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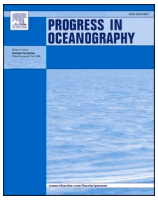

Review

A focus on different types of organic matter particles and their significance in the open ocean carbon cycle

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ABSTRACT

Marine particles are key to the cycling of major elements on Earth and play an important role in the balance of nutrients in the ocean. Three main categories of marine particles link the different parts of the open ocean by shaping carbon distribution: (i) sinking; (ii) suspended, and (iii) ascending. Atmospheric carbon captured by phytoplankton in the surface water, is partly sequestered by sinking particles to the bottom of the ocean and plays an important role in controlling global climate. Suspended particles represent a significant source of organic carbon for heterotrophic microorganisms and are more likely to undergo remineralization compared to sinking particles. Ascending particles, depending on their composition, point of origin, and ascending velocity, may lead to carbon remineralization in the upper layers of the ocean in closer proximity to the atmosphere. Marine particles are hotspots of microbial activity and thus heavily colonized by microorganisms whose dynamics play an important role in organic matter degradation, aggregation and sinking, thus directly influencing the biological carbon pump efficiency. Microbiomes of marine particles differ depending on particle size, source, and age. Nevertheless, these factors are generally overlooked, and particles are mostly studied as "bulk" without considering the high heterogeneity between individual particles. This hinders our understanding of the carbon budget in the ocean and thus future predictions of climate change. In this review we examine known particle-types and associated sampling methods and identify knowledge gaps and emphasize the need for a better understanding of the single-particle ecosystem to enhance global upscaling rates. Furthermore, we introduce a novel concept: the 'lipid carbon shunt'.

1. Introduction

1.1. Particles in the ocean

Marine particles were observed and photographed for the first time in the 1950s by submarines and were termed "Marine Snow" due to their continuous downward migration (Suzuki and Kato, 1953). In the open ocean, particles consist mostly of particulate organic matter (POM), and are initially formed by microorganisms, mostly through photosynthesis in the euphotic zone, and by chemosynthesis deeper in the water column or from hydrothermal-vent plumes. Organic Matter (OM) particles may include homogenous or heterogenous, live and senescent, phytoplankton species (e.g. diatoms, coccolithophores, dinoflagellates, *Cyanobacteria*), zooplankton molts and carcasses, abandoned larvacean houses, pteropod feeding webs, fecal pellets, marine gels, detritus, and also non-biogenic components (e.g., clay, silt, minerals, calcite) (Simon et al., 2002). Colonizing microorganisms are an innate part of any type of OM particles (Bižić-Ionescu et al., 2015). OM particles are aggregated (and disaggregated) via various physical processes (Verdugo et al., 2004; Burd and Jackson, 2009) and further transformed by microbial degradation, and zooplankton grazing (Simon et al., 2002; Burd and Jackson, 2009). OM particles are highly heterogeneous, yet some studies show these exhibit greater similarity when analyzed in terms of season, location, and particle source (Flintrop et al., 2018). In contrast, other studies have shown that even particles of the same source and age can be highly heterogeneous in associated microbial communities (Bizic-Ionescu et al., 2018; Zäncker et al., 2019; Szabo et al., 2022; Baumas et al., 2024).

OM particles can be classified as (i) sinking; (ii) suspended; and (iii) ascending based on their movement in the water column, a property that depends on their size, density, and porosity. Particles are dynamically affected by biotic or abiotic processes, and thus may continuously shift

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between the three main categories. Based on their biological and/or chemical origin and composition, particles can further be divided into several, often interwoven, types within each category, (e.g., phytoplankton/zooplankton-derived particles, bioluminescent particles, marine gels, plastic and other anthropic particles, deep lipid-rich particles, hydrothermal-vents particles).

OM particles are hotspots of microbial activity due to their high concentration of nutrients and OM, as compared to the surrounding water (Alldredge and Cohen, 1987; Alldredge and Silver, 1988; Alldredge and Jackson, 1995; Long and Azam, 1996; Simon et al., 2002). Therefore, these particles are small ecosystems whose physico-chemical characteristics are largely shaped by the attached microorganisms. The diversity and activity of these microorganisms are in turn dictated by the dynamic environmental conditions as the particle moves through the water column. Heterogeneous conditions within particles are distinctly different from those of the surrounding water column. Coupled with high activity of particle attached communities, OM particles are a unique and important topic in biological oceanography.

1.2. *The importance of organic matter particles*

OM particles play a central role in controlling the transport (vertical and horizontal), cycling, and stocks of nutrients (e.g. C, N, P, S, Fe), and trace elements (e.g. Mn, Co, Zn, Mo, Cu, Ni) critical for life in the ocean (Fowler and Knauer, 1986; McDonnell et al., 2015b). By governing the distribution and concentration of carbon in the water column especially, sinking particles play a crucial biogeochemical role storing CO_2 away from the atmosphere at geological timescales via the Biological Carbon Pump (BCP) (Siegel et al., 2016; Le Moigne, 2019). The BCP refers to the capture of atmospheric carbon by phytoplankton in surface waters and its subsequent, partial, sequestration by gravitational sinking of particles to the ocean floor. At depths below 1000 m, particle-bound carbon can remain away from the atmosphere for thousands of years, which plays an important role in regulating the global climate.

In parallel, suspended particles are a major substrate of organic carbon for heterotrophic microorganisms and are more likely to be remineralized shallower in the water column than sinking particles which results in a shorter time frame of carbon being returned to the atmosphere (see sections below). Ascending particles (see sections below), depending on their composition, point of origin and ascending velocity, may in some cases lead to CO_2 being produced, through microbial degradation, in the upper layers of the ocean in closer proximity to the atmosphere (Yayanos and Nevenzel, 1978). Finally, while sinking, ascending, or being transported by currents, marine particles are spread everywhere in the water column and dynamically link the different parts of the ocean also shuttling associated microorganisms.

1.3. *Upscaling from single sites to global scales: The drawbacks of bulk approaches*

The study of OM particles faces several challenges that, if ignored, may lead to incorrect results or to data misinterpretation (Ionescu et al., 2015; Bizic-Ionescu et al., 2018; Armitage and Jones, 2019; Henson et al., 2022). These hurdles are driven, among others, by: 1) difficulties in sample collection (e.g., scuba diving depth is limited, high pressure at great depths); 2) sampling methodologies that select for one type of particles over another; 3) the fragile and complex structure of particles; 4) difficulties in identifying the geographical origin of particles at depth; and, 5) by their heterogeneity in source, age and associated microbial communities (e.g. Alldredge, 1998; McDonnell et al., 2015; Flintrop et al., 2018; Bizic-Ionescu et al., 2018; Baumas et al., 2021). One of the outcomes of these complexities is the common choice to study particles as total bulks. While bulk based approaches aim at generating a representative picture of the particles in the sampled water, it cannot fully resolve the distribution of particle types sampled or type-specific remineralization rates. Furthermore, it fails to provide mechanistic insight into the degradation of different particle-types, information necessary for increasing the prediction power of carbon sequestration models. Additionally, as previously shown, averaging multiple particles is likely to generate an inaccurate representation of the bulk particles microbiome by smoothing the existing heterogeneity (Bizic-Ionescu et al., 2018; Zäncker et al., 2019; Armitage and Jones, 2019; Szabo et al., 2022; Pernthaler et al., 2023; Baumas et al., 2024).

1.4. *Methodological problems arising from heterogeneity among particles*

As a bulk-based approach hides particle heterogeneity and prevents the mechanistic understanding of microbial degradation process, data collected from bulk based approaches cannot be readily applied to large scales. Heterogeneity plays a role at different scales. First, diversity in particle sources, i.e., different biochemical compositions of POM. It was previously suggested that particles of different sources (e.g. different algal species) attract different colonizing prokaryotes (Grossart et al., 2005). However, new experiments show high heterogeneity also in colonizers between particles of the same source (Bizic-Ionescu et al., 2018). A systematic study analyzing multiple individual particles of different source taxa has not been yet conducted to compare the diversity within and between sources. In either case, while Bizic-Ionescu et al. (2018), Bižić-Ionescu et al. (2015) suggested a certain degree of functional similarity between particles colonized by different prokaryotes, this has yet to be transferred into particle degradation rates. The results of such a study will inform on whether community composition can be ignored in rate-upscaling studies or whether it should be incorporated into models in a species-aware manner. A second factor of heterogeneity that plays a role is particle age. Particles located in the same water layer are not necessarily of the same age, meaning elemental composition e.g. C:N:P ratios and carbon quality may vary owing to variable periods of microbial processing and interaction with the surrounding water, despite particles having been from the same source (Schneider et al., 2004). These differences will be transferred into degradation rates with older particles likely being degraded slower, by a community of more specialized microorganisms. Water currents and phytoplankton bloom length may also affect the average particle age in the water column; thus, these factors cannot be taken as constants when upscaling to larger scales. Once more data becomes available on the shift in degradation rate with particle age, a comparison of C:N:P ratios between the source phytoplankton bloom and the resulting particles moving through the water column, may provide an estimate of average particle age.

In this review, we discuss and characterize the different particle-types, as categorized by their motion in the water column and present them as miniaturized ecosystems. We highlight the missing knowledge linking the activities of particle-associated microorganisms to open ocean processes, that need to be addressed to better understand the carbon cycle. Furthermore, we call for supplementing the current bulk-based research with studies targeting single-particles from natural environments and controlled laboratory experiments.

2. Sinking, suspended and ascending particles

2.1. *Sinking particles*

Gravitationally sinking particles (hereafter sinking particles) are key players in the BCP process. Suppressing this process would result in a 50 % rise in present levels of atmospheric CO_2 (Parekh et al., 2006). However, not all the sinking POC reaches the depth (variable across different ecosystems with different water masses which are upwelled sooner than others e.g., Southern Ocean) required for carbon to be stored for millennia. Beyond the mesopelagic zone, where absence of light prevents photosynthesis, biological processes depend almost exclusively on sinking POC as carbon source. As a result, the downward flux of POC decreases with increasing depth as it is processed and remineralized by micro- and macro-organisms. Therefore, all the carbon shuttled down by these sinking particles plays an essential role in the carbon cycle, whether by satisfying the carbon demand of organisms below the photic zone or through sequestration. While L. Joubin recognized their significance already in 1930 (Joubin, 1930), evoking "une pluie alimentaire,[1]" it is only in the last few decades that sinking particles have been extensively studied.

Sinking particles, can be made of single or aggregated phytoplankton cells (DiTullio et al., 2000; Thornton, 2002; Rembauville et al., 2016; Guidi et al., 2016; Leblanc et al., 2018; Michaud et al., 2022), fecal pellets (Turner, 2002; Tamburini et al., 2006; Cavan et al., 2015; Steinberg and Landry, 2017; Eduardo et al., 2020; Saba et al., 2021), and various types of particles coming together following various aggregation and coagulation processes (Alldredge and Jackson, 1995; Verdugo et al., 2004; Riley et al., 2012; Laurenceau-Cornec et al., 2015; Cruz and Neuer, 2022). The contribution of each type of sinking particle to the composition and intensity of the POC sinking flux varies by location and season depending on biological (Piontek et al., 2014; Agusti et al., 2015; Le Moigne et al., 2016; Weber et al., 2016; Cruz and Neuer, 2022), chemical (Edwards et al., 2015), ecological (Cavan et al., 2015; Guidi et al., 2016), and physical (Levy et al., 2013; Taucher et al., 2014; Dall'Olmo et al., 2016) processes. To date, these processes are all poorly constrained and hinder accurate mechanistic prevision. The sinking speed of gravitationally sinking particles ranges from 2 to 1500 m/d (Alldredge and Silver, 1988; Armstrong et al., 2002; Trull et al., 2008; Turner, 2015) with fecal pellets reported to sink at the greatest speeds of this range (Atkinson et al., 2001; Giesecke et al., 2009). The sinking speed can eventually increase with mineral ballast inclusion, either after particle formation or when particle is formed around minerals (Francois et al., 2002; Armstrong et al., 2002, 2009; Klaas and Archer, 2002; Ploug et al., 2008; Iversen and Ploug, 2010; Wilson et al., 2012) and decrease due to the encapsulation of microplastics (Wieczorek et al., 2019; Roberts et al., 2023, and section "plastic particles").

Sinking POC is composed of varying concentrations of amino acids, carbohydrates, lipids, pigments and uncharacterized carbon (Wakeham et al., 1997; Lee et al., 2004; Kharbush et al., 2020). The POC entering the mesopelagic zone is composed of 82 % characterizable compounds, of which 67 % are amino acids (Wakeham et al., 1997; Lee et al., 2004). With increasing depth, and thus increasing age and remineralization stage, the contribution of characterized material decreases dramatically, reaching 20 % at 1000 m (Hedges et al., 2001). Molecular analyses of individual biochemical classes within the characterized portion, reveals exponential loss of plankton remains and increase in heterotrophic biomarkers with depth, and elevated proportions of prokaryotes markers near the sea floor (Wakeham et al., 1997; Lee et al., 2004). The inability to characterize the bulk of the POC at depth confirms the general paradigm of a switch from well characterized, phytoplankton-originating, highly labile POC at the surface, to biologically and analytically refractory material, mostly phytoplankton detritus diluted by zooplankton and microbial material, in the deeper layers (Kharbush et al., 2020). Sinking particles may also include biogenic and lithogenic minerals which serve as dense ballast, possibly minimizing the degradation of POC, and serve as adsorption surfaces for DOC (Hedges et al., 2001; Lee et al., 2004; Lamborg et al., 2008).

While the above provides a general overview on sinking particles, different types of marine sinking particles exhibit different proportions and composition, a trait that still needs to be investigated. For instance, fecal pellets from diurnal migratory organisms such as zooplankton or small fish are shuttled directly into the lower mesopelagic zone. These pellets escape several hundreds of meters of degradation and their composition differs from the pellets that sink from the surface through the euphotic zone (Steinberg and Landry, 2017; Aumont et al., 2018; Hernández-León et al., 2019; Eduardo et al., 2020; Maas et al., 2020; Devries et al., 2021; Saba et al., 2021). In another case, Michaud et al. (2022) showed a link between geographical location and seasonality with the downward fluxes of organic matter particles. This was attributed to differences in particle-forming phytoplankton species and their associated microbial communities subsequently resulting in different remineralization rates over depths and time.

Remineralization rates on particles have been measured on sinking particles obtained from sediment traps (Iversen et al., 2010; McDonnell et al., 2015a; Boyd et al., 2015; Collins et al., 2015; Busch et al., 2017; Le Moigne et al., 2017; Bach et al., 2019), Marine Snow Catchers (Belcher et al., 2016; Cavan et al., 2017), from plankton nets (Cavan and Boyd, 2018); on particles collected by divers (Ploug et al., 1999; Grossart et al., 2003a; Goldthwait et al., 2005), or on lab-made particles (Ploug and Grossart, 2000; Iversen and Ploug, 2010, 2013; Le Moigne et al., 2013; Ploug and Bergkvist, 2015; Stief et al., 2021; Tamburini et al., 2021) and were found to range between 0.001 and 1 d^{-1} (Bach et al., 2019). Reasons for observed variability in remineralization rates across such few studies (~20) has not yet been determined, although it is hypothesized that differences in methodologies coupled with the large heterogeneity in particle characteristics (e.g., origin, source material, size, and age) may drive this. Additionally, remineralization depth is also often ignored. With the exception of Stief et al. (2021) and Tamburini et al. (2021) who simulate a sinking depth of 10 and 1 km, respectively, all other studies focus on the euphotic and shallow mesopelagic zone (0–500 m) despite the fact that carbon remineralization in these regions may not be most important when considering carbon storage efficiency (Fuchs et al., 2022). Prokaryotic Heterotrophic Production (PHP) is commonly used as an indicator for particle remineralization. PHP is linked with carbon remineralization (PR) through prokaryotic growth efficiency (PGE) so that PR = PHP x (1-PGE)/PGE (del Giorgio and Cole, 1998). The choices of conversion factors involved in PHP determination and PGE are a matter of debate (Burd et al., 2010; Giering and Evans, 2022; Baumas et al., 2023) and may require revisions on rate estimations. Despite this, evidence shows that attached prokaryotic cells are more productive (sometimes by a few orders of magnitude) than their free livings counterparts (Turley and Mackie, 1994; Simon et al., 2002; Grossart et al., 2003a; Baumas et al., 2021; Church et al., 2021). This is also confirmed by measurements of enzymatic activities on sinking particles (Smith et al., 1992; Grossart et al., 2003a, 2003b; Tamburini et al., 2006; Kellogg and Deming, 2014; D'Ambrosio et al., 2014; Prairie et al., 2015; Balmonte et al., 2020; Zhao et al., 2020; Lloyd et al., 2022). Since carbon remineralization rates are an integral component in understanding the BCP, it would be worthwhile to establish common protocols for its determination and calculation (Bach et al., 2019).

Living microorganisms (autotrophs and heterotrophs) are an integral part of the particle they inhabit (Caron et al., 1982; Karl et al., 2022; Volkman and Tanoue, 2002; Bižić-Ionescu et al., 2015) both with respect to activity, as well as biomass. Attached prokaryotes are concentrated on particles with prokaryotic abundance reaching thousands of times greater than that of free-living prokaryotes in a comparable sea water volume (Alldredge et al., 1986; Turley and Mackie, 1994; Simon et al., 2002). Additionally, phytoplankton cells which constitute the particle can sometimes remain alive while sinking. For example, it has been shown that diazotrophs such as *Trichodesmium* continue to fix nitrogen in the dark and at great pressures up to depths of 4000 m (Agusti et al., 2015; Poff et al., 2021; Benavides et al., 2022; Bonnet et al., 2022). Karl et al. (2022) showed that live organisms can represent 30 % of total particulate carbon in the euphotic zone, 10 % in the lower mesopelagic, and 3 % below 3000 m. This number may be underestimated due to sampling without keeping *in situ* pressure, but even so, the depth integrated microbial biomass in the aphotic zone exceeds by 25 % that of the euphotic zone.

It has been shown the diversity of colonizing communities on sinking particles from the euphotic zone decreases drastically as a response to environmental parameters from 500 m and below (e.g. increasing pressure and decreasing temperature) (Thiele et al., 2015; Baumas et al.,

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[1] "Une pluie alimentaire"French for "a nutritional rain".

Table 1

Literature review of 58 studies that analyzed the diversity on marine particles (Acinas et al., 1999, 2021; Amacher et al., 2009; Baumas et al., 2021; Bergauer et al., 2018; Bidle and Azam, 2001; Bochdansky et al., 2017; Church et al., 2021; Crespo et al., 2013; Datta et al., 2016; DeLong et al., 1993; Duret et al., 2019; Durkin et al., 2022; Eloe et al., 2011; Flintrop et al., 2018; Fontanez et al., 2015; Frank et al., 2016; Ganesh et al., 2014; Grossart et al., 2003b; Leu et al., 2022; Liu et al., 2018; Luo et al., 2022; Maas et al., 2020; Mestre et al., 2017, 2018; Metfies et al., 2017; Milici et al., 2016a,c, 2017; Pelve et al., 2017; Preston et al., 2020; Rath et al., 1998; Rieck et al., 2015; Riou et al., 2018; Roth Rosenberg et al., 2021; Ruiz-González et al., 2020; Salazar et al., 2016; Steiner et al., 2020; Tamburini et al., 2006, 2009, 2021; Thiele et al., 2015; Valencia et al., 2022; Wenley et al., 2021; Woebken et al., 2007; Yuan et al., 2021; Zäncker et al., 2019; Zorz et al., 2019; Bižić-Ionescu et al., 2015; Boeuf et al., 2019; Dithugoe et al., 2021; Lecleir et al., 2014; Liu et al., 2022; Lloyd et al., 2022; Milici et al., 2016b; Peoples et al., 2018; Poff et al., 2021; Szabo et al., 2022).

	Origins of particles			Type of samples				Type of analyses								Investigation					
	Lab	*In situ*	Location of microbes assemblage	Bulk	Single particle	Sea floor	Single cell	FISH/Card-FISH	DNA Metabarcoding / qPCR or DGGE	RNA Metabarcoding / qPCR	Metatranscriptome	Metagenome	Metaproteome	Metabolomic / metabolites analyse	Activity rates	Locations	Seasons	Methods	Particles degradation or heterogeneity	Depths	Comparison with background
De Long et al. 1993		SCUBA syringes		✓					8F-1492R												✓
Rath et al. 1998		SCUBA syringes	Adriatic Sea	✓					27F-1492R												
Acinas et al. 1999		Van Dorn bottle	Western Mediterranean	✓					27F-1492R											✓	✓
Bidle & Azam 2001	Diatoms		Isolated from diatoms detritus	✓					GC341F-534R, Arch21F-Arch985R & 27F-1492R										✓		
Grossart et al. 2003	Agar		Isolated from marine particles					✓							Interspecific interactions						
Tamburini et al. 2006	Coccolithophorid		Mediterranean Sea	✓				✓							Enzymatic activities				✓	✓	
Woebken et al. 2007		Sea water	Namibian upwelling	✓				✓	GM3F-GM4R, 20F-1392R, Pla46F-1392R, Amx368F-1392R & Amx368F-1392R												✓
Amacher et al. 2009		Free drifting sediment trap	North Atlantic						EukA - EukB											✓	
Tamburini et al. 2009		Net-trap	Ligurian Sea	✓				✓											✓	✓	
Eloe et al. 2011		Sequential filtration of sea water	Puerto Rico Trench	✓			✓		27F-1492R & Arch21F-Arch958R			✓							✓	✓	✓
Crespo et al. 2013		Niskin	Western Mediterranean	✓					A967F-B1046R							✓				✓	✓
Bizic-Ionescu et al. 2014		Niskin	North Sea / North Adriatic	✓				✓	28F and 519R							✓				✓	✓
Ganesh et al. 2014		Niskin	South Pacific	✓					✓			✓									✓
LeCleir et al. 2014		RESPIRE	South Pacific	✓					1050F-1392R & 338F-926R						Enzymatic activities, PHP	✓					✓
Fontanez et al. 2015		Free drifting sediment trap	North Pacific	✓								✓						✓		✓	
Rieck et al. 2015		Sea water	Baltic sea	✓					341F-805R						PHP and respiration	✓					✓
Thiele et al. 2015		Free drifting sediment trap			✓			✓												✓	✓
Datta et al. 2016	Chitin beads		North Atlantic						515F-806R			✓							✓		
Frank et al. 2016		Niskin	North East Atlantic	✓					28F-519R						PHP	✓				✓	✓
Milici et al. 2016a, b, c		Niskin	Atlantic ocean	✓					807F-1050R							✓					✓
Salazar et al. 2016		Niskin	World's oceans	✓					515F-806R							✓					✓
Bochdansky et al. 2017		Niskin	North Atlantic and Arctic	✓				✓											✓		✓
Mestre et al. 2017		Sequential filtration of sea water	Mediterranean Sea	✓					28F-519R								✓				✓
Metfies et al. 2017		Sediment trap, Niskin	Arctic ocean	✓					Euk528F - 1055R								✓	✓			
Milici et al. 2017		Niskin	Southern ocean	✓					807F-1050R							✓					✓

(continued on next page)

Table 1 (*continued*)

Pelve et al. 2017		Free drifting sediment trap	North Pacific	🟩			🟩		27F-907R & Arc344F-Arc915R			🟪								🟦	
Bergauer et al. 2018		Sea water	Atlantic									🟪	🟪							🟦	🟦
Flintrop et al. 2018		MSC, Free drifitng sediment trap	North Atlantic		🟩			🟪										🟦			
Mestre et al. 2018		Sequential filtration of sea water	Mediterranean Sea	🟩					28F-519R								🟦				🟦
Liu et al. 2018		Niskin	New Britain Tranch	🟩					338F-806R & 515F-907R											🟦	🟦
Peoples et al. 2018		Niskin	Kermadec & Mariana trenches	🟩					515F-926R						BONCAT					🟦	🟦
Riou et al. 2018	Diatom		Mediterranean Sea	🟩				🟪											🟦	🟦	
Bœuf et al. 2019		Sediment trap	North Pacific	🟩					515F-806R & Reuk454FWD1 - TAReukREV3		🟪	🟪					🟦				
Duret et al. 2019		MSC	Scotia sea	🟩					Pro341F-Pro805R										🟦	🟦	🟦
Preston et al. 2020		Sediment trap, Niskin, ROV push cores	North East Pacific	🟩		🟩			515F-806R & Euk1391F-EukBr								🟦				🟦
Zancker et al. 2019		Sea water	North Atlantic	🟩	🟩				515F-926R										🟦		
Zorz et al. 2019		Sea water	North Atlantic						B969F-BA1406R							🟦	🟦			🟦	🟦
Maas et al. 2020	Copepod excreta		Bermuda Atlantic	🟩					27F-338 RPL					🟪					🟦		🟦
Poff et al. 2021		Sediment trap	North Pacific	🟩							🟪	🟪					🟦				
Ruiz Gonzales et al. 2020		Niskin	World's oceans	🟩					515F-926R							🟦					🟦
Steiner et al. 2020		SCUBA syringes, Niskin	Northern adriatic sea	🟩					341F-802R			🟪					🟦				🟦
Baumas et al. 2021		MSC, Niskin	North Atlantic	🟩						515F-806R					PHP			🟦	🟦	🟦	🟦
Church et al. 2021		Net-trap, Niskin	North Pacific	🟩					515F-926R						PHP, dark C fixation		🟦				🟦
Dithugoe et al. 2021		MSC	Southern ocean	🟩								🟪				🟦					🟦
Roth Rosenberg et al. 2021		Niskin	Eastern Mediterranean	🟩					515F-926R								🟦				🟦
Acinas et al. 2021		Niskin	World's oceans	🟩								🟪				🟦					🟦
Tamburini et al. 2021	Coccolithophorid		North Atlantic	🟩						515F-806R					O_2 consumption				🟦	🟦	
Yuan et al. 2021		Niskin	South China sea	🟩					515F-806R							🟦					🟦
Wenley et al. 2021		Niskin, onboard pump	South Pacific						515F-806R								🟦			🟦	🟦
Durkin et al. 2022		Polyacrylamide gels from NBST, Niskin	North Pacific	🟩	🟩				Reuk454FWD1 - TAReukREV3									🟦	🟦		🟦
Liu et al. 2022	Diatom		East China sea	🟩					515F-806R & Bac338F-518R											🟦	🟦
Lloyd et al. 2022		Niskin	North Atlantic	🟩					8F-338R						Enzymatic activities	🟦				🟦	🟦
Luo et al. 2022		Sediment traps	North Pacific	🟩								🟪					🟦			🟦	
Leu et al. 2022		Net-trap	North Pacific	🟩								🟪								🟦	🟦
Valencia et al. 2022		Sediment traps, Niskin	North Pacific	🟩					515F-926R & euk 1389F-1510R							🟦					🟦
Szabo et al. 2022	Chitin beads		North Atlantic		🟩							🟪		🟪					🟦		

2021). This likely suggests colonizing microorganisms from the euphotic zone may reach their limit of adaptability and could be gradually replaced by newcomers from a deeper origin as the particles sink deeper. Although this remains to be further confirmed, some studies corroborate this, reporting a high proportion of typical bathypelagic *Gammaproteobacteria* and *Campylobacterota* (formerly *Epsilonproteobacteria*) on particles at 4000 m (Boeuf et al., 2019; Preston et al., 2020; Poff et al., 2021). However, as stated above, sinking particles do not have identical sinking rates and thus differ in the time micro-organisms have for replication suggesting that not all cells that attach have the time to reach the densities necessary to influence diversity or remineralization rates. Although slow- and fast-sinking particles are mixed in sediment traps it is probable that the identified bathypelagic prokaryotes have grown on slow sinking particles. In contrast, fast-sinking particles are primarily colonized by prokaryotes from upper layers, which have withstood the changing in environmental conditions during their rapid descent. Accordingly, fast-sinking particles could seed deep sea free living communities through cells detachment while providing minimally degraded organic matter to the depth, while slow sinking particles could be colonized by deep sea free living bacteria and subsequently be more extensively degraded (Mestre et al., 2018; Ruiz-González et al., 2020; Baumas et al., 2021). Interestingly though, a recent laboratory study (Alcolombri et al., 2021) suggests that fast sinking particles are degraded faster as degradation products are being washed off minimizing the competition for enzymes.

Previously, microscopy was a method of choice to study microbial diversity of particles. For instance, Caron et al. (1982) found that particles form highly enriched heterotrophic micro-environments were colonized by diverse prokaryotes, as determined by shape, (e.g. filamentous, curved and spiral) and diverse eukaryotes, dominated by microflagellates. Nowadays, molecular methods are widespread and financially more accessible, allowing a more in-depth investigation of microbial communities. We compiled existing literature where molecular tools were used to study diversity of microorganisms on sinking particles in the open ocean (Table 1). Most of these studies found common prokaryotic taxa with attached lifestyle including *Bacteroidetes* and *Actinobacteria* in the euphotic zone and *Deltaproteobacteria*, *Marinimicrobia* and *Gammaproteobacteria* in deeper water. Nevertheless, these organisms exhibit different community assemblages and varying degrees of diversity corresponding to different seasons, locations, depths or particle types and sources (ref. within Table 1). Therefore, comparison of results to define key patterns is challenging. In addition, in the studies identified here, many investigate prokaryotes with only 20 % of the studies investigating eukaryotes and even less in the case of viruses, which account for only 7 %.Yet, eukaryotes can dominate microbial biomass on bathypelagic particles (Bochdansky et al., 2017), and have the potential to promote aggregation of particles (Jain et al., 2005; Chang et al., 2014; Hamamoto and Honda, 2019; Xie et al., 2022). Association of viruses with particles has only recently been investigated, though viral lysis of both autotrophic and heterotrophic prokaryotes plays a role in carbon export (Luo et al., 2022) and phage activity may shape prokaryotic diversity at the microscale (Bizic-Ionescu et al., 2018; Szabo et al., 2022). Furthermore, most studies investigate DNA (*ca.* 70 % of those listed in Table 1), not allowing the separation of the active community and their function from the inactive members and their metabolic potential. Overall, as apparent from Table 1, a far greater number studies is needed to understand the high complexity of this "heterogeneous black box".

Sinking particles, are micro-ecosystems, hosting distinct microbial communities (See Table 1 for a summary of diversity studies) with high concentrations of prokaryotes, eukaryotes, and viruses. These communities are influenced by environmental factors and biotic interactions. We hypothesize that differences in sinking particle composition and their associated microbial community drive variations in the remineralization process. However, studies linking microbial activity rates and diversity on particles were only recently undertaken (e.g. Lecleir et al., 2014; Frank et al., 2016; Baumas et al., 2021; Church et al., 2021; Tamburini et al., 2021) and clear patterns remain undefined. Nevertheless, Enke et al. (2018), conducted a controlled lab experiment, demonstrating that microscale ecology of attached prokaryotes can impact carbon turnover rates. They show that particle degradation kinetics depend on the colonization and assembly of primary degraders and secondary consumers (Enke et al., 2018).

Adding further complexity to this, different environmental conditions such as temperature, pressure, OM quality, and absence of light can affect prokaryotic diversity, growth efficiency, enzymatic hydrolysis, and gene expression. In this sense, environmental condition variations caused by sinking of a particle can affect microbial metabolisms potentially shaping POC remineralization and sequestration. For instance, Church et al. (2021) observed greater prokaryotic heterotrophic production on slow-sinking compared to fast-sinking particles. This is further supported by experiments of POC degradation across a variety of substrates which resulted in a range of microbial responses, suggesting that remineralization rates of sinking particles depend on their source material (Davis et al., 2009).

This findings align with ecto-enzymatic activity measurements on sinking particles, which vary with depth and location (Tamburini et al., 2006; Yamada et al., 2012). Inside a single particle, environmental conditions can lead to the formation of micro-niches, favoring various metabolisms, including chemoautotrophy (Karl et al., 1984), sulfur metabolism (Shanks and Reeder, 1993; Raven et al., 2021), and methanogenesis (Shanks and Reeder, 1993). A variety of biological, physical and chemical processes alter the organic composition of sinking particles as they descend, with decomposition and transformation mechanisms, differing based on the molecular structures of individual compounds and substrate availability for heterotrophic metabolism.

Unfortunately, little is known about the distribution of sinking particle types, their attached microbial communities, and associated remineralization rates – essential for comprehending the function of the biological carbon pump and for constraining predictive models. Nguyen et al. (2022) provides mechanistic insights into key microscale dynamics occurring on particles across depth profiles. Their model illustrates that microbial growth dynamics can generate temporal and spatial variability in POC degradation rates, highlighting inadequacies in current parameters used for POC degradation modeling. Additionally, the stochastic assembly of communities on particles results in diverse microbial dynamics over depth. This work (Nguyen et al., 2022) represents a first step in explicitly integrating microscale dynamics into large-scale models and underscores the importance of accurately describing major particle-microbe interactions to predict variability in large-scale carbon cycling.

2.2. Suspended particles

Initially in the field of marine particles, suspended, i.e. neutrally buoyant, particles were considered as a contributing feature of background concentrations pool (e.g. McCave, 1975) likely due to the difficulties in isolating suspended from other categories such as sinking particles which specifically sink into traps. Development of semi-automated platforms and devices enabling high frequency sizing or *in situ* imaging resulted in the discovery that the passive transport of suspended particles was more dynamic than previously thought and have gained increasing interest in recent studies (Picheral et al., 2010; Boss et al., 2015; Dall'Olmo et al., 2016; Le Moigne, 2019; Claustre et al., 2020). While sinking particles control the vertical exchange between the euphotic zone and the deepest zones, neutrally buoyant particles dominate the standing stock of POC in the water column and contribute to horizontal transport of POC (Lam and Marchal, 2015). Two types of suspended particles exist: (i) degraded sinking particles, with no further descent, and (ii) low density particles that cannot sink out of the euphotic zone but can be transported by physical processes down to the mesopelagic zone. In both cases organic carbon stored in such particles and the dispersal of the attached microbes are solely driven by movements of water masses such as the large-scale thermohaline circulation, horizontal currents, advection, subduction, and eddies.

2.2.1. Disaggregated sinking particles

Sinking POC fluxes are attenuated by around 70–85 % in the mesopelagic zone (Martin et al., 1987; Henson et al., 2012; Marsay et al., 2015; Guidi et al., 2015). Zooplankton and attached microbes feed directly on sinking particles, yet their carbon demands explain less than half of the POC flux attenuation (Karl et al., 1988; Giering et al., 2014; Collins et al., 2015; Belcher et al., 2016), highlighting the importance of indirect processes. One potential hypotheses for the remaining, unexplained flux, could be the transformation into smaller, non-sinking particles (Karl et al., 1988; Abramson et al., 2010; Maiti et al., 2010; Kiko et al., 2017; Briggs et al., 2020). The extent to which sinking particles disaggregate can vary with season and less exchanges between both sinking and non-sinking particles occur during high sinking flux period (Cram et al., 2022). This transformation can occur by physical or biological fragmentation, or by microbial degradation.

Physical fragmentation of sinking particles is driven by three shear mechanisms: erosion from the particle's surface, pressure fluctuation across the particle and fracture (Parker et al., 1972). For instance, Riou et al. (2018) observed that disaggregation of sinking particles made of coccolithophorids is enhanced from increasing pressure while sinking. Although few estimates have been made of the forces required to fragment a particle, it has been shown that energy dissipation rates required are between 10^{-4} and 10^{7} m^{2} s^{-3} (Alldredge et al., 1990) with higher values for zooplankton-derived particles than pure diatom-derived. This is also consistent with observations made for robust fecal pellets versus fragile phytoplankton aggregates (Abramson et al., (2010). These numbers are in the range of typical dissipation rates in the ocean, which makes this process significant in determining suspended particle distribution (Burd and Jackson, 2009).

Biological fragmentation of sinking particles is driven by two mechanisms: sloppy feeding or coprorhexy (fragmentation of pellets) by detritivores (Lampitt et al., 1990; Noji et al., 1991; Turner, 2002; Iversen and Poulsen, 2007; Steinberg et al., 2008; Poulsen and Iversen, 2008; Giering et al., 2014; Svensen et al., 2014; Mayor et al., 2020), and fluid flows from zooplankton swimming (Dilling and Alldredge, 2000; Goldthwait et al., 2004; Poulsen and Kiørboe, 2005). Giering et al. (2014) showed that 30 % of sinking particles are fragmented by feeding activities of detritivores and are transformed into suspended particles. Burd and Jackson (2009) revealed that 50 % of surface particles could encounter swimming flows from zooplankton. The large daily migration or mesopelagic zooplankton concentrations (Hernández-León et al., 2019), is potentially also an important fragmentation source in the water column and could efficiently regulate the biological carbon pump (Cavan et al., 2017).

Finally, degradation by microbes also transforms sinking particles into smaller, non-sinking particles (Pomeroy and Deibel, 1980; Biddanda and Pomeroy, 1988; Noji et al., 1991; Smith et al., 1992; Simon et al., 2002). Smith et al. (1992) indicate that the ecto-enzymatic activity on particles is very high. As the amount of DOM produced by solubilization of POC would be 10 to 100 times greater than the absorption capacity of a cell, much of the produced DOC is released into the surrounding environment forming a plume which reduces sinking particle size and sinking velocities (Kiørboe and Jackson, 2001). Microbial degradation can lead to an increase of fractal dimension (Guidi et al., 2008 and ref within) allowing water flows to flush interstitial DOC (Goldthwait et al., 2005) and exposure of the internal particle structures and associated communities to seawater (Bianchi et al., 2018). Grossart et al. (2001) introduce the term of "Sloppy hydrolysis" to refer to these intensive ecto-enzymatic activities resulting in a release of DOC and increased appeal to surrounding microbes and zooplankton communities (Kiørboe and Visser, 1999; Poulsen and Kiørboe, 2005).

Physical and biological processes, as described above, lower the abundance of sinking particles, meaning that the associated gravitational POC fluxes in the mesopelagic zone have a major impact on the BCP (Buesseler and Boyd, 2009; Le Moigne, 2019). The most important mechanism in which suspended particles accumulate in the mesopelagic zone is disaggregation of sinking particles (Burd and Jackson, 2009; Dall'Olmo and Mork, 2014). The major consequence of sinking particle disaggregation is the enhancement of the development of associated microbial communities by providing more time for detritus to be converted into essential compounds conversion (van der Jagt et al., 2020). In turn, non-sinking nutritive material may be harvested by zooplankton (Mayor et al., 2014; Sanders et al., 2016; Cavan et al., 2021). Mayor et al. (2014) speculate that fragmentation of particles could be a deliberate behavior of zooplankton to promote colonization and increased microbial biomass from 'poor' quality POC, termed 'microbial gardening'. It has been deemed that sinking particle fragmentation is a source of prokaryote diversity to the non-sinking pool in the mesopelagic zone (Baumas et al., 2021). In addition, transformation into non-sinking particles increases the availability of POC and energy to small grazers (Belcher et al., 2019). Overall, this likely results in OC retention in the mesopelagic fueling mesopelagic biota and slow remineralization over time (Liszka et al., 2019).

2.2.2. Natively suspended particles

Suspended particles may also be formed by self-assembling DOM and small POM (e.g. Verdugo et al., 2004). Suspended particles are continually produced in the euphotic zone and are exported to depths of 200–1000 m via seasonal and/or physical pathways termed "Particle Injection Pumps" (PIPs) (Boyd et al., 2019) leading to a carbon flux comparable in intensity to the gravitational export (Dall'Olmo and Mork, 2014; Boyd et al., 2019). Suspended particles can be equally transported in all directions in contrast to sinking particles for which vertical export is dominant. PIPs are difficult to quantify because most of methodologies developed are focused on sinking particles. The first PIP described is carbon exported by the 'mixed layer pump' (Bishop et al., (1986). In summer, the mixed layer depth is near the euphotic zone boundary and high stratification leads to important stacking of suspended particles. During spring or fall, intermittent changes in the heat flux result in the vertical movement (e.g., shallowing or deepening) of the mixed layer depth. Variability in the mixed layer depth results in an important redistribution of suspended particles over the water column by subsequent subduction up to 1000 m (Bishop et al., 1986; Ho and Marra, 1994; Gardner et al., 1995; Dall'Olmo and Mork, 2014; Dall'Olmo et al., 2016; Boyd et al., 2019). This phenomenon is fast (in order of a week) and is considered the "largest instantaneous flux of small particles" (Dall'Olmo and Mork (2014). The second PIP is subduction by large scale circulation (Levy et al., 2013; Boyd et al., 2019). This is an advective mechanism driven by Ekman pumping, transporting suspended particles to depth. Although it has been established that subduction rates are typically much slower than those of gravitationally sinking transport, such large subduction occurs over vast areas, boosting the magnitude of carbon export to depth (Marshall et al., 1993; Ho and Marra, 1994). Deep water formation areas are hotspots for such exports (Tamburini et al., 2013b; Levy et al., 2013). The third PIP is termed the 'Eddy subduction pump' and can occur at mesoscale (10–100 km) to sub-mesoscale (1–10 km) frontal circulation (Levy et al., 2013; Omand et al., 2015; Stukel et al., 2017; Boyd et al., 2019). The frontal pump enhances carbon export by subducting surface-rich suspended particles (Omand et al., 2015; Stukel et al., 2017; Boyd et al., 2019) and even living phytoplankton (Pollard and Regier, 1990; Levy et al., 2001; Boyd et al., 2019) on timescales of days (Pollard and Regier, 1990; Niewiadomska et al., 2008; Estapa et al., 2015; Omand et al., 2015; Stukel et al., 2017). Local suspended particle concentration and vigor and penetration of the eddy both govern the subduction strength and efficiency in carbon export (Stukel et al., 2017; Boyd et al., 2019). Eddy subduction export has been mainly investigated using models (e.g. Levy et al., 2001; Karleskind et al., 2011; Nagai et al., 2015). Yet, *in situ* measurements suggest that mesoscale eddy subduction could be responsible for over a quarter of the total OC sequestration in some upwelling ecosystems such as the California current (Stukel et al., 2017). The discrepancy between gravitational carbon export and carbon demand in the aphotic zone has been known for decades (e.g. Burd et al., 2010) and the gap can be partly explained by PIPs (Boyd et al., 2019), although PIPs can often be neglected due to inappropriate sampling techniques. The spread of *in situ* optical devices (e.g. Giering et al., 2020 and optical methods section of this paper) however, likely provide an opportunity to explore this in the future.

2.3. Ascending particles

Biological activity related to particles has largely been studied mostly for its role in the BCP. Accordingly, most studies regard particle movement in the water column as unidirectional with the main recognized particle-classes being the sinking one and to a lesser extent, the suspended ones. Studies addressing the intense biological activity that takes place in the deeper layers of the water column and near the ocean floor are scarce. As a result, evidence of deep zooplankton and microorganism producing large amounts of new organic compounds which can lead to an ascent of POC and it's recycling back to upper layers, is often overlooked. Two main types of such ascending particles were identified (but see also section on marine gels): (i) deep lipid rich particles, and (ii) hydrothermal plumes particles.

2.3.1. Deep lipid rich particles

The "rising particle hypothesis" was first suggested in 1978, stating that lipid-rich particles produced near the deep benthos, due to buoyancy nature of lipids, would promote the fast shuttling of POC from the deep to the surface (Yayanos and Nevenzel, 1978). The hypotheses was founded in the demonstration that benthic amphipods from hadal zone (the zone below 6000 m) are lipid rich (26 % of dry weight of their bodies) and it was suggested after decay, predation or cannibalism, this could be a source of fast rising/ascending particles as lipid rich carcasses or fecal pellets (Yayanos and Nevenzel, 1978). Dissections of benthic amphipods revealed lipids are mainly in the form of visible liquid droplets. Nevertheless, analyses were performed at atmospheric pressure after decompression of the organisms (Yayanos and Nevenzel, 1978) and under *in situ* conditions of pressure and temperature, these lipids could be solid. Therefore, it is necessary to consider the hydrostatic pressure when modelling the release of these lipids, their ability to form particles, and their ascending velocity. Eggs are yet another source of rising lipid-rich particles (Robison and Lancraft, 1984; Smith et al., 1989; Grimalt et al., 1990). Apart from a few species with benthic ancestors, the majority of meso and bathypelagic zooplankton and fish have positively buoyant eggs, due to the presence of oil droplets allowing larvae to gain access to highly productive upper water layers (Robison and Lancraft, 1984). The time it would take such a particle to reach the surface starting from 5000 m was estimated between a week and a year (Yayanos and Nevenzel, 1978), equivalent to about 14 to 714 md^{-1}. This ascension speed is far greater than diffusion or normal mixing processes, indicating their potential significance in nutrient and biogeochemical processes.

To evaluate the relative importance of upward compared to downward fluxes, upright and inverted sediment traps were used

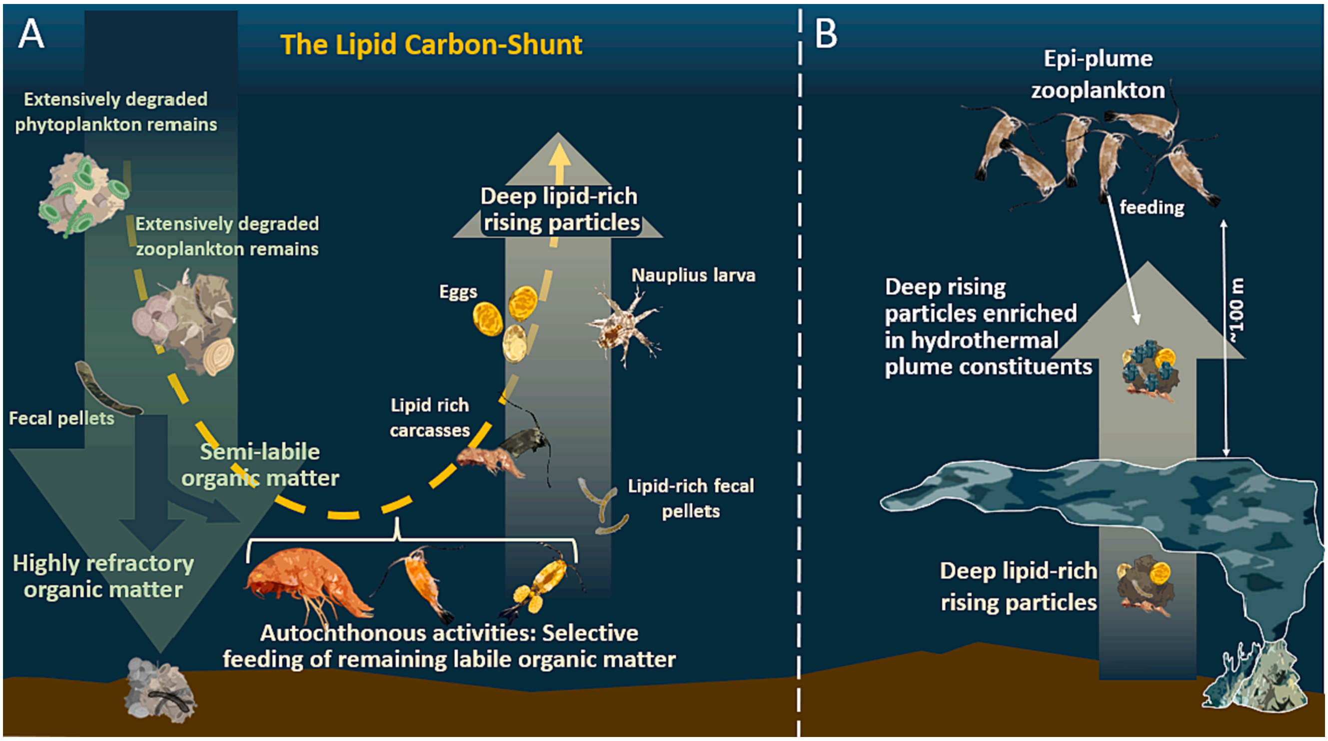


Fig. 1. (A) In bathyal and hadal zones (that are zones below 1000 m to the sea floor), strong zooplankton autochthonous activities occur, specifically with reproductive efforts during spring. This leads to a selective feeding of remaining labile organic matter which will rise as lipid rich carcasses or fecal pellets or as eggs and larva containing yolk stores. Lipid-rich particles ascending from the deep ocean may form “lipid carbon shunt”, allowing only the most refractory POC to reach the bottom while most labile POC that reach the depth is returned to shallower layers as buoyant particles. (B) Zooplankton are accessing hydrothermal vent constituents by feeding on deep lipid rich particles which cross the plume while ascending. That way they access labile food and plume constituents while avoiding the toxic plume (see section below). Sinking and suspended particles though co-occurring with ascending ones, are not shown in this figure for the sake of clarity.

concomitantly in the North Pacific at different stations, seasons and depths from around 1200 to 5000 m (Simoneit et al., 1986; Smith et al., 1989; Grimalt et al., 1990). The three studies agree that the upward flux is systematically lower than the downward flux, although the upward flux varies ranging between 1 and 68 % of the downward flux (Simoneit et al., 1986; Smith et al., 1989). No significant spatial differences in upward fluxes were noted between eutrophic and oligotrophic zones. However seasonally, the upward flux was systematically higher in spring (Smith et al., 1989). After hatching, larvae with imperfect appendage development, depend on their yolk stores for buoyancy. Their high abundance in spring in inverted sediment traps suggests high upward fluxes correspond to reproductive efforts of deep sea animals (Smith et al., 1989). Additionally, this constitutes the first evidence that the upward flux is independent of the downward flux, and rather, that it is linked to biological activities in the deep sea (Grimalt et al., 1990). Despite that the upward flux in most cases is a small portion of the downward flux, such a balance must be considered in the context of the particle quality and composition. Indeed, focusing on lipids, the upward flux represents between 0.19 and 190 % of the downward flux and more precisely 15 and 13,000 % for the sterols and fatty acids, respectively (Grimalt et al., 1990). Specifically, the downward lipid fluxes of particles consists of fecal pellets, diatoms frustule, foraminifera tests, and pteropods shells and showed a decrease with depth of fatty acids, wax esters and hydrocarbons concentrations (Simoneit et al., 1986; Grimalt et al., 1990). The identified hydrocarbons are characteristic of microbial degradation, oxidation and dissolution of algal detritus (Simoneit et al., 1986). Sediment lipids are consistent with the downward fluxes as they reveal POC from the same source (phytoplankton) but further degraded with signatures of degradation products by anaerobic prokaryotes related to sulfur metabolisms (Simoneit et al., 1986). In contrast, at comparable depths, upward flux was composed of small (<2mm diameter) transparent spherical globules, eggs, gelatinous masses and were rich in, fatty acid, wax esters, ketones and various polar compounds (Simoneit et al., 1986; Smith et al., 1989; Grimalt et al., 1990). Lipids found in particles collected in inverted sediment traps were associated with the signature of excretion, reproduction (eggs) and decay of copepods and amphipods (Simoneit et al., 1986; Smith et al., 1989). This demonstrates that at the same depth, the downward flux is characterized by highly degraded or refractory POC while the upward flux of POC are derived from recent autochthonous biogenic production (Simoneit et al., 1986; Grimalt et al., 1990). The strong contrast between the composition of sinking and sediment POC vs. rising POC makes it unlikely that the upward flux depends on the downward flux or the resuspension of sediment. While it has been established that deep lipid-rich particles are formed from eggs or decomposed amphipods and copepods, to fully understand the carbon cycle, food source of these indigenous, heterotrophic organisms should be investigated.

On a global scale deep lipid-rich ascending particles may represent an important pathway in biogeochemical cycles. Lipid-rich particles ascending from the deep ocean may form a “lipid carbon shunt”, allowing only the most refractory POC to reach the bottom while most of the labile POC that reaches the depth is shunted to shallower layers as buoyant particles (Fig. 1). As evidence suggests that upward fluxes of lipid-rich particles could be significant, ascending particles should be better characterized at different locations and across a greater depth resolution to determine to what extent they contribute to biogeochemical cycles to allow proper integration into models. Currently, the only model that includes these data is the “Upward P-flux model” which investigates uptake and assimilation of phosphorus by *Trichodesmium* (Karl et al., 1992).

Studies on lipid-rich ascending particles have been mainly conducted between the 1980 and the early 2000s. Recently, Flores et al. (2022) investigated the hadal production of labile lipids, yet a link to upward fluxes was not considered. This indicates a pause in deep lipid-rich particle research which should be filled by applying modern methods to allow characterization of the eco-sphere of ascending particles including the particle itself and activity and diversity of the associated microbial communities and their link to the upper layers.

2.3.2. Hydrothermal vents particles

Mechanisms involved in hydrothermal plumes are so strong that ocean water residence time in vent areas is comparable to deep ocean mixing caused by thermohaline circulation, meaning deep hydrothermal vents have the potential to have a global influence on ocean biogeochemistry. Deep hydrothermal-vent particles have been a point of interest since the 1980s (Comita et al., 1984). Some studies indicate hydrothermal plumes, including black and white smokers, are enriched in POC compared to the surrounding water (Comita et al., 1984; Maruyama et al., 1993; Bennett et al., 2011b, 2011a; Hoffman et al., 2018). Hydrothermal plumes can be divided into two distinct parts, both characterized by steep gradients: 1) the rising plume with residence time of minutes to hours and a spatial scale of up to hundreds of vertical meters; and 2) the suspended plume with residence time of days to years and a spatial scale of up to thousands of horizontal kilometers (German and Seyfried, 2014). Both plume zones are driven by different chemical, physical and biological processes (Dick et al., 2013; Reed et al., 2015; Hoffman et al., 2018). In the first zone, vent fluids undergo an abrupt change in temperature upon contact with background seawater, causing rapid precipitation of minerals and metals in the first meter of ascension. The rising fluids exhibit high concentrations of reduced chemicals which provide the energy necessary to maintain an abundant prokaryotic population relying on chemoautotrophy. Prokaryotes in the rising plume are mainly entrained from the background (immediate seawater, vent chimneys, near-vent animal symbionts, subsurface environments, near-bottom waters, and recirculation of aged plume), however, the rising rate is too high compared to growth processes and they have insufficient time to grow (Dick et al., 2013; Reed et al., 2015; Lin et al., 2020). Thus, POC enrichment in the rising part of the plume originates mostly from physicochemical processes such as aggregation of near-vent (organic and inorganic) debris with minerals, chemical alteration of entrained debris, and continued mineral precipitation (Roth and Dymond, 1989; Bennett et al., 2011b, 2011a). The second zone begins when the vent fluids reach a matching density to the surrounding seawater, and divert horizontally away from the source, driven by density and currents (Lin et al., 2020). The suspended plume is characterized by long-distance (thousands km) shuttling and dilution of hydrothermally derived solutes, particles, and prokaryotes, providing sufficient residence time relevant for *in situ* biological activity (Bennett et al., 2011a; Dick et al., 2013; Hoffman et al., 2018). Suspending plumes contain complex microbial communities consisting of chemoautotrophs, heterotrophs and viruses (Maruyama et al., 1993; Yoshida-Takashima et al., 2012; Dick et al., 2013). Major sources of POC into the suspended plume were identified as originating from the rising plume, from DOC adsorption to hydrothermal particles, and from microbial activity (POC production, exudates and lysis) within the suspended plume (Bennett et al., 2011b, 2011a; Dick et al., 2013; Hoffman et al., 2018). Many studies report elevated microbial biomass (2–3 times higher), and activity in plumes, relative to the background, suggesting intensified carbon cycling (Maruyama et al., 1993; Dick et al., 2013; Lin et al., 2020; Cathalot et al., 2021). The production by plume-suspended biomass (between ≈1 to 10 mg C m^{-2} d^{-1}) is comparable to the downward flux from photosynthetically derived POC (Cowen et al., 2001; Dick et al., 2013; German et al., 2015) making hydrothermal plumes a likely a significant source of POC in the deep ocean (Cathalot et al., 2021). Plumes are enriched with raw inorganic hydrothermal compounds fueling chemoautotrophy and with fresh and labile POC as suggested by exceptionally low C/N ratios (Roth and Dymond, 1989; Cowen et al., 2001; Bennett et al., 2011b, 2011a). Hoffman et al. (2018) report POC losses during lateral transport that could not be explained only by parallel sinking. Three possible explanations exist for these losses: 1) heterotrophic prokaryotic degradation into smaller or dissolved compounds (Roth and Dymond, 1989); 2) predation of prokaryotes by microzooplankton, and 3) the presence of more nutritious POC compared to the heavily degraded sinking POC in the surrounding water, attracts zooplankton which contributes to the attenuation of the lateral plume's POC fluxes (Roth and Dymond, 1989; Cowen et al., 2001; Lin et al., 2020).

The "eat & run scenario" from Roth and Dymond (1989) was reinforced by the detection of anomalously high congregating zooplanktons within a 100 m layer above the hydrothermal plumes (hereafter "epi-plume zooplankton") whose carbon demand matches the POC contribution from the plume (Fig. 1). However, bioacoustics data and net tows indicate that zooplankton avoid the plume itself (Cowen et al., 2001). A link between zooplankton and their food located in the toxic plume water could be the ascending lipid rich particles coming from below (see section above and Fig. 1) which act as vehicles for vertical transport of hydrothermal constituents when passing through the plume (Fig. 1) (Cowen et al., 2001; Bertram, 2002). Additionally, as iron and other metals can be adsorbed, stabilized and may rise with deep lipid-rich particles (see section above), POC and trace metals entrained into ascending particles can provide another source to the water column above including those large distances away from the originating vent (Cowen et al., 2001; Toner et al., 2009; German et al., 2015; Hoffman et al., 2018). From the downward view, seasonal pulses of sinking fluxes can scavenge plume particles in the opposite way, and thus Fe and other metals, when passing through the plume (Bertram, 2002). As a result, both sinking phytoplankton-originating particles and rising chemosynthetic/lipid-rich particles may sustain local deep and mid-water secondary production. Such mixed ingestion is supported by composition of fecal pellets containing coccolithophorids and sulfides (Roth and Dymond, 1989). No evidence shows an increase in fecal pellet below the epi-plume zooplankton suggesting that defecation occurs at another site, depending on vertical or lateral migrations, therefore spreading part of the hydrothermal POC and other compounds elsewhere (Roth and Dymond, 1989).

By significantly enhancing prokaryotic activities, providing labile POC in the food-depleted bathypelagic zone, and promoting 3D connectivity (of POC, metals and microorganisms), hydrothermal plumes must be accounted for in global carbon fluxes ocean budgets (Cathalot et al., 2021). Carbon budgets of hydrothermal plumes result from the balance between carbon sinks through plume chemoautotrophic processes and carbon release via heterotrophic remineralization. Suspended particles in the plume are not heterogeneous as seen by studies of how microbial composition, particles composition and morphology change through a dispersing plume (Bennett et al., 2011b; Dick et al., 2013; Hoffman et al., 2018). This research field would benefit from additional multidisciplinary studies (e.g., OMICS, stable- and radio-isotope labelling, isotopic fractionation analyses and *in situ* measurements) to elucidate the dynamic evolution of microbial communities, autotrophic and heterotrophic activities and the carbon cycle following a plume's advection in time and space. Such studies could support or refute the hypothesis that microbial activity in hydrothermal plumes contributes significantly to the conversion of inorganic carbon into refractory POC and thus to carbon sequestration as part of the "microbial carbon pump" (Jiao et al., 2010).

3. Additional types of marine particles

3.1. Bioluminescent particles

Amongst the first reports of bioluminescent particles, Orzech and Nealson (1984) noticed that 20–63 % of aggregates at 60 m were luminous. Similarly, Andrews et al. (1984), revealed light emission in 70 % of the samples collected from sediment traps between 30 and 1900 m depth. Bioluminescence associated with particles can be provided from various sources such as dinoflagellates (Herren et al., 2004) and coelenterazine (a molecule of the enzymatic reaction of bioluminescence) which can be taken up together with particles by filter feeders such as echinoderms and tunicates to produce their own light (Mirza et al., 2021). In addition, around 30 species of marine bacteria, some colonizing particles, are known to emit light (Dunlap, 2014). Bacterial bioluminescence manifests itself as a continuous glow in the presence of oxygen typically at cell concentrations greater than quorum-sensing levels (Nealson et al., 1970; Eberhard, 1972; Nealson, 1977; Hastings and Nealson, 2003) but occurs also in single cells (Tanet et al., 2019). Bioluminescence requires much energy and the benefits of bioluminescence for prokaryotes have not been fully resolved. Most of them are known to have a surface attached (e.g. particles) life style or as symbionts in fish, squids or zooplankton organs or guts (Dunlap and Kita–Tuskamoto, 2006; Zarubin et al., 2012). Luminous bacteria are regularly released into the water column through fecal pellets, light-organs maintenance, or through organic detritus after their host dies. From the water column bioluminescent bacteria are likely attaching to the particle through chemotaxis or already attached being expelled into the fecal pellets (Dunlap and Kita–Tuskamoto, 2006; Tanet et al., 2020).

These particles are not physically different from those mentioned in the categories above and may be sinking, rising, or suspended. Nevertheless, in the dark ocean, below the photic zone, bioluminescence likely makes them more attractive to grazers than other particles altering the particles fate (Tanet et al., 2020; Zarubin et al., 2012). Some bioluminescent bacteria can resist exposure to increasing pressure whilst particles are sinking (Brown et al., 1942) and some produce more light and have higher growth rates under pressure (Martini et al., 2013). This allows them to develop on sinking particles and to reach the seafloor where they can be resuspended by oceanographic physical conditions (such as deep sea convection) and potentially consumed by epi-benthic organisms (Tamburini et al., 2013b; Tanet et al., 2020). Large bioluminescent particles may be ingested, respired, and packed as faster sinking fecal pellets. Despite lacking any ability for visual detection or selection, filter feeders can eventually aggregate luminous organic matter in their transparent bodies and fecal pellets. Concentrating bioluminescent bacteria in packed fecal pellets or in transparent bodies promotes predation by upper trophic levels (Pinti et al., 2022). Alternatively, such particles may be shredded, resulting in reduced sinking velocities or in their contribution to smaller particle fractions or suspended particles which may lead to greater and earlier remineralization. Overall, bioluminescent organic matter is likely remineralized faster and higher in the water column than non-bioluminescent organic matter leading to the “bioluminescence shunt hypothesis” (Tanet et al., 2020). The link between bioluminescence and organic matter particles was for a long time ignored but in view of its potential importance, a better quantification of its contribution to the BCP is important.

3.2. Marine gels (TEP and CSP particles)

Marine gels, first described nearly 4 decades ago (Emery et al., 1984) consist mainly of two types of natural hydrogel particles in the oceanic water column: Transparent Exopolymer Polysaccharide (TEP) and Coomassie stainable particles (CSP), (Verdugo, 2012). These two particle types differ in their major constituents where TEP is dominated by Alcian-Blue stainable polysaccharides, and CSP by Coomassie brilliant blue stainable proteins (Alldredge et al., 1993; Long and Azam, 1996; Cisternas-Novoa et al., 2015). TEP and CSP originate from different phases of phytoplankton blooms (Taylor et al., 2014; Cisternas-Novoa et al., 2015; Zamanillo et al., 2019) and are also produced by prokaryotes (Stoderegger and Herndl, 1999; Yamada et al., 2017). Like other organic matter particles in aquatic environments, both TEP and CSP are heavily colonized by prokaryotes (Passow, 2002; Busch et al., 2017; Zäncker et al., 2019; Cai, 2020) with individual particles containing different prokaryotic communities from each other and from the surrounding water (Zäncker et al., 2019). TEP acts as a biological glue that promotes the aggregation of suspended particles with each other, and is essential to the formation of diatom aggregates and their subsequent sinking (Passow et al., 2001; Verdugo et al., 2004).

TEP particles are normally formed near the surface, trapping some water with specific salinity and density inside the impermeable gel. Accordingly due to their low density, TEP particles may also accumulate in the surface microlayer, i.e. the boundary interface between the atmosphere and ocean (Mari et al., 2017; Sun et al., 2018). While sinking, the density of the gel does not change and as these particles sink into the halocline, they become more buoyant relative to the surrounding water and eventually stop their descent (Alldredge and Crocker, 1995). Passow et al. (2001) reported that only a small fraction of TEP particles reached 500 m, suggesting possible upper remineralization by prokaryotes (Nagata et al., 2021; Guo et al., 2022). However, TEP has been documented at depths exceeding 3000 m (Busch et al., 2017), and was positively correlated with prokaryotic abundance and prokaryotic heterotrophic production even at great depths (Yamada et al., 2017). According to models, only 0.5 to 2 % of the particle volume occupied by gel are necessary to obtain neutral buoyancy around density discontinuities such as a halocline (Alldredge and Crocker, 1995). It takes several days for salinity balance to be achieved through diffusion through the gel. Even if a particle becomes dense enough to sink again, the equilibration period is likely to be long enough to allow trapped gas bubbles to form following microbial activities making them rise again (Riebesell, 1992; Alldredge and Crocker, 1995; Rinaldi et al., 1995). This leads to two accumulating zones, the halocline and the surface micro-layer. While ascending, TEP can shuttle biological and chemical elements as well as micro-organisms (Azetsu-Scott and Passow, 2004). The flux of positively buoyant TEP increases the collision frequency of TEP with sinking particles, affecting the carbon export efficiency (Azetsu-Scott and Passow, 2004). As a result of these collisions, TEP may also clog the pore space within the particles, altering the fractal dimension and decreasing the drag of water through sinking particles (De La Rocha and Passow, 2007). Particle density, a factor of particle porosity, OM and porewater composition, volume ratio TEP/particle, and gas trapped bubbles, is a main determinant of the fate of TEP particles. However, density values of TEP particles are provided only in one study (Azetsu-Scott and Passow (2004). Thus, while TEP can play a major role in the biological carbon pump (Kiørboe et al., 1998; Santschi et al., 2003; Engel, 2004; De La Rocha and Passow, 2007; Nagata et al., 2021, Guo et al., 2022) it can also enhance CO_2 release back to the atmosphere and influence the air–water gas exchange (Calleja et al., 2009).

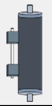
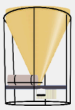
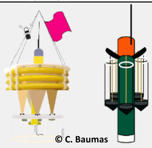
The contribution of CSP to the biological carbon pump is still unclear. Like TEP, CSP has been detected in deep water samples, exceeding 4000 m (Cisternas-Novoa et al., 2015). CSP are considered to be less sticky than TEP (Thornton, 2018) and are known to accumulate more than TEP in the surface micro layer (Thornton et al., 2016; Busch et al., 2017). Therefore, it may indicate that despite their abundance in the water, CSP may contribute less to carbon sequestration than TEP does. In both cases, TEP and CSP, gel particles exhibit complex dynamics involving microbial communities which experience variability in hydrostatic pressure, temperature, and OM composition resulting from sinking, suspension or ascent of gel particles. The difficulty of sampling gel particles at each of these phases and knowledge gap in the mechanisms of gel degradation by micro-organisms (e.g. linked to CAZymes enzymes (Arnosti et al., 2021)) hinders our ability to understand the role of gel particles in the BCP. Future research efforts should endeavor to include both laboratory and *in situ* observations to determine the contribution of gel particles and associated microbial action to the BCP.

3.3. Plastic particles

Plastic debris was first reported at the surface of the ocean in the early 1970s. Since then, the amount of plastic entering the ocean has increased to an estimated of roughly 10 million tons of plastic ending up in the ocean each year (Jambeck et al., 2015). Once introduced into the ocean, only 1 % of the plastic accumulates at the surface as floating debris. This indicates that the remaining 99 % is retained elsewhere, i.e.,

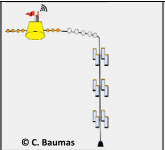
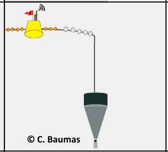
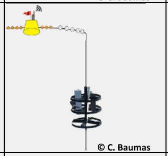
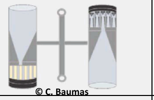
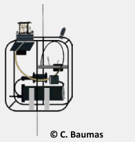
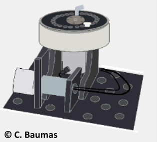
Table 2

Literature review of 17 marine particles sampling instruments (Knauer et al., 1979; Jannasch et al., 1980; Bishop et al., 1985, p. 1985; Honjo and Doherty, 1988; Smith et al., 1989; Heussner et al., 1990; Alldredge, 1991; Lampitt et al., 1993, 2008; Peterson et al., 1993, 2005, 2009; Valdes and Price, 2000; Cowen et al., 2001; Scholten et al., 2001; Simon et al., 2002; Buesseler et al., 2007; Kiørboe, 2007; Breier et al., 2009, 2010; Lee et al., 2009; Riley et al., 2012; Planquette and Sherrell, 2012; McDonnell et al., 2015a; Boyd et al., 2015; Mestre et al., 2018; Garel et al., 2019; Bressac et al., 2019; Estapa et al., 2020; Puigcorbé et al., 2020; Baumas et al., 2021).

Sampling	Picture	Method Description	Fraction catched	Depth range	Time	Operational considerations	Approach	Advantages	Disadvantages	Manufacturers	References
Scuba diving	 © C. Baumas	Hand collection by divers of undisturbed individual particles in syringes	Individual macroscopic particles	0 to ≈60m	≈ 1h	Constraints related to depth and duration of human dives	Snapshot	Most delicate and effective way to recover intact particles in minimal amount of water	Feasible only at shallow coastal depths & depends on the visibility of the particles by divers, tedious task	-	(Alldredge 1991; Simon et al. 2002)
Water sampler (e.g. Niskin or GoFlo)	 © C. Baumas	Water samples followed by differential filtrations (e.g. filters with pore sizes of 0.2, 0.8, 3, 5, 10 µm)	Suspended particles retained on filters	Surface to bottom	Instant	Requires a cable or a rosette with messenger	Snapshot	Easily accessible as it is the most common oceanographic water sampler	Inadequate to the study of sinking particles. Filtration done on board (not in situ) thus can affect microbial processes. Filtered volume too low to represent the particles (often not abundant)	General Oceanics	(Planquette and Sherrell 2012; Mestre et al. 2018; Garel et al. 2019; Puigcorbé et al. 2020; Baumas et al. 2021)
Marine Snow Catcher	 © C. Baumas	After 2 h of decantation on deck particles are seggregated: Suspended particles (in the top 93L), Slow sinking (in the 7L base) and Fast sinking (in the bottom plate)	Suspended, Slow sinking and Fast sinking, separately	Surface to bottom	Instant	Requires a cable with a messenger. Must stay upright for ca. 2 hours on deck	Snapshot	Avoids turbulence so harvested particles are not altered. Individual particles don't collide with eachother	When particle concentration is too low, 100 L of water are not sufficient to sample enough. If we can see and harvest individual Fast sinking with the naked eye, it is not the case of the suspended & slow sinking which are drowned in surrounding water	OSIL	(Lampitt et al. 1993; Riley et al. 2012)
Sea Core Sampler	 © C. Baumas	After sampling of 50 L of undistrurbed water column, the Sea Core is enclosed by a casing fitted with light sources and camera	All types	Tested up to 1,700 m	Instant	Requires a cable with a messenger	Snapshot	Allow to observe and record specific process around a partilce without disturbing it	When particle concentration is low events that occur in the field of the camera are rare. The light emitted for cameras may differ from natural light and may disturb zooplancton behaviour.	NA	(Kiørboe 2007)
Conical time-series sediment trap (e.g. McLane, PPS5 or Kiel trap)	 © C. Baumas	Sediment Traps collect vertically settling particles into individual sample bottles set on caroussel which are sealed when not in collection mode	Sinking particles	McLane : 10,000 m, PPS5 & Kiel trap : up to 6,000 m	Annual or few months	Requires a fixed long-term mooring and a cruise to recover it after planned sampling time is over	Eulerian	Provides a long time series, sampling of discrete samples for up to 24 months	Sample fixation prevents mesurements of micro-organisms activities. Shear or lateral advection create biases in sinking flux measurements	McLane , Technicap , KUM-Kiel	(Honjo and Doherty 1988; Scholten et al. 2001; McDonnell et al. 2015)
Cylindroconical time-series sediment trap (e.g. PPS3)	 © C. Baumas	Sediment Traps collect vertically settling particles into individual sample bottles which are sealed when not in collection mode	Sinking particles	Up to 6,000m	Annual or few months	Requires a fixed long term mooring and a cruise to recover it after sampling time	Eulerian or Lagrangian	Provides a long time series, sampling of discrete samples for up to 24 months. Can be use in moored or surface drifting configurations	Sample fixation prevents mesurements of micro-organisms activities. Shear or lateral advection create biases in sinking flux measurements	Technicap	(Heussner et al. 1990; McDonnell et al. 2015)
Neutrally buoyant sediment trap (e.g. PELAGRA or NBST)	 © C. Baumas	Particles are collected while sinking in cones (PELAGRA) or tubes (NBST) which follow current at targeted density. When collection mission ends, it releases weights and floats to the surface	Sinking particles	PELAGRA up to 1,000 m, NBST : up to 500 m	Few days	A CTD and a short deployment is required to ajust ballast. Recovered location is hard to predict , requiring extra ship time to be held as reserve	Lagrangian	Free from surface currents/wind stress minimizing hydrodynamic interference & is almost uncontaminated by swimmers	Sample fixation prevents mesurements of micro-organisms activities. Recovery may be straining as the devices can drift everywhere, in different, unpredictable, directions after days of deployment	PELAGRA : Custom made NOC-Southampton, NBST : WHOI	(Valdes and Price 2000; Buesseler et al. 2007; Lampitt et al. 2008; McDonnell et al. 2015; Estapa et al. 2020)

(*continued on next page*)

Table 2 (*continued*)

Surface tethered trap, PITS	 © C. Baumas	Particles are collected while sinking in tubes which follow currents during a short term deployement	Sinking particles	Up to 1,000 m	Few days	Deployment and recovery can be achieved in ≈1h. During deployment period other core operations can be conducted while following the sediment trap	Lagrangian	Collection of sinking particles along a depth profile in different tube settings (poisoned , unpoisoned, polyacrylamide gels)	Sensitive to surface currents and wind stress. The particles tend to almagate to form a homogeneous bulk with more particle-to-particle contact than in nature	Kc-Denmark	(Knauer et al. 1979; Jannasch et al. 1980; McDonnell et al. 2015; Le Moigne et al. 2017)
Free floating net trap	 © C. Baumas	Particles are collected while sinking in a trap designed as a closing plankton net (50 µm mesh size). Design can be mixed with IRS system (see below)	Sinking partidles	**?**	Few days	Sometimes requires to be towed by the boat if it does not drift properly. Other core operations can be conducted while following the sediment trap	Lagrangian	Enables the collection of large quantities of fresh sinking particles in a short period of time due to the large diameter. Samples can be used in microbial degradations radionuclide-uptake experiments	The particles tend to almagate to form a homogeneous bulk with more particles-to-particles contact than in nature. The large size, weight and flotation package of the NetTrap created some concern that the entire instrument might not drift effectively with the current while causing disturbing currents across the opening of the net.	Custom made University of Washington, WA, USA	(Peterson et al. 2005, 2009)
Indented Rotating Sphere trap (WM-IRSC, IRS, IRSC)	 © C. Baumas	Sinking particles are intercepted either in a cylinder or in a funnel and settle on a sphere that will rotate and collect them in a simple collector or in collectors of a caroussel depending on the IRS model	Sinking particles	Up to 6,000 m	Ca. one year	Requires one day for collection	Eulerian or Lagrangian	Sample cups are isolated from ambient water by the IRS valve, minimizing degradation, and contact with living organisms, Allows separation of particles at *in situ* settling velocity	Possible reduction in measured flux due to particle degradation on the sphere prior to rotation. Rotation of the sphere might cause turbulence that may alter particle properties	Prime Focus Inc	(Peterson et al. 1993, 2005, 2009; Lee et al. 2009)
RESPIRE	 © C. Baumas	Sinking particles are intercepted in a cylinder on top of a sphere which will rotate to collecte particles underneath in an incubation chamber for O_2 consumption measurments	Sinking particles	Up to 300 m	Few days	Some parameters can to be set only via a special software prior each deployment. Other core operations can be conducted while following the sediment trap	Lagrangian	Allows measurments of *in situ* O_2 consumption. The chamber is isolated from ambient water and swimmers	Cannot be used to differentiate patterns in time on timescales shorter than the interception period. Transmorfation may occur during incubation (e.g. aggregation, microbial developpment and community shift, exchange of microbial consortia between individual particles), possibly changing the O_2 consumption	Custom made IMAS-UTAS Hobart	(Boyd et al. 2015; Bressac et al. 2019)
Upright sediment trap	 © C. Baumas	Coupled collection of sinking and ascending particles using inverted sediment trap with carousel cups for multiple time points	Sinking and Ascending separatly	Tested up to 5,200 m	Few months to a year	Requires a fixed long term mooring and a cruise to recover it after sampling time	Eulerian or Lagrangian	Allows to determine both, upright and downward fluxes at the same time and location	The ascending particles must wait until they lose their buoyancy before sinking into the cup where they will be fixed by poison. Particles may be subject to biological degradation during this time.	**?**	(Smith et al. 1989; Cowen et al. 2001)
***In situ* pumps (e.g. MUL- VFS, McLane pumps, SAPS, submersible pump Antarctic CRC)**	 © C. Baumas	*In situ* water pump that sucks large amounts of water through filters of different pore sizes, leaving particles on the filters for resuspension or direct analysis	All types mixed	Up to ca. 6,000 m	Few hours	Requires a long boat-imobilisation time	Eulerien	Direct filtration under *in situ* conditions. Can be used when sediment traps are impracticable. Due to the high filtration capacity, this method is not limited by a low concentration of particles	The samples are in bulk on a filter without the possibility of recovering intact particles , no possibility to segregate Non-, Slow-, and Fast-sinking particles. The flow can destroy particles. Different designs and filters types generate different results	McLane , Challenger Oceanic (no longer exists)	(Bishop et al. 1985, 2012; Planquette and Sherrell 2012; McDonnell et al. 2015)
Suspended Particulate Rosette multi-sampler (SUPR)	 © C. Baumas	*In situ* filtration of 24 discrete large volume samples (30-100 L) by multistage filtering to collect separate particles size classes simultaneously. It is programmed to stop before a filter rupture	Suspended or rising particles from deep rising or non-boyant hydrothermal plumes	At least up to 5,500m	Few minutes to a few months	Requires an ROV dive or a fixed long term mooring coupled with a cruise to recover it after sampling time	Snapshot, Eulerian or Lagrangian	Can be mounted on an ROV to follow a rising plume, on a rosette for discrete sampling of suspended plumes or on a fixed mooring for time series. It is compatible with optical in situ sensors enabling particles characterization before alteration during deployement time. Designed to facilitate sample processing after recovery	Take several minutes to filter one sample which may be not compatible with some shorter time scale process	WHOI	(Breier et al. 2009; Breier et al. 2010)

at the sediment, in the water column, or in the food web (Pabortsava and Lampitt, 2020). Plastic in the oceans is dominated by microplastic, defined as plastic particles smaller than 5 mm in size (Zettler et al., 2013; Cozar et al., 2014). Choy et al. (2020) recently demonstrated that key species of particle-feeding zooplankton greatly shape the distribution of microplastic by shuttling it after ingestion within the water column. As a result, microplastic particles are widespread through the oceans with a reported maximum contained in the mesopelagic zone (Choy et al., 2020). In contrast, Wieczorek et al. (2019) found that though microplastic decrease the sinking rate of OM particles by 1.5 folds, at present they are rare within pellets suggesting that ingestion of microplastic by zooplankton have actually a minimal impact on the biological carbon pump (Wieczorek et al., 2019). Presently, Galgani et al. (2022) estimated that microplastic can represent 3.8 % of the sinking POC flux in the mesopelagic zone. However, if the concentration of plastic waste continues to increase in the ocean, up to 46 % of fecal pellets could contain microplastic in the future which could dramatically lower the biological carbon pump efficiency (Wieczorek et al., 2019; Shen et al., 2020) and increase microplastic export to the deep ocean through the "biological plastic pump" introduce by (Galgani et al., 2022).

Similarly to natural particles, microplastic are highly colonized by microbial communities: termed the "Plastisphere", composed of prokaryotes, single-cell algae and fungi (Wright et al., 2020). Due to their hydrophobic surface, microplastics act as artificial "microbial reef" stimulating biofilm formation (Zettler et al., 2013). It is now evident that microplastic do not select for specific taxa compared to other marine particles classes (Oberbeckmann and Labrenz, 2020; Wright et al., 2020). Evidence shows microbial activity can be stimulated by plastic leachates and enhance microplastic degradation even in the deep sea (Zettler et al., 2013; Romera-Castillo et al., 2018; Fauvelle et al., 2021; Vaksmaa et al., 2022). However, plastic leachates are consumed in few days after the first contact between the plastic and the sea water and only micro-organisms located at the interface between biofilm and micro-plastic can interact with them, making plastic degraders a minority outcompeted within the plastisphere (Romera-Castillo et al., 2018; Wright et al., 2020). Finally, environmental variables are suggested to play a greater role in influencing plastisphere diversity than plastic composition (Wright et al., 2020; Vaksmaa et al., 2022). Plastisphere primary colonizers are dominated by photosynthetic autotrophs such as heavy diatom cells. This can increase the density of the particle and force the particle to sink to the mesopelagic zone where photosynthesis is unable to take place. Without photosynthesis to provide a carbon source, the biofilm will likely self-consume and combined with the mortality of taxa which are unable to withstand high pressure and low temperature changes during the sinking process, these particles may regain buoyancy until they are recolonized by primary producers in the euphotic zone starting a new cycle. These cycles create oscillations of the microplastics in the water column, concentrating microplastics between 200 and 600 m (Kooi et al., 2017).

Though, the effect of microplastic on the biological carbon pump seems minimal at present (Shen et al., 2020), under future scenarios, higher concentration may negatively affect the carbon sequestration by several mechanisms: toxic effect on photosynthesis and zooplankton; by catching natural OM and preventing it from sinking; and by decreasing the density and hence the sinking speed of sinking particles (Wieczorek et al., 2019; Shen et al., 2020; Roberts et al., 2023).

4. Methods to study particles

4.1. *In situ sampling devices*

Studying particles in their natural environment has the potential of providing the least biased results. Such an analysis would encompass the interaction of particles with their natural chemical, physical, and biological surroundings, however, for obvious reasons, one cannot conduct experiments throughout a water column of several hundreds to thousands of meters. Therefore, we must rely on *in situ* observations coupled with sampling and preservation for analyses. These methods range from sampling and inspection of particles by depth limited SCUBA divers, through moored or drifting sediment traps, to automated particle samplers that can be deployed at various depths down to the oceanic hadal zone (Table 2). During cruises, researchers continuously bring water to the surface, as a source for water and of particulate organic matter for different studies. However it has been identified that the routine use of Niskin bottles captures almost exclusively suspended particles (Planquette and Sherrell, 2012; Puigcorbé et al., 2020; Baumas et al., 2021). Therefore, different water samplers have been developed to allow the separation and collection of sinking, suspended, and ascending particles from one water mass. These include, among others, Marine Snow Catcher, Sea Core sampler, different sediment trap designs (downward and upward), *in situ* pumps, and the Suspended Particulate Rosette Multi-sampler. A comparative summary of these methods is featured in Table 2. These methods have been extensively reviewed and discussed in dedicated papers (e.g. Bloesch and Burns, 1980; McDonnell et al., 2015; Baker et al., 2020) and will not be discussed here in depth.

4.2. *Optical devices*

The use of optical devices have been thoroughly reviewed in Giering et al. (2020). However, given their innovation and growing significance we will address them here in short. Optical devices are divided into 3 classes: photodetectors, holographic systems, and photographic systems. Photodetectors measure a bulk optical property empirically correlated with particle concentration in the ocean (e.g. Bishop, 1986; Reynolds et al., 2016), and with POC where POC dominate particles composition (e.g. Gardner et al., 2001; Cetinić et al., 2012). Examples of photodetectors are the Optical Backscatter Sensor (OBS) (Briggs et al., 2011), the transmissometer or beam attenuation (Briggs et al., 2013), the fluorimeter (Briggs et al., 2011), The Laser Optical Plankton Counter (LOPC) (Herman et al., 2004) and the Laser *In situ* Scattering Transmissometer (LISST) (Gartner et al., 2001). Holographic systems illuminate a sample volume with a laser. As the beam hits a particle, an interference pattern is generated and is recorded by a camera. The result is used to reconstruct a holographic image of the particle. These devices allow the recognition of particle size and shape. Key examples include the HoloSea (4Deep, Canada) and the LISST-Holo (Sequoia Scientific, USA). Finally, photographic systems have become the preferred method for the observation of *in situ* particles, most likely because the resulting images are similar to those obtained from traditional microscopic analyses (Giering et al., 2020). There are numerous commercially available or custom-made devices available from various oceanic research groups such as the Video Plankton Recorder (VPR) (Davis et al., 2005) or the Continuous Particle Imaging and Classification system (CPICS) (Giering et al., 2020) for colored images, and the Underwater Vision Profiler (UVP) (Picheral et al., 2010, 2022), the *In Situ* Ichthyoplankton Imaging System (ISIIS) (Giering et al., 2020), the Shadowed Image Particle Profiling and Evaluation (SIPPER) (Samson et al., 2004), the profiling underwater camera system KIELVISION (Taucher et al., 2018), ParCa system (Ratmeyer and Wefer, 1996), or the Lightframe On-Sight Key-species Investigation (LOKI) (Schmid et al., 2016) for monochrome images. The advantages mainly result in their deployment from ships or on autonomous platforms which can deliver large datasets covering the spatial and temporal distribution of particles. For example, data from Bio-Argo floats have already shown that multiyear, high-resolution, vertically resolved observations can revolutionize our understanding of particles distribution and carbon cycle (Dall'Olmo and Mork, 2014). In addition, some robots equipped with photographic devices or cameras are currently under development. This is the case of the MINION Robot[2] from Woods Hole Oceanographic Institution which allows particles to settle on a clear glass panel from where a camera will record particle type and accumulation rates while drifting in the water column. In the near future, BATHYBOT,[3] a benthic crawler from the Mediterranean Institute of Oceanography deployed at 2400 m deep in the Mediterranean Sea, will start a long-term study recording with a dedicated camera deep-organism activities (specifically including bioluminescence ones) and, with a UVP, particles accumulation rates at the sea floor (i.e., flux of sinking POC at the end of its way down). *In situ* optical devices provide greater identification capabilities across greater vertical and horizontal resolutions than pump or sediment traps by not inducing particle fragmentation or transformation of particle shapes. Nevertheless, despite these advances further research is still required to translate imaged objects into carbon content and sinking rates (Fender et al., 2019; Giering et al., 2020).

4.3. *Laboratory experimental set ups*

The study of particles in the laboratory (lab-based) encompasses the many aspects of the natural environment, in an attempt to generate adequate data for modelling efforts. Lab-based setups overcome technological limitations in following particles through the water column by allowing observation from formation to sequestration. These studies make use of various particles types which can be freshly sampled (e.g. (Sempéré et al., 2000; Panagiotopoulos et al., 2002; Hwang et al., 2006; Panagiotopoulos and Sempéré 2007; Tamburini et al., 2009; Le Moigne et al., 2017), fecal pellets (e.g. Tamburini et al., 2009; Maas et al., 2020), phytoplankton cultures (some of which with added minerals) often aggregated with roller tanks (e.g. (Bidle and Azam, 1999, 2001; Passow et al., 2003; Passow and De La Rocha, 2006; Tamburini et al., 2006, 2021; Le Moigne et al., 2013; Riou et al., 2018; Bizic-Ionescu et al., 2018; Liu et al., 2022), or artificial particles with homogenous composition and structures made for example from agar (e.g. Grossart et al., 2003) or chitin (e.g. (Datta et al., 2016; Szabo et al., 2022). The latter provide a uniform and reproducible experimental system but fail to represent the structural complexity of natural particles (Maerz et al., 2020). Many studies incubate particles inside glass or polycarbonate bottles (mainly between 100 mL and 2000 mL) under varying environmental conditions for purposes such as: degradation of specific compounds (e.g. Bidle and Azam, 1999; Panagiotopoulos et al., 2002; Passow et al., 2003; Panagiotopoulos and Sempéré 2007), exchange between POC and DOC pools (e.g. Hwang et al., 2006), measurements of prokaryotic bacterial productivity and respiration (e.g. Bidle and Azam, 1999; Sempéré et al., 2000; Panagiotopoulos et al., 2002; Richardson et al., 2013), quantification of enzymatic activities (e.g. Smith et al.,

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[2] https://www.youtube.com/watch?v=TaNZH1sXGEo.

[3] mio.osupytheas.fr/en/seas-and-oceans-global-change/emso-wl-underwater-observatory-follow-antares-telescope.

1992; Bidle and Azam, 1999, 2001), microbial diversity (e.g. Bidle and Azam, 2001; Grossart et al., 2003; Tamburini et al., 2006, 2021; Datta et al., 2016; Riou et al., 2018; Bizic-Ionescu et al., 2018; Maas et al., 2020; Liu et al., 2022), or to study microbial interactions (e.g. Grossart et al., 2003). All those experiments in little volume bottles provide insightful information about particles dynamics and mechanistic over time and under different conditions. However, they are biased by artificial settling and aggregation of particles at the bottom of bottles which can cause dramatic biases. This led to a need to maintain particles in suspension and thus simulating their free sink through the water column either by hand (e.g. Sempéré et al., 2000; Hwang et al., 2006), mixing (Roberts et al., 2020), strapping bottles on a rotating axes (e.g. Richardson et al., 2013), using a plankton wheel (Passow et al., 2003; Le Moigne et al., 2017; Bach et al., 2019), applying semi revolution rotation to bottles (Tamburini et al., 2006, 2009, 2021; Riou et al., 2018) or applying a constant flow of ambient water through a dedicated roller tank (Ionescu et al., 2015). Additionally, in order to study disaggregation processes, a specific roller tanks which combine rotating and oscillating action can be used to generate diatom aggregates subsequently exposed to calibrated laminar shear (Song and Rau, 2022).

As the majority of the water column is under high pressure, some specific experimental setups are used to expose particles to pressure (Tamburini et al., 2006, 2009, 2021; de Jesus Mendes et al., 2007; Grossart and Gust, 2009; Mendes and Thomsen, 2012; Dong et al., 2018; Stief et al., 2021; Liu et al., 2022). To mimic as closely as possible the *in situ* pressure and temperature variations experienced by sinking particles, Tamburini et al. (2009) designed the “PASS” system. The PASS system allows the tracking of geochemical conditions and microbial activity, and diversity during a simulated sinking of particles through continuous increase of pressure and temperature variations, both adapted to the sinking speed of particles. However, polycarbonate or glass bottles, hyperbaric bottles or roller tanks, are all prone to biases occurring in long incubations (Lee and Fuhrman, 1991; Baltar et al., 2012; Herlemann et al., 2019) termed “the bottle effect”. These biases result in rapid community shifts, drive the experimental system towards different metabolisms and accelerate processes within the system, as compared to open experimental systems which have recently become available (Ionescu et al., 2015; Bizic-Ionescu et al., 2018). The flow-through rolling tank system (Ionescu et al., 2015) allows the incubation of particles while ambient water is continuously exchanged, ideally connected to an environmental source of water. This system provides a major step forward in bringing the natural environment into the lab. However, when simulating oceanic environments, it cannot account for the increasing pressure and the effect this has on microbial community composition and particle degradation. Additionally, this system cannot be easily supplied with deep water beyond what can be directly pumped from the shore or research vessel or can be brought up daily to maintain the usage of fresh water.

In an attempt to limit the bottle effect and the biases related to the study of large-scale processes in tanks of a few liters, some indoor experimental setups such as microcosms (ca. 150 L) (e.g. Christaki and Van Wambeke, 1995), mesocosms (ca. 1500 L) (e.g. KOSMOS system by Riebesell et al. (2013)) or macrocosms (larger than 10^5 L) may provide alternatives for short- to long term, experiments, respectively. Meso- and macro-cosms are reduced models of an ecosystem which allow for the control- and combination of environmental gradients to disentangle and understand underlying mechanisms controlling particle dynamics under more realistic environmental conditions. For instance, Alldredge et al. (1995) used mesocosms to investigate formation of diatoms particles following a bloom of several species and found that non phytoplankton particles can have an important role in the aggregation process. Later, Piontek et al. (2009) studied, using mesocosms, the effect of a temperature increase on aggregation and on microbial degradation of diatom particles and conclude that microbial degradation is stimulated under higher temperature and implying the vertical export of carbon through diatom particles may change in the future. However, even such large experimental systems are limited in size. The accuracy of various biological observations made in the field is greatly influenced by the constantly shifting distribution of physical, chemical, and biological properties of a water column. The uncertain effects of the boundary conditions associated with small systems also require caution when interpreting laboratory observations of biological events. Macrocosms require large infrastructure and manpower and are therefore not very widespread. To our knowledges, 3 major ones were built between 1939 and 1977: the “large plankton culture” 150 m^3 by 12 m height at Göteborg in Sweden (Pettersson et al., 1939), the “deep tank” 282 m^3 by 10 m in California (Strickland et al., 1969; Mullin and Evans, 1974), and the “Aquatron tower tank” 502 m^3 by 10 m in Canada (Conover and Paranjape, 1977). The outlined macrocosms are still in current use to study marine particles or POC degradations (e.g. Jiao et al., 2018; Zhang et al., 2021; He et al., 2022). Such large-scale controlled experiments can bridge the gap between small-scale experiments and *in situ* measurements (Conover and Paranjape, 1977; Robinson et al., 2018).

The major link between all the studies mentioned in this section is the carbon cycle and specifically carbon sequestration on a global scale. In this sense, increasing the scales of the controlled experiments seems obvious. However, we are still not able to constrain the carbon balance correctly towards a closed budget (Reinthaler et al., 2006; Steinberg et al., 2008; Burd et al., 2010; Collins et al., 2015; Boyd et al., 2019). Particle attached microorganisms are important players, therefore, zooming into their the micro-scale, i.e., individual particle could give key insights on the overall carbon cycling. Very few experimental setups devoted specifically to single particles investigation have been published. The flow rate chamber from Ploug and Jørgensen (1999) is dedicated to measure O_2 respiration gradient from the center to the periphery of one single particles and was used in lab and during cruises (Ploug and Grossart, 1999; Grossart and Ploug, 2001; Belcher et al., 2016). This setup can be further adjusted to any solute measurable by microelectrodes. The setup from Stief et al. (2021) allows to study the effect of pressure on single aggregates. See section “Shifting paradigm” for further discussions about individual particles studies. Though they will never substitute field work, controlled laboratory experiments are essential for developing mechanistic interpretations of environmental observations and should not be omitted.

4.4. Mathematical models

Mathematical models provide a means of capturing our current knowledge of a given system in an unambiguous mathematical description. Despite models not providing a complete picture, model results can be used to identify missing or misunderstood key processes, and for hypothesis testing by extrapolating our current understanding across variable environmental dynamics or potential scenarios. Key questions identified through the study of marine particles resulted in a wide range of mathematical models aiming to decipher the role of particles in carbon sequestration. Some models focus on global scale processes to understand the global ecosystem dynamic and include several trophic levels (e.g. (Anderson and Ducklow, 2001; Anderson and Turley, 2003; Anderson and Tang, 2010; Anderson et al., 2015; Aumont et al., 2018; Countryman et al., 2022; Serra-Pompei et al., 2022; Stukel et al., 2022; Galí et al., 2022; Wilson et al., 2022; Rohr et al., 2023), whilst others focus or smaller scale processes including particle colonization or microbial interactions or particles dynamics (e.g. (Kiørboe et al., 1990; Kiørboe and Jackson, 2001; Armstrong et al., 2002; Kiørboe, 2003; Kiorboe et al., 2003; Bearon, 2007; Bianchi et al., 2018; Styles et al., 2021; Nguyen et al., 2022). Using Tara Ocean’s data Guidi et al. (2016) reveal a correlation between the carbon flux at 150 m and the occurrence of specific taxa. Yet this data does not go beyond the photic zone and has not yet been incorporated into quantitative carbon export models. To our knowledge, efforts have been made to couple global scale models to small scale studies, such as at the level of single particle, although results are yet unpublished.

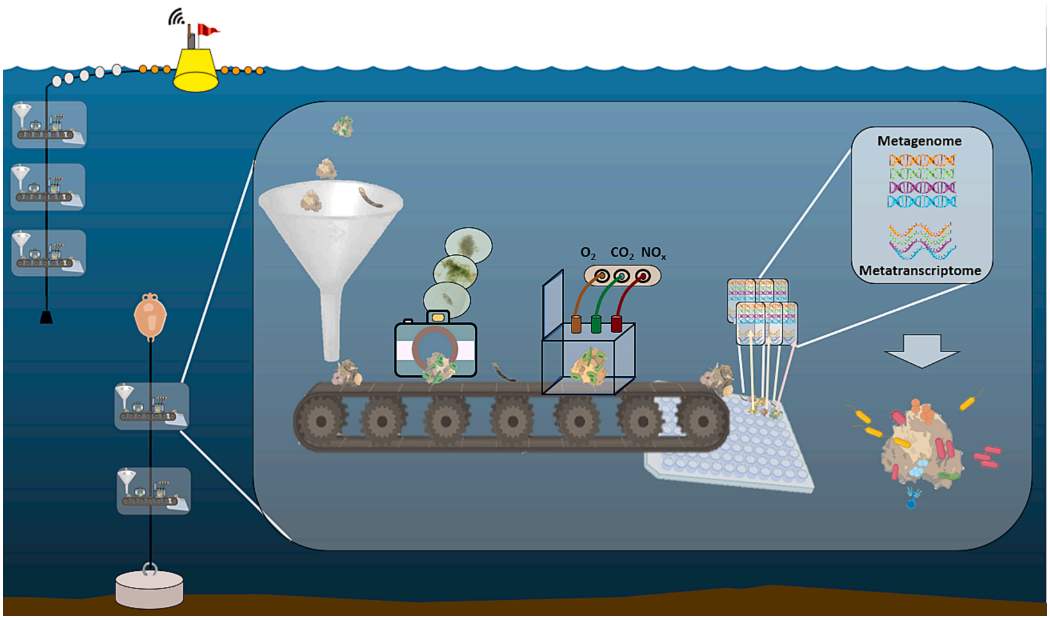

Fig. 2. Conceptual moored or drifting single-particle-focused analysis system. Sinking particles are imaged individually. The images are linked to optode-based activity measurements of each particle. Eventually, each particle is preserved in a multi-well plate for later metagenomic, metatranscriptomic, or metabarcoding analysis. Such a system could potentially contain magazines of such plates, resulting in the preservation of thousands of well characterized individual particles.

5. Shifting paradigm

The study of organic matter particles has come a long way since its early days, conceptually and technologically. We are now able to sample and image more particles and obtain a highly detailed picture of the composition, metabolic potential, and measured metabolism of microbial communities colonizing particles, using metagenomics, metatranscriptomics, metaproteomics, and meta-metabolomics. In a seminal paper, Fuhrman (1992), concluded that it is not sufficient to look at the bulk, but one should rather look into the individual components of the microbial food web in order to understand of the deterministic processes that shape it. Yet, 30 years later, while we possess the technology to isolate and sequence individual viruses, particulate organic matter is still mostly studied as lumps of matter found between two filter fractions. The simultaneous analysis of thousands of individual particles of different size, source, age and history, has been suggested to provide misleading information (Bizic-Ionescu et al., 2018; Armitage and Jones, 2019; Baumas et al., 2024). Furthermore, such data cannot provide information on the synergistic or antagonistic interactions between the microorganisms colonizing a particle, inform on the specificity of a microbial community to certain particle types, or changes in community composition and activity in response to environmental changes. For reasons other than quantification of particle fluxes, there is a need to enhance the focus on individual particles, both during *in situ* sampling as well as in experimental systems. The tools required to achieve this are already in existence. For decades, sediment traps or rolling tank experiments, whether flow-through or traditional, allowed access to individual particles. Additionally, the ability to sequence samples deeply at a low cost, coupled with the ability to amplify low amounts of DNA, can in- part remove barriers to obtaining single-particle metagenomics or metatranscriptomics data for a large enough number of particles to provide meaningful results. Nevertheless, to date there are only a handful of studies focusing on individual particles. Amongst identified studies, few have measured activity of individual particles ((Ploug and Jørgensen, 1999; Ploug, 2001; Ionescu et al., 2015; Belcher et al., 2016; Stief et al., 2021; Karthäuser et al., 2021), and few have obtained sequencing data (Bizic-Ionescu et al., 2018; Zäncker et al., 2019; Szabo et al., 2021; Vaksmaa et al., 2022; Baumas et al., 2024). Yet to the best of our knowledge no study has been published yet, combining both. This hinders our understanding of the carbon budget and its future prediction since no work has included molecular information in biological carbon pump models as taxa are not quantitatively coupled to the pathways involved in POC fluxes. Genomic and transcriptomic data obtained from particles can be used for the calculation of genome-scale metabolic models of colonizing bacteria to predict carbon usage (Saifuddin et al., 2019; Ofaim et al., 2021). Similarly, data obtained from entire particles can be used for Metagenome-scale metabolic models (metaGEMs; (Zorrilla et al., 2021). Such models can be coupled with activity measurements of single particles to better predict carbon fluxes under different environmental and taxonomic scenarios.

Ionescu et al. (2015) have shown that by using a flow-through rolling tank system, processes in nature may occur at a slower rate. Bizic-Ionescu et al. (2018) have shown, using the same system, that microbial succession on organic matter particles are initially driven by stochasticity and antagonistic interactions, rather than a change in carbon quality. Szabo et al. (2021), though still using a closed experimental system, revealed as well a high heterogeneity in colonizers of homogenous artificial particles, reaching similar conclusions as Bizic-Ionescu et al. (2018), Bižić-Ionescu et al. (2015), results unachievable by analyzing bulk samples. Similar trends have been shown also on TEP particles, which are far less studied than other types (Zäncker et al., 2019). Activity rates have also been shown to be heterogenous between single aggregates with great ranges of values (Belcher et al., 2016) even under high pressure (Stief et al., 2021).

Therefore, we call for a shift in concept and encourage the analysis of individual organic matter particles for the purpose of gaining mechanistic understanding of the processes related to their colonization and degradation. Given the current technology we can envision an *in-situ* system (Fig. 2) in which sinking particles are run through a “conveyor belt” through imaging, optode-based, activity analysis, and preservation for molecular analysis in large batches of multi-well plates. From a lab experimental point of view, the flow-through rolling tank systems from Ionescu et al. (2015) allow to apply constant flow rates around particles as if they were truly sinking. However, this set up was built to study lake particles and does not consider the increase of the pressure. Ocean water column is deeper and effect of the pressure is shown to have an important effect on microbial life (Tamburini et al., 2013a; Garel et al., 2019). In that sense, the particle sinking simulator from Tamburini et al., 2009 seems more suitable allowing to adapt pressure and temperature variation to the sinking speed of particles and to measure respiration rates (Tamburini et al., 2021). However, samples are closed into 500 mL bottles and are not liberated from bottle effect without a system to apply a flow rate as in Ionescu et al. (2015). Later Stief et al. (2021) developed a slightly different system allowing to simulate the sinking of particles individually placed each into 6 mL high pressure incubation vials. However, this system is also not exempt from the bottle effect and does not allow to continuously increase pressure as in Tamburini et al. (2009), instead graduated increases in steps of 24 h not reflective of real sinking velocity of particles. Here we envisage a system which merges the three: a system to mimic depth profile of pressure and temperature (Tamburini et al.,2009), whilst applying a constant flow rate with water and associated free living microbial communities from different depths (Ionescu et al., 2015) which can separate particles into individual high pressure vials (Stief et al., 2021). The flow rates could be stopped at some sinking phases to allow single particles respiration measurements and single aggregates could be retrieved at the end of the experiment for imaging and diversity analyses.

We further recommend that analyses of individual particles focus not only on sinking particles as obtained in sediment traps but also on suspended and ascending particles. Upon closer inspection, each particle can be a completely different world with a different composition, density, sinking speed, size, microbial communities, as correctly stated by McDonnell "*In a sense, they're like a little galaxy of their own in a huge, enormous universe of the ocean*".[4] It is now crucial to bridge the gap between small scale mini environments and big scales to improve our understanding of Earth's carbon budget.

CRediT authorship contribution statement

Chloé Baumas: Writing – original draft, Writing – review & editing. **Mina Bizic:** Writing – original draft, Writing – review & editing.

Declaration of competing interest

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Data availability

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