34$, df = 10, and $p = 0.73$). However, the relationship was not so clear for the BP rates (Figure S4b), as the BP measured in bulk waters collected with Niskin bottles was c.a. two-fold greater than the sum of the volume-scaled BP measured in the MSC in ∼50% of the data from April and July.

4. Discussion

4.1. Metabolism of Sinking Fractions

Microbial respiration in the fast-sinking fraction was lower than in the slow-sinking fraction, confirming our hypothesis, and both fractions made only a small contribution to the remineralization of organic carbon in the water column. Similar results were reported for respiration rates of sinking particles in the upper mesopelagic of the Southern Ocean (Belcher et al., 2016). Our 3 orders of magnitude lower bacterial production in the fast-sinking fraction than in the suspended fraction agrees with a recent study in the open Atlantic Ocean (Baumas et al., 2021), with the low contribution (<2%) of attached bacteria to total bacterial production in the NE Atlantic Ocean (Turley & Mackie, 1994), with the lower bacterial production estimated in different marine snows compared to the surrounding seawater of samples collected in surface waters off the coast of California (Simon et al., 1990), and the lower incorporation of thymidine by particle-attached bacteria in aphotic waters (Cho & Azam, 1988). The scarcity of sinking POC material in this study may explain the low contribution of the sinking fractions to the water column metabolism. Our observations of low POC associated with sinking particles are not unusual, as previous studies in the Atlantic Ocean indicated that most of the POC was associated with suspended particles (Baker et al., 2017; Riley et al., 2012).

Our results suggest that BP in the slow- and fast-sinking fraction was limited or decoupled from R, as the R was on average 15- and 95-times greater than BP, respectively. Higher R rates than BP have been previously reported in aggregates (Ploug & Grossart, 2000) and in bulk waters of North Atlantic shelf seas (García-Martín, Daniels et al., 2019; Reinthaler et al., 2005; Sintes et al., 2010). The R measurements in our sinking fractions include the respiration of free-living and particle-associated microorganisms. To calculate bacterial growth efficiencies in this study, we have assumed that bacteria were responsible for 50% of the respiration rates. This is in the range of the bacterial contribution to community respiration reported for a recompilation of data from diverse oceanographic regions (average 45%, Robinson, 2008) and a similar contribution proposed in Collins et al. (2015). Our results suggest that most of the carbon resources in the sinking fractions were used to maintain bacterial cellular activity, and a small proportion was used for cell production, therefore, indicating low bacterial growth efficiencies, based on the 15-fold and 95-fold higher R rates compared to BP in the slow- and fast-sinking fractions, respectively. Our averaged BGE values for the suspended and slow-sinking fractions (0.21 ± 0.03 and 0.15 ± 0.02) are within the average value ± standard error (0.19 ± 0.16) reported for coastal waters (Robinson, 2008), and within the lower range of bacterial growth efficiencies measured in aggregates from cultured phytoplankton (0.1–0.5, Ploug & Grossart, 2000). These BGE values from cultured phytoplankton should be considered as minimum BGE values, as the total respiration of the particle was assumed to be bacterial respiration (Ploug & Grossart, 2000). Our average value for the fast-sinking fraction (0.06 ± 0.01) is lower than these published values, but higher than the BGE reported for sinking particles in the North West Atlantic (average 0.01 ± 0.004) (Collins et al., 2015). Our average BGE values are also lower than the average BGE in bulk waters measured during the same cruises (average 0.38 ± 0.02, García-Martín, Daniels et al., 2019). Discrepancies between BGE values reported for the fractions collected with the MSCs and from bulk waters (García-Martín, Daniels et al., 2019) could be attributed to the different methodologies used in the two studies (dissolved oxygen consumption

vs. INT reduction), including the different incubation times used by the methods (24 h for dissolved oxygen consumption vs. <4 h for INT reduction; see García-Martín, Aranguren-Gassis et al., 2019 for a further discussion on the limitations of both methods). Nevertheless, our statement that most of the organic carbon assimilated by bacteria in the slow- and fast-sinking fractions is used in respiratory processes rather than growth would be valid for a varying proportion of respiration attributable to bacteria, as the R was 15-times and nearly 2 orders of magnitude greater than BP, respectively.

Our POC-specific respiration of the slow-sinking (0.02–0.8 d^{-1}, median 0.17 d^{-1}) and fast-sinking fractions (0.01–0.5 d^{-1}, median 0.08 d^{-1}) are within or in the lower range of those measured in sinking particles collected by sediment traps in the North Atlantic (0.007–0.173 d^{-1} (Collins et al., 2015)), of aggregates formed by algal cultures (0.01–0.45 d^{-1} (Iversen & Ploug, 2010)), or particles collected by a RESPIRE trap at the base of the euphotic zone in the Sargasso Sea (0.3–1.5 d^{-1} (McDonnell et al., 2015)). However, they are greater than POC-specific respiration measured in particles collected during mesocosm experiments in the northeast Atlantic (0.007–0.1 d^{-1} (Bach et al., 2019)) and fecal pellets collected in the Southern Ocean (0.01–0.065 (Belcher et al., 2016)). The great variability in the turnover rates of the organic carbon in the fractions associated with the sinking particles indicated that the POC in the slow-sinking fraction could be completely remineralized from 3 days in April and July to 20 days in November in the UML, whereas, the POC in the fast-sinking fraction would take from 4 to ∼125 days in early April to be completely remineralized.

4.2. Seasonal Variability in the Celtic Sea

One of the main objectives of this study was to study the seasonal variability of the microbial respiration and bacterial production rates in different sinking fractions. The three cruises sampled winter mixing in November, a spring plankton bloom during April, and summer stratification in July (Davis et al., 2019; García-Martín, Daniels et al., 2019; Poulton et al., 2019). The Celtic Sea is characterized by seasonal variability in POC, with higher concentrations in spring and summer and lower concentrations in autumn (Davis et al., 2019) that reflect the seasonal variability in primary production and plankton community structure (Giering et al., 2019; Poulton et al., 2019). Our results showed a similar seasonality in respiration in the three fractions and in bacterial production in the suspended and slow-sinking fractions. However, BP in the fast-sinking fraction was, on average, higher in November than in the other 2 months. The seasonality in the suspended and slow-sinking fractions was similar to that observed in bulk waters collected during the same cruises (García-Martín, Aranguren-Gassis et al., 2019; García-Martín, Daniels et al., 2019). Thus, we suggest that R and BP in these two fractions were regulated by the same environmental factors as those regulating the metabolic activity in bulk waters (temperature and dissolved organic carbon). Whereas, in the fast-sinking fraction it is likely that other environmental factors, such as the quality and quantity of particulate organic matter, had a greater influence. The BP of marine particle-attached bacteria can depend on the origin of the particle (Alldredge & Gotschalk, 1989; Simon et al., 1990) and on the quality of the organic matter (Grossart & Ploug, 2001). Furthermore, a seasonal study of estuarine particles showed that the BP of particle-attached bacteria was related, specifically, to the quantity of labile particulate organic nitrogen while the variability of free-living bacteria was mainly related to chlorophyll and primary production (Crump et al., 2017). The plankton community during our study varied seasonally from one dominated by gelatinous zooplankton in November, to a high abundance of autotrophic organisms during the spring bloom in April followed by an increase in mesozooplankton, such as copepods, in July (Giering et al., 2019; Poulton et al., 2019). Hence, although we lack specific data on the origin of the particles, it is likely that the sinking particles had a zooplankton origin in November and July and a phytoplankton origin in April. Unfortunately, the high variability in the POC:PON ratio measured in the fast-sinking fraction, especially in November and April, meant that there was no difference in POC:PON seen between the suspended, slow-, and fast-sinking fractions.

The low turnover rates of the organic carbon associated with the slow- and fast-sinking fractions and the shallower seasonal thermocline in April (∼50 m) and July (∼55 m) than November (∼96 m) implied that a large proportion of the original POC measured in the UML could reach the BML. Thus, 86%, 95%, and 90% of the fast-sinking POC and ∼99% of the slow-sinking POC could have reached the BML in November, April, and July, respectively. However, these percentages should be considered maximum POC export flux estimates, as zooplankton grazing on particles and particle fragmentation are important factors in the

attenuation of the organic carbon (Briggs et al., 2020; Goldthwait et al., 2004; Ploug & Grossart, 2000). The higher contribution of the fast-sinking fraction to POC export during April supports the suggestion of a higher contribution of POC flux associated with fast-sinking particles during bloom conditions as a result of higher concentrations of plankton cells (Belcher et al., 2016). However, our percentages correspond to a negligible POC export associated with the fast-sinking fraction, due to the ∼50-times lower POC concentration in the fast-sinking fraction compared to the suspended fraction (Davis et al., 2019, Figure S3), and to an export of ∼5% of the total POC in the UML associated with the slow-sinking fraction. A similar major contribution of the slow-sinking fraction, rather than the fast-sinking fraction, to POC export flux was reported in the studies in the Atlantic Ocean (Baker et al., 2017; Riley et al., 2012) and in a model study (Henson et al., 2015). Once in the BML, sinking POC could reach the sediment or be transported off the shelf, especially in November, when there was low POC-specific respiration and an off-shelf flow of bottom waters (Ruiz-Castillo et al., 2019). The low potential off-shelf POC export calculated in this study agrees with results derived from offshore particulate and dissolved carbon analysis in the NW European shelf (Painter et al., 2016) where the off-shelf carbon flux was predominantly in the form of dissolved inorganic and organic carbon, and POC represented only 0.3% of the off-shelf flux.

4.3. Limitations and Future Considerations

This study presents the first seasonal view of microbial respiration and bacterial production associated with suspended, slow-sinking, and fast-sinking fractions including estimates of carbon-specific respiration rates. We acknowledge that the data presented here have limitations that include the use of the MSCs to collect and separate sinking particles and the need to dilute the fast-sinking fraction. As mentioned in the material and methods section, the fast-sinking fraction contains suspended and slow-sinking as well as fast-sinking particles, and therefore, it is difficult to estimate the respiration of fast-sinking particles per se. However, sinking particles are not found in isolation, but surrounded by suspended particles, which benefit from the dissolved organic matter released during the remineralization of the sinking particles (Kiørboe & Jackson, 2001).

Most of the studies reporting metabolic activities measured in sinking particles have collected and incubated particles individually (Alldredge & Gotschalk, 1989; Belcher et al., 2016; Iversen & Ploug, 2010; Ploug & Grossart, 2000) or collectively (Bach et al., 2019; Cavan et al., 2015, 2017; Collins et al., 2015; McDonnell et al., 2015; Ploug & Grossart, 1999). The method employed (individual or collective incubation) could lead to differences in the measured rates. In a comparative study of BP associated with individual particles and particles clustered together, Ploug and Grossart (1999) showed that clustered particles had higher BP compared to individual particles. As far as we know, there is no previous information on the possible effect of the method employed on the particle-associated respiration, making it hard to compare the results between studies. Nevertheless, this study is not the first to require dilution of the sinking material (Bach et al., 2019; Baumas et al., 2021; Collins et al., 2015). In the three former studies, dilutions of the sinking fraction were performed with bulk waters collected with Niskin bottles, or water samplers, which could be considered as the suspended fraction. Furthermore, respiration rate or bacterial production rate associated with the sinking material was calculated as the difference between the rate estimated in the bottles containing the diluted sinking fraction and the rate measured in the suspended fraction. Based on the results from our dilution experiments (Supporting Information S1), particularly the possible dilution effect on the rates of bacterial production (diluted:undiluted ratio >0.5), we recommend avoiding dilution if at all possible. However, if this is not possible, perhaps due to the lack of sample volume to undertake all the required measurements, then we suggest determining and applying a diluted:undiluted ratio, as done here rather than calculating the rates associated with the sinking material as the difference between fractions with sinking and without sinking material. Since, this ratio can be applied irrespective of whether the rates in the suspended fraction are higher or lower than the rates in the fast-sinking fraction, it will solve the potential problem of obtaining negative values for the sinking fraction when the rates in the suspended fraction are greater than the rates in the sinking fraction (Bach et al., 2019; Collins et al., 2015).

However, the determination of a dilution ratio needs to be undertaken frequently enough to be representative of the particular sample. Here, we undertook one dilution experiment at each month at each depth and so had to assume that the dilution ratio did not vary between experimental days within that month. Since

particle disaggregation may lead to variation in the rates of the free-living microbes (Collins et al., 2015), and thus, may influence whether dilution is conservative or not, we cannot be certain that this assumption was fulfilled. However, the consistent diluted:undiluted respiration ratio in the three sampling months, even when the sinking material was likely to have a different origin, gives us some confidence that dilution was conservative at least for microbial respiration. Unfortunately, the variability observed in the diluted:undiluted bacterial production ratio suggests that this assumption may not hold for bacterial production. Future studies may need to determine the diluted: undiluted ratio over successive days, to better characterize the variability for bacterial production.

Nevertheless, based on the following observations, we suggest that any potential limitation due to sampling with the MSC and diluting the fast-sinking fraction, did not significantly impact the conclusions. First, POC-specific respiration rates were comparable with previous observations made using different techniques (Bach et al., 2019; Belcher et al., 2016; Collins et al., 2015; McDonnell et al., 2015). Second, our BP rates in the fast-sinking fraction are within the range in the North Atlantic (BP for depths <100 m: 0.002–0.005 μg C L^{-1} d^{-1} (Baumas et al., 2021)). Finally, the sum of the R and BP rates in the three fractions was similar or in the range of the rates measured in bulk waters within the previous 24 h. The variability between the BP rates from Niskin or MSC sampling (~40% of the BP measurements collected with Niskin bottles were 2-fold greater than the BP measured in the corresponding samples collected with the MSC) could be due to daily variability (Niskin and MSC samples were taken 24 h apart), or diel variability (Niskin samples were collected predawn and MSC samples after sunset), or the settling process of the MSC could negatively affect BP. Diel and daily variability are likely to be the basis for the variability seen here, based on the 1.5-fold diel variability in BP measured in the North Pacific (Viviani & Church, 2017) and the >2-fold daily and diel variability in BP in the Mediterranean Sea (Ruiz-González et al., 2012).

The seasonal variability in POC, with higher concentrations in spring and summer and lower concentrations in autumn (Davis et al., 2019) reflected the seasonal variability in primary production and plankton community structure (Giering et al., 2019; Poulton et al., 2019). However, despite the increase observed in sinking POC concentration in April, the POC concentrations in the sinking fractions were lower than we expected from this productive shelf sea. Biogeochemical models suggest a time lag of 20–30 days between the peak in primary production and the export of sinking particles for the North Atlantic region (Henson et al., 2015). This time lag could mean that our sampling campaign in April missed the time of greatest sinking particulate organic material (early-mid May 2015). It is also possible that the low POC concentration in the fast-sinking fraction was a result of the dominance of phytoplankton in the 2–20 μm size fraction (Giering et al., 2019), which tend to be rapidly recycled by the microbial loop (Azam et al., 1983; Laws et al., 2000), rather than large silicifying diatoms.

5. Conclusions

The contribution of slow- and fast-sinking fractions to the remineralization of organic carbon in the water column was between 1 and 2 orders of magnitude lower than the remineralization associated with the suspended fraction suggesting minor contributions to water column metabolism. There was a seasonal variability in microbial respiration, with higher rates in April and July, for the suspended, slow-, and fast-sinking fractions in the upper mixed layer and for the suspended and slow-sinking fractions in the bottom mixed layer. Whereas, bacterial production only showed seasonal differences in the suspended and slow-sinking fractions in both layers. There was a modest amount of sinking POC during our study. Our results indicate that ~5% of the total POC in surface waters can be exported below the seasonal thermocline, mainly as slow-sinking particles, which then have a high potential to reach the sediment or be exported off-shelf unless consumed or fragmented by zooplankton.

Data Availability Statement

All data used in this study are available at the British Oceanographic Data Centre (BODC) (BODC reference number for bacterial production data: DML170161 and for dissolved oxygen consumption UEA170099).

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