Did you say marine snow? Zooming into different types of organic matter particles and their importance in the open ocean carbon cycle

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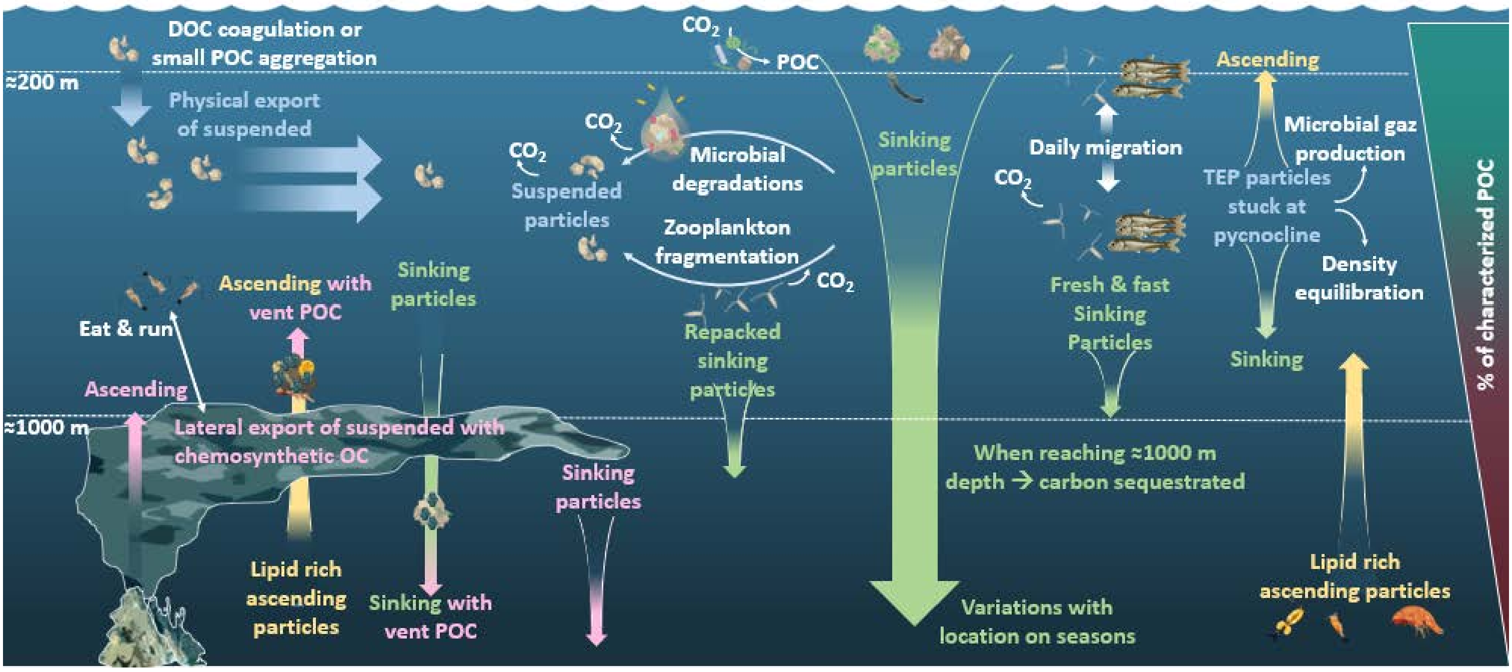
Graphical abstract



Key words:

Marine particles, attached microorganisms, sinking particles, suspended particles, ascending particles, marine gels, plastic pollution, bioluminescent particles, biological carbon pump, hydrothermal vents, lipid-carbon shunt.

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, having an important role in controlling global climate. Suspended particles represent a major substrate of organic carbon for heterotrophic microorganisms, being more likely to get remineralized. Ascending particles, depending on their content, 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 discuss characteristics of known particle-types and associated sampling methods. We further identify gaps in knowledge and highlight the need to better understand the single particles ecosystem to improve upscaling rates to the global scale.

Short 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 (i) Sinking, (ii) Suspended, and (iii) Ascending, link the different parts of the open ocean by shaping carbon distribution. In this review we discuss the significance of each group to carbon sequestration in the ocean, of the associated microbiomes, and, current sampling methods associated with each particle type. We further identify gaps in knowledge and highlight the need to better understand the highly heterogeneous single particles as mini-ecosystems before upscaling rates to the global scale.

Introduction

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 these particles consist mostly of particulate organic matter, and are initially formed by microorganisms, mostly through photosynthesis in the euphotic zone, 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, faecal 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 2014). OM particles are aggregated (and disaggregated) via various physical processes (Verdugo et al. 2004; Burd and Jackson 2009) and further transformed by microbial and fungal degradation, and zooplankton grazing (Simon et al. 2002; Burd and Jackson 2009). OM particles are highly heterogeneous, yet some studies show these are closely related to the season, location, and origin of the primary particles (Flintrop et al. 2018). In contrast, other studies have shown that even particles of the same source and age can be highly heterogeneous (Bižić-Ionescu et al. 2018; Zäncker et al. 2019; Szabo et al. 2022).

Marine particles can be classified as (i) Sinking; (ii) Suspended; and (iii) Ascending based on their motion 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 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 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. The heterogeneous conditions within these particles are distinctly different from those of the surrounding water, thus, coupled with the high activity of the attached communities, making OM particles a unique and important topic in biological oceanography.

The importance of organic matter particles

Marine 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). Governing the distribution and concentration of carbon in the water column, 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 sinking particles to the ocean floor. There, and especially, when reaching zones below 1000 m, the carbon remains away from the atmosphere for thousands of years, thus having an important role in controlling global climate. In parallel, suspended particles are a major substrate of organic carbon for heterotrophic microorganisms and are more likely to be remineralized, thus, redistributing CO_2 in the water column resulting in a shorter-term sequestration (see sections below). Ascending particles (see sections below), depending on their content, 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.

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; Bižić-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; Bižić-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 this approach aims at generating a representative picture of the particles in the sampled water, it provides neither information on the distribution of different types of particles nor on 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 incorrect picture of the bulk particles microbiome (Bižić-Ionescu et al. 2018; Zäncker et al. 2019; Armitage and Jones 2019; Szabo et al. 2022).

Methodological problems arising from heterogeneity among particles

Particle heterogeneity prevents the mechanistic understanding of the microbial degradation process and therefore bulk data cannot be readily applied to large scales. Heterogeneity plays a role at different scales. First, diversity in particle sources, i.e., the first building organisms. It was previously suggested that particles of different sources (e.g. different algal species) attract different colonizing prokaryotes (Grossart et al. 2005). However, in contrast to these closed-vessel experiments, new experiments show high heterogeneity also in colonizers between particles of the same source (Bižić-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 Bižić-Ionescu et al. (2018) 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. Thus, due to shorter or longer periods of microbial processing and interaction with the surrounding water, even particles of the same source may differ in the elemental composition e.g. C:N:P ratios and carbon quality, with fresh particles containing more labile organic carbon and a lower C:N:P ratio (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.

Sinking, suspended and ascending particles

Sinking particles

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 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, unlike suspended and ascending, 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 to the composition

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[1] “Une pluie alimentaire“French for “a nutritional rain”

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 an accurate mechanistic prevision. The sinking speed of marine snow ranges from 2 to 1500 m d^{-1} (Alldredge and Silver 1988; Armstrong et al. 2002; Trull et al. 2008; Turner 2015) with fecal pellets being on the faster end of this range (Atkinson et al. 2001; Giesecke et al. 2009). The sinking speed can eventually increase with mineral ballast inclusion (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, 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 difference 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). However, to date there are only about 20 studies addressing the topic and the reasons for this large range cannot be determined as no patterns emerge, possibly due to the different methods used, coupled with the large heterogeneity in particle characteristics (e.g. origin, source material, size, and age). 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 early mesopelagic zone (0-500m) though this is not necessarily where carbon remineralization is most important in the context of carbon storage efficiency (Fuchs et al. 2022). Prokaryotic Heterotrophic Production (PHP), is commonly used as an indicator for particles 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 matter of debate (Burd et al. 2010; Giering and Evans 2022) and may require revisions on rates estimations. Regardless it is by now evident 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; b; 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 a parameter of paramount importance regarding 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; Volkman and Tanoue 2002; Bižić-Ionescu 2014; Karl et al. 2022) both with respect to activity as well as biomass. Attached prokaryotes are concentrated on particles and their population can reach 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 even far from light and at great pressure 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 that sinking particles are colonized by communities of microorganisms from the euphotic zone whose diversity drastically decreases while experiencing strong environmental variations down to 500 m and beyond (e.g. increasing pressure and decreasing temperature) (Thiele et al. 2015; Baumas et al. 2021). Accordingly, microorganisms from the euphotic zone could 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 to replicate suggesting that not all cells that attach have the time to reach the densities necessary to influence diversity or remineralization rates. Though 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 that have withstood the change in environmental parameters during sinking. 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.

In the past, microscopy was a method of choice to study microbial diversity on 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 to investigate microbial communities more in depth. We compiled existing literature where molecular biology techniques were used to study diversity of microorganisms on sinking particles from open ocean (Table. 1). Most of these studies found common prokaryotic taxa with attached lifestyle such as *Bacteroidetes* and *Actinobacteria* in the euphotic zone and *Deltaproteobacteria*, *Marinimicrobia* and *Gammaproteobacteria* in deeper water. Nevertheless, these organisms exhibit different community assemblages and degrees of diversity corresponding to different seasons, locations, depths or particle types and sources (ref. within Table. 1). Thus, comparing and merging the different studies to define certain key patterns becomes challenging. In addition, these studies mostly investigate prokaryotes with only 20 % of the studies investigating eukaryotes and even less in the case of viruses, which account for only 7 % of the studies presented in Table. 1. 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). Virus association with marine snow was only recently 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 (Bižić-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, there are still too few studies as compared to the high complexity of this “heterogeneous black box”.

Table 1 : Literature review of 58 studies that analyzed the diversity on marine particles

	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							●					●

Table 1 : Literature review of 58 studies that analyzed the diversity on marine particles

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		🟩							🟪		🟪					🟦		

Sinking particles, are small ecosystems, harboring distinct communities of microorganism (See Table 1 for a summary of diversity studies) in which prokaryotes, eukaryotes, and virus, are highly concentrated, and are constrained by environmental factors as well as by their interactions. We therefore support the hypothesis that differences in composition of the sinking particles and their associated microbial community drive differences in the remineralization process. However, studies relating 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 we lack data to define clear patterns of diversity and associated remineralization rate. Nevertheless, Enke et al. (2018), by performing a controlled lab experiment, demonstrated that microscale ecology of attached prokaryotes affect carbon turnover rates. More precisely, they show that particle degradation kinetics depend on the colonization and the assembly of primary degraders and secondary consumers (Enke et al. 2018). This is further complicated when considering that different environmental conditions such as temperature, pressure, organic matter quality, and absence of light can affect prokaryotic diversity, growth efficiency, enzymatic hydrolysis, or gene expression. In this sense, environmental variations caused by the sinking of a particle could affect microbial metabolisms and hence could shape POC remineralization and sequestration. For instance, Church et al. (2021) found that prokaryotic heterotrophic production is higher on slow sinking rather than fast sinking particles. Further supportive of this hypothesis, experiments of POC degradation with different substrates resulted in different microbial responses, suggesting that remineralization rates of sinking particles depend on their source material (Davis et al. 2009). This was further corroborated by ecto-enzymatic activities measurement on sinking particles which vary with depth and location (Tamburini et al. 2006; Yamada et al. 2012). Inside single particle, environmental conditions can lead to the formation of micro-niches, favoring different metabolisms for instance chemoautotrophy (Karl et al. 1984), sulfur (Shanks and Reeder 1993; Raven et al. 2021), or methanogenesis (Shanks and Reeder 1993). A variety of biological, physical and chemical processes alter the organic composition of particles as they sink. Decomposition and transformation mechanisms, rates and extent vary depending on the molecular structure of individual compounds and their availability as substrates for heterotrophic metabolism. Unfortunately, very little is known about the distribution of type of sinking particles, their attached microbial communities and associated remineralization rates, despite the crucial need to understand how the biological carbon pump works and to constrain models predicting what will happen in future scenarios. Nguyen et al. (2022) provides mechanistic insight into key microscale dynamics occurring on particles over depth profiles. Their model shows that microbial growth dynamics can generate temporal and spatial variability in POC degradation rates and thus suggest that current parameters used for POC degradation modeling are inadequate. It further shows that stochastic assembly of communities on particles results in different microbial dynamics over depth. This work (Nguyen et al. 2022) provides a first step to explicitly integrate microscale dynamics into large scale models and should be taken as an example that accurately describing major particle-microbe interactions seems necessary and urgent to predict variability in large scale carbon cycling.

Suspended particles

Suspended, i.e. neutrally buoyant, particles have been distinguished from sinking particles early in the field but were considered at first mainly as a background concentration pool (e.g. McCave 1975). Suspended particles are technically hard to isolate 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 allowed to discover that the passive transport of these particles was more dynamic than previously thought and suspended particles gain more importance 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 its horizontal transport (Lam and Marchal 2015). We can distinguish between two types of suspended particles: (i) strongly degraded sinking particles, stopping their 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.

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). As stated above, zooplankton and attached microbes are feeding directly on sinking particles. However, their carbon demand can 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), thus highlighting the importance of indirect processes.

The remaining, unexplained part, 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 with less exchanges between both sinking and non-sinking particles during high sinking flux period (Cram et al. 2022). This transformation can occur by physical or biological fragmentation, or by microbial degradation.

Physical break-up 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 by the 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 purely diatoms. 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 break-up of sinking particles is driven by two mechanisms: sloppy feeding or coprorhexy (fragmentation of pellets) of 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 detritivores feeding activities and are thus 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 ones (Pomeroy and Deibel 1980; Biddanda and Pomeroy 1988; Noji et al. 1991; Smith et al. 1992; Simon et al. 2002). Indeed, Smith et al. (1992) indicate that the ectoenzymatic activity on particles is very high. The amount of DOM produced by solubilization of POC would be 10 to 100 times greater than the absorption capacity of a cell. Thus, DOC is released into the surrounding environment in the form of a plume, reducing sinking particle size and sinking velocities (Kiørboe and Jackson 2001). Microbes degradation can lead to an increase of fractal dimension (Guidi et al. 2008 and ref within) allowing sinking water flows to flush interstitial DOC (Goldthwait et al. 2005) and to expose micro-environmements to sea water (Bianchi et al. 2018). Grossart et al. (2001) introduce the term of “Sloppy hydrolysis” to refer to these intensive ectoenzymatic activities resulting in a release of DOC which intensifies surrounding microbes and zooplankton attraction (Kiørboe and Visser 1999; Poulsen and Kiørboe 2005).

These physical and biological processes lower the abundance of sinking particles and hence the associated gravitational POC fluxes in the mesopelagic zone having a major impact on the biological carbon pump (Buesseler and Boyd 2009; Le Moigne 2019). The most important mechanism by 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 into essential compounds conversion (van der Jagt et al. 2020). In turn, these non-sinking nutritive materials could be efficiently harvested by zooplankton (Mayor et al. 2014; Sanders et al. 2016; Cavan et al. 2021). Mayor et al. (2014) speculate that fragmentation could be a deliberate behavior of zooplankton to promote harvestable production of microbial biomass from poor quality POC, terming this phenomenon “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). The general effect is that OC would be retained in the mesopelagic zone where it can fuel mesopelagic biota and be slowly remineralized over time (Liszka et al. 2019).

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 sinking 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 export by the so-called 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 makes the mixed layer depth moving. These event 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 Eddy subduction pump and can occur by 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). This 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 particles concentration with 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 was mainly investigated using models (e.g. Levy et al. 2001; Karleskind et al. 2011; Nagai et al. 2015). However, some measurements were performed and for instance, Stukel et al. (2017) show that mesoscale eddies subduction could be responsible for over a quarter of the total OC sequestration in some upwelling ecosystems such as the California current. A discrepancy between gravitational carbon export and carbon demand in the aphotic zone has been known for decades (e.g. Burd et al. 2010). This gap can be partly explained, among others, by PIPs (Boyd et al. 2019), yet it is too often neglected due to inappropriate sampling techniques. Even if we still cannot sample them properly, the spread of *in situ* optical devices (e.g. Giering et al. 2020 and optical methods section of this paper) should give crucial information in the future.

Ascending particles

The biological activity related to marine snow has been and still is studied mostly for its role in the BCP. Accordingly, most studies regard particle movement in the water column unidirectionally 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 microorganisms 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.

Deep lipid rich particles

The "Rising particle hypothesis" was first suggested in 1978, stating that lipid-rich particles produced near the deep benthos would promote the fast shuttling of POC from the deep to the surface (Yayanos and Nevenzel 1978). They supported this hypothesis by demonstrating that benthic amphipods from hadal zone (the zone below 6000 m) contain large amount of lipids (26 % of dry weight of their bodies) which, after decay predation or cannibalism could be a source of fast rising particles in the shape of lipid rich carcasses or fecal pellets (Yayanos and Nevenzel 1978). Dissections reveal that those lipids are mostly in the form of visible liquid droplets. Nevertheless, these 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). With the exception of 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. This allows the larvae to gain access to the 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) This is equivalent to about 14 to 714 md^{-1} which is, in both cases, much faster than diffusion or normal mixing processes, indicating their potential significance in nutrient and biogeochemical processes.

In an attempt to evaluate the relative importance of upward compared to downward fluxes, upright and inverted sediment traps were used 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, the upward flux is systematically lower than the downward flux. However the upward flux varied, ranging between 1 to 68 % of the downward flux (Simoneit et al. 1986; Smith et al. 1989). No significant spatial difference in upward fluxes was noted between eutrophic and oligotrophic zones. However, seasonally, the upward flux was systematically higher in spring (Smith et al. 1989). After hatching, larvae whose appendages did not perfectly developed, depend on their yolk stores for buoyancy. Their high abundance in spring in inverted sediment traps confirms that the high upward fluxes correspond to reproductive efforts of deep sea animals (Smith et al. 1989). This constituted a first proof that the upward flux is independent of the downward one, and that it is rather linked to biological activities in the deep sea (Grimalt et al. 1990). Even though the upward flux is in most cases a small portion of the downward flux, such a balance must be considered in the context of the particle composition. Indeed, focusing on lipids, the upward flux represents between 0.19-190 % 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 consisting 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 was 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 these particles are formed from eggs or decomposed amphipods and copepods, to fully understand the carbon cycle, the food source of these indigenous, heterotrophic organisms should be investigated.

On a global scale these 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). Given all the evidence that upward fluxes of lipid-rich particles could be significant, rising particles should be better characterized at different locations and at higher depths to determine to what extent they contribute to biogeochemical cycles for proper integration into models. Currently, the only model that includes these data is the “Upward P-flux model” whose purpose is to investigate uptake and assimilation of phosphorus by *Trichodesmium* (Karl et al. 1992). Studies on lipid rich ascending particles were mainly conducted between 1980 and the early 2000s. Recently, Flores et al. (2022) investigated the hadal production of labile lipids but without evoking a link to upward fluxes. This forms a large gap in knowledge which should be filled by applying modern methods that will allow us to characterize the eco-sphere of the ascending particles including the particle itself and activity and diversity of the associated microbial communities and their link to the upper layers.

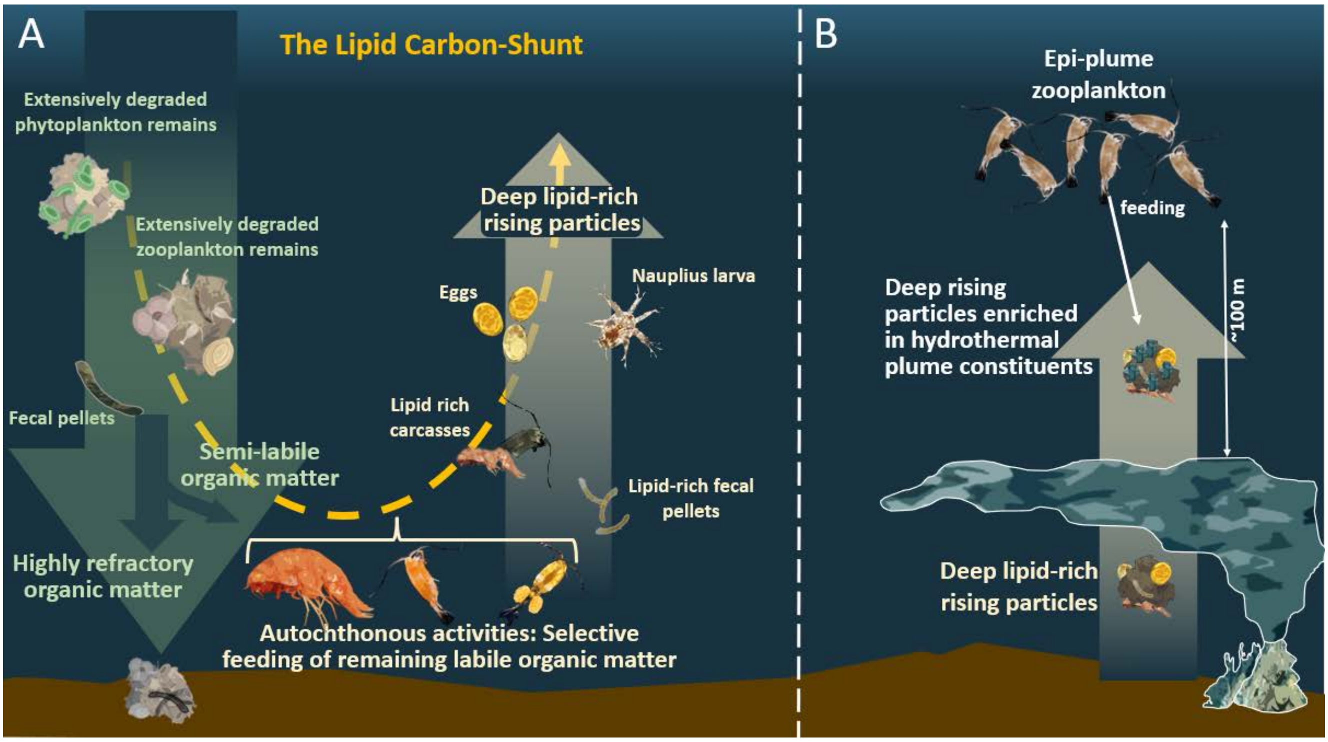


Figure 1. A) In bathyal and hadal zones (that are zones below 1000m to the sea floor), strong zooplankton autochthonous activities occur, specifically with reproductive efforts during spring. This leads to a selective feeding remaining labile organic matter which will rise as lipid rich carcasses or 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 to 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

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. Thus, 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). The results of different studies indicate that hydrothermal plumes, either black or white smokers, are enriched in POC compared to the surrounding water (Comita et al. 1984; Maruyama et al. 1993; Bennett et al. 2011b; a; 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 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 sea water, 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; a). The second zone begins when the vent fluids have reached the same density as the background water, and advert 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). In the suspended plume, the microbial community is rather complex; 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; a; Dick et al. 2013; Hoffman et al. 2018). Many studies have reported elevated microbial biomass (2 to 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 really low C/N ratios (Roth and Dymond 1989; Cowen et al. 2001; Bennett et al. 2011b; a). 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 already intensively degraded sinking POC from the surrounding water, attracts zooplankton, which in turn contribute 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). In addition, Fe and other metals can be adsorbed, stabilized and can rise with deep lipids rich particles (see section above), providing a source of POC and trace metals in the upper water column and at large distances 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. The 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).

Additional types of marine particles

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 to 1900 m depth. Bioluminescence associated with particles can be provided from various sources such as dinoflagellates (Herren et al. 2004), 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 a lot of 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-Tsukamoto 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 bioluminescence is likely transferred to the particle through chemotaxis or is already attached being expelled into the fecal pellets (Dunlap and Kita-Tsukamoto 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, their luminescence makes them attractive to grazers, which will feed on the particle and alter its fate (Zarubin et al. 2012; Tanet et al. 2020). Some bioluminescent bacteria resist the increasing pressure to which they are exposed while particles are sinking (Brown et al. 1942) and some produce more light and have a higher growth rate 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 luminescent particles may be ingested, partly respired, and partly 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, deeming the smaller fractions as suspended or significantly lowering their sinking velocity, leading to a stronger and earlier remineralization. Overall, luminous 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 impacts on the biological carbon pump would be interesting.

Marine gels (TEP and CSP particles)

Marine gels, first described nearly 4 decades ago (Emery et al. 1984) consist mainly of Transparent Exopolymer Particles (TEP) and Coomassie stainable particles (CSP), two types of natural hydrogel particles in the oceanic water column (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 differing 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 some TEP particles can 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. 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 among others, possible upper remineralization by prokaryotes (Nagata et al. 2021; Guo et al. 2022). Nevertheless, 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 halocline (Alldredge and Crocker 1995). It takes several days for salinity balance to be achieved through diffusion through the gel. Even if the particles 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). Nevertheless, 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 be that, despite their abundance in the water, they lead to less carbon sequestration than TEP does. In both cases, TEP and CSP, gel particles exhibit a complex dynamic involving microbial communities undergoing all the variations of 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 the gap in knowledge regarding the mechanisms of gel degradation by micro-organisms (specially linked to CAZymes enzymes (Arnosti et al. 2021)) hinders our ability to understand the role of gel particles in the biological carbon pump. This field needs future research efforts in this direction, both in the laboratory and *in situ*.

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., at the sediment, in the water column, or in the foodweb (Pabortsava and Lampitt 2020). Plastic in the oceans is dominated by microplastic, defined as particles smaller than 5 mm (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 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: the “Plastisphere”, composed of prokaryotes, single-cell algae and fungi (Wright et al. 2020). Because of 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). Some evidence shows that microorganism activities can be stimulated by plastic leachates and can 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, the 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 have a much higher influence on the plastisphere diversity than the plastic component (Wright et al. 2020; Vaksmaa et al. 2022). Plastisphere primary colonizers are in majority, photosynthetic autotrophs such as heavy diatom cells. This increases the density of the particle which will sink until it reaches the mesopelagic zone where photosynthesis can no longer take place. Without photosynthesis to provide a carbon source, the biofilm will self-consume. Combined with the mortality of taxa that do not withstand the high pressure and low temperature changes across the sinking process, the particles 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).

Methods to study particles

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. To this extent, it was concluded that the routinely used Niskin bottles capture 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.

Table 2 : Literature review of 17 marine particles sampling instruments

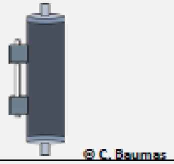
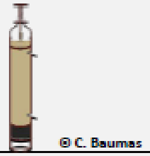
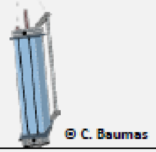
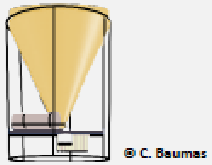
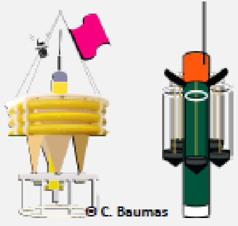
Sampling	Picture	Method Description	Fraction catched	Depth range	Time	Operational considerations	Approach	Advantages	Disadventages	Manufacturers	References
Scuba diving		Hand collection by divers of undisturbed individual particles in syringes	Individual macroscopic particles	0 to ≈60m	≈ 1h	Constraints 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)		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		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		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)		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)		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)		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)

Table 2 : Literature review of 17 marine particles sampling instruments

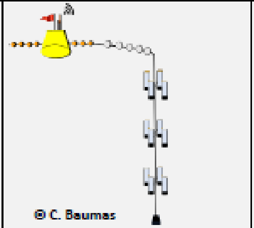
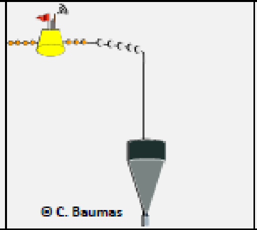
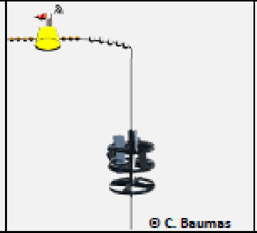
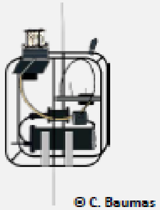
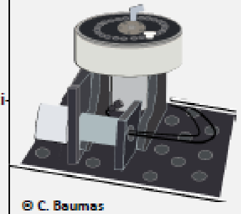
Surface tethered trap, PITS		Particles are collected while sinking in tubes which follow currents during a short term deployement	Sinking particles	Up to 1,000 m	Few days	Deployment and recovery can be achieved in ≈1h. During deployment period other core operations can be conducted while following the 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		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)		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		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		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)

Table 2 : Literature review of 17 marine particles sampling instruments

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)

Optical devices

This group of devices has 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. Main examples are 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 Keyspecies Investigation (LOKI) (Schmid et al. 2016) for monochrome images. Their advantages mainly result in their deployment from ships or on autonomous platforms and can deliver large datasets covering spatially and temporally distribution of particles. Indeed, 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 or close to deployment. 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, will be deployed at 2400m deep in the Mediterranean Sea and will start a long-term study recording with a dedicated camera deep-organism activities (specifically including bioluminescent 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, with minimum disturbance, much higher vertical and horizontal resolutions than sampling devices do, and a much better identification of individual particle structure without fragmenting them or changing their shape as pump systems or sediment traps do. 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).

Lab experimental set ups

The study of particles in the lab encompasses the many aspects of the natural environment, in an attempt to generate adequate data for modeling. This responds to technological limitations in following particles through the water column 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), formed in the lab using 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; Bižić-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 to 2000 mL) under varying environmental conditions for purposes such as: degradation of specific compounds (e.g. Bidle and Azam 1999; Panagiotopoulos et al. 2002;

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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

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. 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; Bižić-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 give precious 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), by strapping bottles on a rotating axes (e.g. Richardson et al. 2013), by using a plankton wheel (Passow et al. 2003; Le Moigne et al. 2017; Bach et al. 2019), by applying semi revolution rotation to bottles (Tamburini et al. 2006, 2009, 2021; Riou et al. 2018) or by applying a constant flow of ambient water through a dedicated roller tank (Ionescu et al. 2015). To study disaggregation processes a specific roller tank that combined rotating and oscillating action was used to generate diatom aggregates which were 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 apply a pressure on particles (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. This 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, whether it is polycarbonate or glass bottles, hyperbaric bottles or roller tanks, they are all prone to biases occurring in long incubations (Lee and Fuhrman 1991; Baltar et al. 2012; Herlemann et al. 2019) which have been grouped under the term “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; Bižić-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 a natural environment. 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 daily brought up 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 whose advantage is that environmental gradients of interest can be controlled or combined to disentangle and understand the underlying mechanisms. Such experiments can also give an idea of what to expect if something were to happen in that ecosystem. 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 that 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). Those are still used nowadays 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 interrelation 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 microorganism are among others, important players. Zooming to their 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.

Mathematical models

Mathematical models provide a means of capturing our current knowledge of a given system in an unambiguous mathematical description. In most cases, these models do not give a complete picture, however, such results can be used to point out missing or misunderstood key processes, and to test some hypothesis by extrapolating our current understanding to other times and situations. Key questions brought up 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 focus more 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; C.E. Countryman et al. 2022; Serra-Pompei et al. 2022; Stukel et al. 2022; Galí et al. 2022; Wilson et al. 2022; Rohr et al. 2022) and some on small scale processes such as 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). Guidi et al. (2016) reveal using the Tara Oceans dataset, a correlation between the carbon flux at 150 m and the occurrence of certain taxa. Yet this data, that does not go beyond the photic zone, has not been incorporated so far into quantitative carbon export models. To our knowledge, efforts have been done to couple global scale models to small scale studies, such as at the level of single particle, yet none of these results have been published yet.

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 actual metabolism of the microbial community colonizing particles, by means of 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 to reach an understanding 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 (Bižić-Ionescu et al. 2018; Armitage and Jones 2019). Furthermore, such data cannot provide information on the synergistic or antagonistic interactions between the microorganisms colonizing a particle. This data can also not inform on the specificity of a microbial community to certain particle types, nor can it inform on the change in community composition and activity in response to environmental changes incurred by the increasing depth. Thus, 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 to make this leap in concept have been there for a long while. Sediment traps or rolling tank experiments, whether flow-through or traditional, have been offering for decades access to individual particles. And last, the ability to sequence samples deeply at a low cost, coupled with the ability to amplify low amounts of DNA, removes the financial and methodological barrier to obtaining single-particle metagenomic or metatranscriptomic data for a large enough number of particles to lead to meaningful results. Nevertheless, to date there are only a handful of studies focusing on individual particles. Among these 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 (Bižić-Ionescu et al. 2018; Zäncker et al. 2019; Szabo et al. 2021; Vaksmaa et al. 2022). 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. Bižić-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 Bižić-Ionescu et al. (2018). These phenomena would not have been identified 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 was 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 free from the bottle effect and does not allow to increase continuously the pressure as in Tamburini et al. 2009 but a pressure increase in steps of 24 h which does not reflect the real sinking velocity of particles. Given this observation, we can also envision a system merging the three: Tamburini et al. 2009 system to mimic depth profile of pressure and temperature, Ionescu et al. 2015 system to apply a constant flow rate with water and associated free living microbial communities from different depths and Stief et al. (2021) to separate particles into individual high pressure vials. 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.

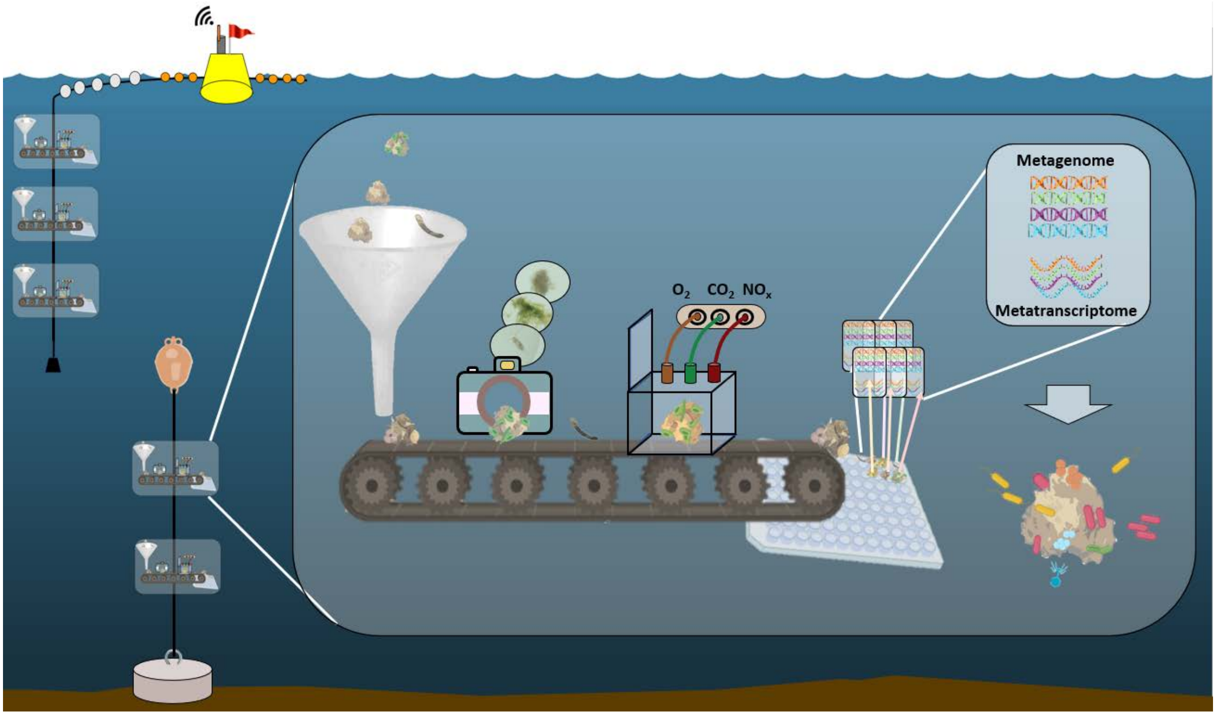

Figure 3. Conceptual moored or drifting single-particle-focused analysis system. Sedimenting particles are imaged individually. The images are linked to optode-based activity measurements of each particle. Eventually, each particle is preserved in a multi-well plate for later metagenomic, metatranscriptomic, or metabarcoding analysis. Such a system could potentially contain magazines of such plates, resulting in the preservation of thousands of well characterized individual particles.

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.

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Bibliography

Abramson, L., C. Lee, Z. Liu, S. G. Wakeham, and J. Szlosek. 2010. Exchange between suspended and sinking particles in the northwest Mediterranean as inferred from the organic composition of in situ pump and sediment trap samples. Limnology and Oceanography **55**: 725–739. doi:10.4319/lo.2010.55.2.0725

Acinas, S. G., J. Antón, and F. Rodríguez-Valera. 1999. Diversity of Free-Living and Attached Bacteria in Offshore Western Mediterranean Waters as Depicted by Analysis of Genes Encoding 16S rRNA. Applied and Environmental Microbiology **65**: 514–522. doi:10.1128/AEM.65.2.514-522.1999

Acinas, S. G., P. Sánchez, G. Salazar, and others. 2021. Deep ocean metagenomes provide insight into the metabolic architecture of bathypelagic microbial communities. Commun Biol **4**: 1–15. doi:10.1038/s42003-021-02112-2

Agusti, S., J. I. González-Gordillo, D. Vaqué, M. Estrada, M. I. Cerezo, G. Salazar, J. M. Gasol, and C. M. Duarte. 2015. Ubiquitous healthy diatoms in the deep sea confirm deep carbon injection by the biological pump. Nat Commun **6**: 7608. doi:10.1038/ncomms8608

Alcolombri, U., F. J. Peaudecerf, V. I. Fernandez, L. Behrendt, K. S. Lee, and R. Stocker. 2021. Sinking enhances the degradation of organic particles by marine bacteria. Nat. Geosci. **14**: 775–780. doi:10.1038/s41561-021-00817-x

Alldredge, A. 1998. The carbon, nitrogen and mass content of marine snow as a function of aggregate size. Deep Sea Research Part I: Oceanographic Research Papers **45**: 529–541. doi:10.1016/S0967-0637(97)00048-4

Alldredge, A. L. 1991. In Situ Collection and Laboratory Analysis of Marine Snow and Large Fecal Pellets, p. 43–46. *In*.

Alldredge, A. L., and Y. Cohen. 1987. Can microscale chemical patches persist in the sea? Microelectrode study of marine snow, fecal pellets. Science **235**: 689–691. doi:10.1126/science.235.4789.689

Alldredge, A. L., J. J. Cole, and D. A. Caron. 1986. Production of heterotrophic bacteria inhabiting macroscopic organic aggregates (marine snow) from surface waters1. Limnology and Oceanography **31**: 68–78. doi:10.4319/lo.1986.31.1.0068

Alldredge, A. L., and K. M. Crocker. 1995. Why do sinking mucilage aggregates accumulate in the water column? Science of The Total Environment **165**: 15–22. doi:10.1016/0048-9697(95)04539-D

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[4] https://mashable.com/article/marine-snow-bioluminescence-oceanx

Alldredge, A. L., C. Gotschalk, U. Passow, and U. Riebesell. 1995. Mass aggregation of diatom blooms: Insights from a mesocosm study. Deep Sea Research Part II: Topical Studies in Oceanography **42**: 9–27. doi:10.1016/0967-0645(95)00002-8

Alldredge, A. L., T. C. Granata, C. C. Gotschalk, and T. D. Dickey. 1990. The physical strength of marine snow and its implications for particle disaggregation in the ocean. Limnology and Oceanography **35**: 1415–1428. doi:10.4319/lo.1990.35.7.1415

Alldredge, A. L., and G. A. Jackson. 1995. Aggregation in marine systems. Deep-sea res., Part 2, Top. stud. oceanogr **42**.

Alldredge, A. L., U. Passow, and B. E. Logant. 1993. The abundance and significance of a class of large, transparent organic particles in the ocean.

Alldredge, A. L., and M. W. Silver. 1988. Characteristics, dynamics and significance of marine snow. Progress in Oceanography **20**: 41–82. doi:10.1016/0079-6611(88)90053-5

Amacher, J., S. Neuer, I. Anderson, and R. Massana. 2009. Molecular approach to determine contributions of the protist community to particle flux. Deep Sea Research Part I: Oceanographic Research Papers **56**: 2206–2215. doi:10.1016/j.dsr.2009.08.007

Anderson, T., and H. Ducklow. 2001. Microbial loop carbon cycling in ocean environments studied using a simple steady-state model. Aquatic Microbial Ecology **26**: 37–49. doi:10.3354/ame026037

Anderson, T. R., W. C. Gentleman, and A. Yool. 2015. EMPOWER-1.0: an Efficient Model of Planktonic ecOsystems WrittEn in R. Geoscientific Model Development **8**: 2231–2262. doi:10.5194/gmd-8-2231-2015

Anderson, T. R., and K. W. Tang. 2010. Carbon cycling and POC turnover in the mesopelagic zone of the ocean: Insights from a simple model. Deep Sea Research Part II: Topical Studies in Oceanography **57**: 1581–1592. doi:10.1016/j.dsr2.2010.02.024

Anderson, T. R., and C. M. Turley. 2003. Low bacterial growth efficiency in the oligotrophic eastern Mediterranean Sea: A modelling analysis. Journal of Plankton Research **25**: 1011–1019. doi:10.1093/plankt/25.9.1011

Andrews, C. C., D. M. Karl, L. F. Small, and S. W. Fowler. 1984. Metabolic activity and bioluminescence of oceanic faecal pellets and sediment trap particles. Nature **307**: 539–541. doi:10.1038/307539a0

Armitage, D. W., and S. E. Jones. 2019. How sample heterogeneity can obscure the signal of microbial interactions. The ISME Journal **13**: 2639–2646. doi:10.1038/s41396-019-0463-3

Armstrong, R. A., C. Lee, J. I. Hedges, S. Honjo, and S. G. Wakeham. 2002. A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. Deep Sea Research Part II: Topical Studies in Oceanography **49**: 219–236. doi:10.1016/S0967-0645(01)00101-1

Armstrong, R. A., M. L. Peterson, C. Lee, and S. G. Wakeham. 2009. Settling velocity spectra and the ballast ratio hypothesis. Deep Sea Research Part II: Topical Studies in Oceanography **56**: 1470–1478. doi:10.1016/j.dsr2.2008.11.032

Arnosti, C., M. Wietz, T. Brinkhoff, J.-H. Hehemann, D. Probandt, L. Zeugner, and R. Amann. 2021. The Biogeochemistry of Marine Polysaccharides: Sources, Inventories, and Bacterial Drivers of the Carbohydrate Cycle. Annual Review of Marine Science **13**: 81–108. doi:10.1146/annurev-marine-032020-012810

Atkinson, A., M. J. Whitehouse, J. Priddle, G. C. Cripps, P. Ward, and M. A. Brandon. 2001. South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. Marine Ecology Progress Series **216**: 279–308.

Aumont, O., O. Maury, S. Lefort, and L. Bopp. 2018. Evaluating the Potential Impacts of the Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry. Global Biogeochemical Cycles **32**: 1622–1643. doi:10.1029/2018GB005886

Azetsu-Scott, K., and U. Passow. 2004. Ascending marine particles: Significance of transparent exopolymer particles (TEP) in the upper ocean. Limnology and Oceanography **49**: 741–748. doi:10.4319/lo.2004.49.3.0741

Bach, L. T., P. Stange, J. Taucher, E. P. Achterberg, M. Algueró-Muñiz, H. Horn, M. Esposito, and U. Riebesell. 2019. The Influence of Plankton Community Structure on Sinking Velocity and Remineralization Rate of Marine Aggregates. Global Biogeochemical Cycles **33**: 971–994. doi:10.1029/2019gb006256

Baker, C. A., M. L. Estapa, M. Iversen, R. Lampitt, and K. Buesseler. 2020. Are all sediment traps created equal? An intercomparison study of carbon export methodologies at the PAP-SO site. Progress in Oceanography **184**: 102317. doi:10.1016/j.pocean.2020.102317

Balmonte, J. P., H. Hasler-Sheetal, R. N. Glud, T. J. Andersen, M. K. Sejr, M. Middelboe, A. Teske, and C. Arnosti. 2020. Sharp contrasts between freshwater and marine microbial enzymatic capabilities, community composition, and DOM pools in a NE Greenland fjord. Limnology and Oceanography **65**: 77–95. doi:10.1002/lno.11253

Baltar, F., M. V. Lindh, A. Parparov, T. Berman, and J. Pinhassi. 2012. Prokaryotic community structure and respiration during long-term incubations. MicrobiologyOpen **1**: 214–224. doi:10.1002/mbo3.25

Baumas, C. M. J., F. A. C. Le Moigne, M. Garel, and others. 2021. Mesopelagic microbial carbon production correlates with diversity across different marine particle fractions. The ISME Journal **15**: 1695–1708. doi:10.1038/s41396-020-00880-z

Bearon, R. N. 2007. A Model for Bacterial Colonization of Sinking Aggregates. Bull. Math. Biol. **69**: 417–431. doi:10.1007/s11538-005-9038-8

Belcher, A., S. A. Henson, C. Manno, and others. 2019. Krill faecal pellets drive hidden pulses of particulate organic carbon in the marginal ice zone. Nature Communications **10**: 889. doi:10.1038/s41467-019-08847-1

Belcher, A., M. Iversen, S. Giering, V. Riou, S. A. Henson, L. Berline, L. Guilloux, and R. Sanders. 2016. Depth-resolved particle-associated microbial respiration in the northeast Atlantic. Biogeosciences **13**: 4927–4943. doi:10.5194/bg-13-4927-2016

Benavides, M., S. Bonnet, F. A. C. Le Moigne, and others. 2022. Sinking Trichodesmium fixes nitrogen in the dark ocean. ISME J 1–8. doi:10.1038/s41396-022-01289-6

Bennett, S. A., R. L. Hansman, A. L. Sessions, K. Nakamura, and K. J. Edwards. 2011a. Tracing iron-fueled microbial carbon production within the hydrothermal plume at the Loihi seamount. Geochimica et Cosmochimica Acta **75**: 5526–5539. doi:10.1016/j.gca.2011.06.039

Bennett, S. A., P. J. Statham, D. R. H. Green, and others. 2011b. Dissolved and particulate organic carbon in hydrothermal plumes from the East Pacific Rise, 9°50′N. Deep-Sea Research Part I: Oceanographic Research Papers **58**: 922–931. doi:10.1016/j.dsr.2011.06.010

Bergauer, K., A. Fernandez-Guerra, J. A. L. Garcia, R. R. Sprenger, R. Stepanauskas, M. G. Pachiadaki, O. N. Jensen, and G. J. Herndl. 2018. Organic matter processing by microbial communities throughout the Atlantic water column as revealed by metaproteomics. Proceedings of the National Academy of Sciences **115**: E400–E408. doi:10.1073/pnas.1708779115

Bertram, M. A. 2002. Compositional variability in the ascending fluxes from a hydrothermal plume. Journal of Geophysical Research **107**: 3191. doi:10.1029/2000JC000223

Bianchi, D., T. S. Weber, R. Kiko, and C. Deutsch. 2018. Global niche of marine anaerobic metabolisms expanded by particle microenvironments. Nature Geoscience **11**: 263–268. doi:10.1038/s41561-018-0081-0

Biddanda, B. A., and L. R. Pomeroy. 1988. Microbial aggregation and degradation of phytoplankton-derived detritus in seawater. Microbial Succession **42**: 79–88.

Bidle, K. D., and F. Azam. 1999. Accelerated dissolution of diatom silica by marine bacterial assemblages. Nature **397**: 508–512. doi:10.1038/17351

Bidle, K. D., and F. Azam. 2001. Bacterial control of silicon regeneration from diatom detritus: Significance of bacterial ectohydrolases and species identity. Limnol. Oceanogr. **46**: 1606–1623. doi:10.4319/lo.2001.46.7.1606

Bishop, J. K. B. 1986. The correction and suspended particulate matter calibration of Sea Tech transmissometer data. Deep Sea Research Part A. Oceanographic Research Papers **33**: 121–134. doi:10.1016/0198-0149(86)90111-1

Bishop, J. K. B., M. H. Conte, P. H. Wiebe, M. R. Roman, and C. Langdon. 1986. Particulate matter production and consumption in deep mixed layers: observations in a warm-core ring. Deep Sea Research Part A. Oceanographic Research Papers **33**: 1813–1841. doi:10.1016/0198-0149(86)90081-6

Bishop, J. K. B., D. Schupack, R. M. Sherrell, and M. Conte. 1985. A Multiple-Unit Large-Volume In Situ Filtration System for Sampling Oceanic Particulate Matter in Mesoscale Environments, p. 155–175. *In*.

Bižić-Ionescu, M., D. Ionescu, and H.-P. Grossart. 2018a. Organic Particles: Heterogeneous Hubs for Microbial Interactions in Aquatic Ecosystems. Frontiers in Microbiology **9**: 1–15. doi:10.3389/fmicb.2018.02569

Bižić-Ionescu, M., D. Ionescu, and H.-P. Grossart. 2018b. Organic Particles: Heterogeneous Hubs for Microbial Interactions in Aquatic Ecosystems. Frontiers in Microbiology **9**: 1–15. doi:10.3389/fmicb.2018.02569

Bloesch, J., and N. M. Burns. 1980. A critical review of sedimentation trap technique 1). **4211**.

Bochdansky, A. B., M. A. Clouse, and G. J. Herndl. 2017. Eukaryotic microbes, principally fungi and labyrinthulomycetes, dominate biomass on bathypelagic marine snow. The ISME Journal **11**: 362–373. doi:10.1038/ismej.2016.113

Boeuf, D., B. R. Edwards, J. M. Eppley, and others. 2019. Biological composition and microbial dynamics of sinking particulate organic matter at abyssal depths in the oligotrophic open ocean. Proceedings of the National Academy of Sciences of the United States of America **116**. doi:10.1073/pnas.1903080116

Bonnet, S., M. Benavides, F. A. C. Le Moigne, and others. 2022. Diazotrophs are overlooked contributors to carbon and nitrogen export to the deep ocean. ISME J 1–12. doi:10.1038/s41396-022-01319-3

Boss, E., L. Guidi, M. J. Richardson, L. Stemmann, W. Gardner, J. K. B. Bishop, R. F. Anderson, and R. M. Sherrell. 2015. Optical techniques for remote and in-situ characterization of particles pertinent to GEOTRACES. Progress in Oceanography **133**: 43–54. doi:10.1016/j.pocean.2014.09.007

Boyd, P. W., H. Claustre, M. Levy, D. A. Siegel, and T. Weber. 2019. Multi-faceted particle pumps drive carbon sequestration in the ocean. Nature. doi:10.1038/s41586-019-1098-2

Boyd, P. W., A. McDonnell, J. Valdez, D. LeFevre, and M. P. Gall. 2015. RESPIRE: An in situ particle interceptor to conduct particle remineralization and microbial dynamics studies in the oceans' Twilight Zone. Limnology and Oceanography: Methods **13**: 494–508. doi:10.1002/lom3.10043

Breier, J. A., C. G. Rauch, K. McCartney, B. M. Toner, S. C. Fakra, S. N. White, and C. R. German. 2009. A suspended-particle rosette multi-sampler for discrete biogeochemical sampling in low-particle-density waters. Deep-Sea Research Part I: Oceanographic Research Papers **56**: 1579–1589. doi:10.1016/j.dsr.2009.04.005

Breier, J. A., S. N. White, and C. R. German. 2010. Mineral–microbe interactions in deep-sea hydrothermal systems: a challenge for Raman spectroscopy. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences **368**: 3067–3086. doi:10.1098/rsta.2010.0024

Bressac, M., C. Guieu, M. J. Ellwood, and others. 2019. Resupply of mesopelagic dissolved iron controlled by particulate iron composition. Nature Geoscience **12**: 995–1000. doi:10.1038/s41561-019-0476-6

Briggs, N., G. Dall'Olmo, and H. Claustre. 2020. Major role of particle fragmentation in regulating biological sequestration of CO 2 by the oceans. Science **367**: 791–793. doi:10.1126/science.aay1790

Briggs, N., M. J. Perry, I. Cetinić, C. Lee, E. D'Asaro, A. M. Gray, and E. Rehm. 2011. High-resolution observations of aggregate flux during a sub-polar North Atlantic spring bloom. Deep Sea Research Part I: Oceanographic Research Papers **58**: 1031–1039. doi:10.1016/j.dsr.2011.07.007

Briggs, N. T., W. H. Slade, E. Boss, and M. J. Perry. 2013. Method for estimating mean particle size from high-frequency fluctuations in beam attenuation or scattering measurements. Appl. Opt., AO **52**: 6710–6725. doi:10.1364/AO.52.006710

Brown, D. E., F. H. Johnson, and D. A. Marsland. 1942. The pressure, temperature relations of bacterial luminescence. Journal of Cellular and Comparative Physiology **20**: 151–168. doi:10.1002/JCP.1030200204

Buesseler, K. O., A. N. Antia, M. Chen, and others. 2007. An assessment of the use of sediment traps for estimating upper ocean particle fluxes. Journal of Marine Research **65**: 345–416. doi:10.1357/002224007781567621

Buesseler, K. O., and P. W. Boyd. 2009. Shedding light on processes that control particle export and flux attenuation in the twilight zone of the open ocean. Limnology and Oceanography **54**: 1210–1232. doi:10.4319/lo.2009.54.4.1210

Burd, A. B., D. A. Hansell, D. K. Steinberg, and others. 2010. Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: What the @$#! is wrong with present calculations of carbon budgets? Deep-Sea Research Part II: Topical Studies in Oceanography 1557–1571. doi:10.1016/j.dsr2.2010.02.022

Burd, A. B., and G. A. Jackson. 2009. Particle Aggregation. Annual Review of Marine Science **1**: 65–90. doi:10.1146/annurev.marine.010908.163904

Busch, K., S. Endres, M. H. Iversen, J. Michels, E.-M. Nöthig, and A. Engel. 2017. Bacterial Colonization and Vertical Distribution of Marine Gel Particles (TEP and CSP) in the Arctic Fram Strait. Frontiers in Marine Science **4**: 1–14. doi:10.3389/fmars.2017.00166

Cai, Y. 2020. Non-surface Attached Bacterial Aggregates: A Ubiquitous Third Lifestyle. Frontiers in Microbiology **11**: 1–18. doi:10.3389/fmicb.2020.557035

Calleja, M. L., C. M. Duarte, Y. T. Prairie, S. Agustí, and G. J. Herndl. 2009. Evidence for surface organic matter modulation of air-sea CO&lt;sub&gt;2&lt;/sub&gt; gas exchange. Biogeosciences **6**: 1105–1114. doi:10.5194/bg-6-1105-2009

Caron, D. A., P. G. Davis, L. P. Madin, and J. M. N. Sieburth. 1982. Heterotrophic bacteria and bacterivorous protozoa in oceanic macroaggregates. Science **218**: 795–797. doi:10.1126/science.218.4574.795

Cathalot, C., E. G. Roussel, A. Perhirin, and others. 2021. Hydrothermal plumes as hotspots for deep-ocean heterotrophic microbial biomass production. Nature Communications **12**: 6861. doi:10.1038/s41467-021-26877-6

Cavan, E., and P. Boyd. 2018. Effect of anthropogenic warming on microbial respiration and particulate organic carbon export rates in the sub-Antarctic Southern Ocean. Aquatic Microbial Ecology **82**: 111–127. doi:10.3354/ame01889

Cavan, E. L., S. Kawaguchi, and P. W. Boyd. 2021. Implications for the mesopelagic microbial gardening hypothesis as determined by experimental fragmentation of Antarctic krill fecal pellets. Ecology and Evolution **11**: 1023–1036. doi:10.1002/ece3.7119

Cavan, E. L., F. A. C. Le Moigne, A. J. Poulton, G. A. Tarling, P. Ward, C. J. Daniels, G. M. Fragoso, and R. J. Sanders. 2015. Attenuation of particulate organic carbon flux in the Scotia Sea, Southern Ocean, is controlled by zooplankton fecal pellets. Geophysical Research Letters **42**: 821–830. doi:10.1002/2014GL062744

Cavan, E. L., M. Trimmer, F. Shelley, and R. Sanders. 2017. Remineralization of particulate organic carbon in an ocean oxygen minimum zone. Nature Communications **8**. doi:10.1038/ncomms14847

C.E. Countryman, D.K. Steinberg, and A.B. Burd. 2022. Modelling the effects of copepod diel vertical migration and community structure on ocean carbon flux using an agent-based model. Ecological modelling **470**: 110003-. doi:10.1016/j.ecolmodel.2022.110003

Cetinić, I., M. J. Perry, N. T. Briggs, E. Kallin, E. A. D'Asaro, and C. M. Lee. 2012. Particulate organic carbon and inherent optical properties during 2008 North Atlantic Bloom Experiment. Journal of Geophysical Research: Oceans **117**. doi:10.1029/2011JC007771

Chang, K. J. L., C. M. Nichols, S. I. Blackburn, G. A. Dunstan, A. Koutoulis, and P. D. Nichols. 2014. Comparison of Thraustochytrids Aurantiochytrium sp., Schizochytrium sp., Thraustochytrium sp., and Ulkenia sp. for Production of Biodiesel, Long-Chain Omega-3 Oils, and Exopolysaccharide. Mar Biotechnol 16.

Choy, C. A., B. H. Robison, T. O. Gagne, and others. 2020. Author Correction: The vertical distribution and biological transport of marine microplastics across the epipelagic and mesopelagic water column. Scientific Reports **10**: 620. doi:10.1038/s41598-020-57573-y

Christaki, U., and F. Van Wambeke. 1995. Simulated phytoplankton bloom input in top-down manipulated microcosms: comparative effect of zooflagellates, ciliates and copepods. Aquat. Microb. Ecol. **9**: 137–147. doi:10.3354/ame009137

Church, M. J., E. Kyi, R. O. Hall, D. M. Karl, M. Lindh, A. Nelson, and E. K. Wear. 2021. Production and diversity of microorganisms associated with sinking particles in the subtropical North Pacific Ocean. Limnology and Oceanography lno.11877. doi:10.1002/lno.11877

Cisternas-Novoa, C., C. Lee, and A. Engel. 2015. Transparent exopolymer particles (TEP) and Coomassie stainable particles (CSP): Differences between their origin and vertical distributions in the ocean. Marine Chemistry **175**: 56–71. doi:10.1016/j.marchem.2015.03.009

Claustre, H., K. S. Johnson, and Y. Takeshita. 2020. Observing the Global Ocean with Biogeochemical-Argo. Annu. Rev. Mar. Sci. **12**: 23–48. doi:10.1146/annurev-marine-010419-010956

Collins, J. R., B. R. Edwards, K. Thamatrakoln, J. E. Ossolinski, G. R. DiTullio, K. D. Bidle, S. C. Doney, and B. A. S. Van Mooy. 2015. The multiple fates of sinking particles in the North Atlantic Ocean. Global Biogeochemical Cycles **29**: 1471–1494. doi:10.1002/2014GB005037

Comita, P. B., R. B. Gagosian, and P. M. Williams. 1984. Suspended particulate organic material from hydrothermal vent waters at 21° N. Nature **307**: 450–453. doi:10.1038/307450a0

Conover, R. J., and M. A. Paranjape. 1977. Comments on the use of a deep tank in planktological research. Helgolander Wiss. Meeresunters **30**: 105–117. doi:10.1007/BF02207829

Cowen, J. P., M. A. Bertram, S. G. Wakeham, R. E. Thomson, J. William Lavelle, E. T. Baker, and R. A. Feely. 2001. Ascending and descending particle flux from hydrothermal plumes at Endeavour Segment, Juan de Fuca Ridge. Deep Sea Research Part I: Oceanographic Research Papers **48**: 1093–1120. doi:10.1016/S0967-0637(00)00070-4

Cozar, A., F. Echevarria, J. I. Gonzalez-Gordillo, and others. 2014. Plastic debris in the open ocean. Proceedings of the National Academy of Sciences **111**: 10239–10244. doi:10.1073/pnas.1314705111

Cram, J. A., C. A. Fuchsman, M. E. Duffy, and others. 2022. Slow Particle Remineralization, Rather Than Suppressed Disaggregation, Drives Efficient Flux Transfer Through the Eastern Tropical North Pacific Oxygen Deficient Zone. Global Biogeochemical Cycles **36**: e2021GB007080. doi:10.1029/2021GB007080

Crespo, B. G., T. Pommier, B. Fernández-Gómez, and C. Pedrós-Alió. 2013. Taxonomic composition of the particle-attached and free-living bacterial assemblages in the Northwest Mediterranean Sea analyzed by pyrosequencing of the 16S rRNA. MicrobiologyOpen **2**: 541–552. doi:10.1002/mbo3.92

Cruz, B. N., and S. Neuer. 2022. Particle-associated bacteria differentially influence the aggregation of the marine diatom Minutocellus polymorphus. ISME COMMUN. **2**: 1–11. doi:10.1038/s43705-022-00146-z

Dall'Olmo, G., J. Dingle, L. Polimene, R. J. W. Brewin, and H. Claustre. 2016. Substantial energy input to the mesopelagic ecosystem from the seasonal mixed-layer pump. Nature Geoscience **9**: 820–823. doi:10.1038/ngeo2818

Dall'Olmo, G., and K. A. Mork. 2014. Carbon export by small particles in the Norwegian Sea. Geophysical Research Letters **41**: 2921–2927. doi:10.1002/2014GL059244

D'Ambrosio, L., K. Ziervogel, B. MacGregor, A. Teske, and C. Arnosti. 2014. Composition and enzymatic function of particle-associated and free-living bacteria: a coastal/offshore comparison. ISME J **8**: 2167–2179. doi:10.1038/ismej.2014.67

Datta, M. S., E. Sliwerska, J. Gore, M. F. Polz, and O. X. Cordero. 2016. Microbial interactions lead to rapid micro-scale successions on model marine particles. Nature Communications **7**: 11965. doi:10.1038/ncomms11965

Davis, C. S., F. T. Thwaites, S. M. Gallager, and Q. Hu. 2005. A three-axis fast-tow digital Video Plankton Recorder for rapid surveys of plankton taxa and hydrography. Limnology and Oceanography: Methods **3**: 59–74. doi:10.4319/lom.2005.3.59

Davis, J., K. Kaiser, and R. Benner. 2009. Amino acid and amino sugar yields and compositions as indicators of dissolved organic matter diagenesis. Organic Geochemistry **40**: 343–352. doi:10.1016/j.orggeochem.2008.12.003

DeLong, E. F., D. G. Franks, and A. L. Alldredge. 1993. Phylogenetic diversity of aggregate-attached vs. free-living marine bacterial assemblages. Limnology and Oceanography **38**: 924–934. doi:10.4319/lo.1993.38.5.0924

Devries, T., T. Norin, C. Serra-pompei, and others. 2021. Metazoans , migrations , and the ocean ' s biological carbon pump. 1–12. doi:10.1101/2021.03.22.436489

Dick, G. J., K. Anantharaman, B. J. Baker, M. Li, D. C. Reed, and C. S. Sheik. 2013. The microbiology of deep-sea hydrothermal vent plumes: Ecological and biogeographic linkages to seafloor and water column habitats. Frontiers in Microbiology **4**: 1–16. doi:10.3389/fmicb.2013.00124

Dilling, L., and A. L. Alldredge. 2000. Fragmentation of marine snow by swimming macrozooplankton: A new process impacting carbon cycling in the sea. Deep Sea Research Part I: Oceanographic Research Papers **47**: 1227–1245. doi:10.1016/S0967-0637(99)00105-3

Dithugoe, C. D., E. L. Cavan, and W. P. Froneman. 2021. Prokaryotes Regulate Particulate Organic Carbon Export in Suspended and Sinking Particle Fractions. 1–24. doi:10.21203/rs.3.rs-952425/v1

DiTullio, G. R., J. M. Grebmeier, K. R. Arrigo, and others. 2000. Rapid and early export of Phaeocystis antarctica blooms in the Ross Sea, Antarctica. Nature **404**: 595–598. doi:10.1038/35007061

Dong, S., A. V. Subhas, N. E. Rollins, J. D. Naviaux, J. F. Adkins, and W. M. Berelson. 2018. A kinetic pressure effect on calcite dissolution in seawater. Geochimica et Cosmochimica Acta **238**: 411–423. doi:10.1016/j.gca.2018.07.015

Dunlap, P. 2014. Bioluminescence: Fundamentals and Applications in Biotechnology - Volume 1. **144**. doi:10.1007/978-3-662-43385-0

Dunlap, P. V., and K. Kita-Tsukamoto. 2006. Luminous Bacteria, p. 863–892. *In* The Prokaryotes. Springer New York.

Duret, M. T., R. S. Lampitt, and P. Lam. 2019. Prokaryotic niche partitioning between suspended and sinking marine particles. Environmental Microbiology Reports **11**: 386–400. doi:10.1111/1758-2229.12692

Durkin, C. A., I. Cetinić, M. Estapa, Z. Ljubešić, M. Mucko, A. Neeley, and M. Omand. 2022. Tracing the path of carbon export in the ocean though DNA sequencing of individual sinking particles. The ISME Journal 1–11. doi:10.1038/s41396-022-01239-2

Eberhard, A. 1972. Inhibition and Activation of Bacterial Luciferase Synthesis. Journal of Bacteriology **109**: 1101–1105. doi:10.1128/jb.109.3.1101-1105.1972

Eduardo, L. N., F. Lucena-Frédou, M. M. Mincarone, A. Soares, F. Le Loc'h, T. Frédou, F. Ménard, and A. Bertrand. 2020. Trophic ecology, habitat, and migratory behaviour of the viperfish Chauliodus sloani reveal a key mesopelagic player. Sci Rep **10**: 20996. doi:10.1038/s41598-020-77222-8

Edwards, B. R., K. D. Bidle, and B. A. S. Van Mooy. 2015. Dose-dependent regulation of microbial activity on sinking particles by polyunsaturated aldehydes: Implications for the carbon cycle. Proceedings of the National Academy of Sciences **112**: 5909–5914. doi:10.1073/pnas.1422664112

Eloe, E. A., C. N. Shulse, D. W. Fadrosh, S. J. Williamson, E. E. Allen, and D. H. Bartlett. 2011. Compositional differences in particle-associated and free-living microbial assemblages from an extreme deep-ocean environment. Environmental Microbiology Reports **3**: 449–458. doi:10.1111/j.1758-2229.2010.00223.x

Emery, K. O., I. A. Johns, and S. Honjo. 1984. Organic films on particulate matter in surface waters off eastern Asia. Sedimentology **31**: 503–514. doi:10.1111/j.1365-3091.1984.tb01816.x

Engel, A. 2004. Distribution of transparent exopolymer particles (TEP) in the northeast Atlantic Ocean and their potential significance for aggregation processes. Deep Sea Research Part I: Oceanographic Research Papers **51**: 83–92. doi:10.1016/j.dsr.2003.09.001

Enke, T. N., G. E. Leventhal, M. Metzger, J. T. Saavedra, and O. X. Cordero. 2018. Microscale ecology regulates particulate organic matter turnover in model marine microbial communities. Nature Communications **9**: 2743. doi:10.1038/s41467-018-05159-8

Estapa, M. L., D. A. Siegel, K. O. Buesseler, R. H. R. Stanley, M. W. Lomas, and N. B. Nelson. 2015. Decoupling of net community and export production on submesoscales in the Sargasso Sea. Global Biogeochemical Cycles **29**: 1266–1282. doi:10.1002/2014GB004913

Estapa, M., J. Valdes, K. Tradd, J. Sugar, M. Omand, and K. Buesseler. 2020. The neutrally buoyant sediment trap: Two decades of progress. Journal of Atmospheric and Oceanic Technology **37**: 957–973. doi:10.1175/JTECH-D-19-0118.1

Fauvelle, V., M. Garel, C. Tamburini, and others. 2021. Organic additive release from plastic to seawater is lower under deep-sea conditions. Nature Communications **12**. doi:10.1038/s41467-021-24738-w

Fender, C. K., T. B. Kelly, L. Guidi, M. D. Ohman, M. C. Smith, and M. R. Stukel. 2019. Investigating Particle Size-Flux Relationships and the Biological Pump Across a Range of Plankton Ecosystem States From Coastal to Oligotrophic. Frontiers in Marine Science **6**.

Flintrop, C. M., A. Rogge, S. Miksch, S. Thiele, A. M. Waite, and M. H. Iversen. 2018. Embedding and slicing of intact in situ collected marine snow. Limnology and Oceanography: Methods **16**: 339–355. doi:10.1002/lom3.10251

Flores, E., S. I. Cantarero, P. Ruiz-Fernández, N. Dildar, M. Zabel, O. Ulloa, and J. Sepúlveda. 2022. Bacterial and eukaryotic intact polar lipids point to in situ production as a key source of labile organic matter in hadal surface sediment of the Atacama Trench. Biogeosciences **19**: 1395–1420. doi:10.5194/bg-19-1395-2022

Fontanez, K. M., J. M. Eppley, T. J. Samo, D. M. Karl, and E. F. DeLong. 2015. Microbial community structure and function on sinking particles in the North Pacific Subtropical Gyre. Frontiers in Microbiology **6**. doi:10.3389/fmicb.2015.00469

Fowler, S. W., and G. A. Knauer. 1986. Role of large particles in the transport of elements and organic compounds through the oceanic water column. Progress in Oceanography **16**: 147–194. doi:10.1016/0079-6611(86)90032-7

Francois, R., S. Honjo, R. Krishfield, and S. Manganini. 2002. Factors controlling the flux of organic carbon to the bathypelagic zone of the ocean. Global Biogeochemical Cycles **16**: 34-1-34–20. doi:10.1029/2001GB001722

Frank, A. H., J. A. L. Garcia, G. J. Herndl, and T. Reinthaler. 2016. Connectivity between surface and deep waters determines prokaryotic diversity in the North Atlantic Deep Water. Environmental Microbiology **18**: 2052–2063. doi:10.1111/1462-2920.13237

Fuchs, R., C. M. J. Baumas, M. Garel, D. Nerini, F. A. C. Le Moigne, and C. Tamburini. 2022. A RUpture-Based detection method for the Active mesopeLagIc Zone (RUBALIZ): A crucial step toward rigorous carbon budget assessments. Limnology and Oceanography: Methods **n/a**. doi:10.1002/lom3.10520

Fuhrman, J. 1992. Bacterioplankton Roles in Cycling of Organic Matter: The Microbial Food Web, p. 361–383. *In* Primary Productivity and Biogeochemical Cycles in the Sea. Springer US.

Galgani, L., I. Goßmann, B. Scholz-Böttcher, X. Jiang, Z. Liu, L. Scheidemann, C. Schlundt, and A. Engel. 2022. Hitchhiking into the Deep: How Microplastic Particles are Exported through the Biological Carbon Pump in the North Atlantic Ocean. Environ. Sci. Technol. doi:10.1021/acs.est.2c04712

Galí, M., M. Falls, H. Claustre, O. Aumont, and R. Bernardello. 2022. Bridging the gaps between particulate backscattering measurements and modeled particulate organic carbon in the ocean. Biogeosciences **19**: 1245–1275. doi:10.5194/bg-19-1245-2022

Ganesh, S., D. J. Parris, E. F. DeLong, and F. J. Stewart. 2014. Metagenomic analysis of size-fractionated picoplankton in a marine oxygen minimum zone. The ISME Journal **8**: 187–211. doi:10.1038/ismej.2013.144

Gardner, W. D., J. C. Blakey, I. D. Walsh, and others. 2001. Optics, particles, stratification, and storms on the New England continental shelf. Journal of Geophysical Research: Oceans **106**: 9473–9497. doi:10.1029/2000JC900161

Gardner, W. D., S. P. Chung, M. J. Richardson, and I. D. Walsh. 1995. The oceanic mixed-layer pump. Deep Sea Research Part II: Topical Studies in Oceanography **42**: 757.

Garel, M., P. Bonin, S. Martini, S. Guasco, M. Roumagnac, N. Bhairy, F. Armougom, and C. Tamburini. 2019. Pressure-Retaining Sampler and High-Pressure Systems to Study Deep-Sea Microbes Under In Situ Conditions. Frontiers in Microbiology **10**: 453. doi:10.3389/FMICB.2019.00453

Gartner, J. W., R. T. Cheng, P.-F. Wang, and K. Richter. 2001. Laboratory and field evaluations of the LISST-100 instrument for suspended particle size determinations. Marine Geology **175**: 199–219. doi:10.1016/S0025-3227(01)00137-2

German, C. R., L. L. Legendre, S. G. Sander, N. Niquil, G. W. Luther, L. Bharati, X. Han, and N. Le Bris. 2015. Hydrothermal Fe cycling and deep ocean organic carbon scavenging: Model-based evidence for significant POC supply to seafloor sediments. Earth and Planetary Science Letters **419**: 143–153. doi:10.1016/j.epsl.2015.03.012

German, C. R., and W. E. Seyfried. 2014. Hydrothermal Processes, p. 191–233. *In* Treatise on Geochemistry. Elsevier.

Giering, S. L. C., E. L. Cavan, S. L. Basedow, and others. 2020. Sinking Organic Particles in the Ocean—Flux Estimates From in situ Optical Devices. Frontiers in Marine Science **6**. doi:10.3389/fmars.2019.00834

Giering, S. L. C., and C. Evans. 2022. Overestimation of prokaryotic production by leucine incorporation—and how to avoid it. Limnology and Oceanography 1–13. doi:10.1002/lno.12032

Giering, S. L. C., R. Sanders, R. S. Lampitt, and others. 2014. Reconciliation of the carbon budget in the ocean's twilight zone. Nature **507**: 480–483. doi:10.1038/nature13123

Giesecke, R., H. E. González, and U. Bathmann. 2009. The role of the chaetognath Sagitta gazellae in the vertical carbon flux of the Southern Ocean. Polar Biology **33**: 293.

del Giorgio, P. A., and J. J. Cole. 1998. BACTERIAL GROWTH EFFICIENCY IN NATURAL AQUATIC SYSTEMS. Annual Review of Ecology and Systematics **29**: 503–541. doi:10.1146/annurev.ecolsys.29.1.503

Goldthwait, S. A., C. A. Carlson, G. K. Henderson, and A. L. Alldredge. 2005. Effects of physical fragmentation on remineralization of marine snow. Marine Ecology Progress Series **305**: 59–65. doi:10.3354/meps305059

Goldthwait, S., J. Yen, J. Brown, and A. Alldredge. 2004. Quantification of marine snow fragmentation by swimming euphausiids. Limnology and Oceanography **49**: 940–952. doi:10.4319/lo.2004.49.4.0940

Grimalt, J. O., B. R. T. Simoneit, J. I. Gómez-Belinchón, K. Fischer, and J. Dymond. 1990. Ascending and descending fluxes of lipid compounds in North Atlantic and North Pacific abyssal waters. Nature **345**: 147–150. doi:10.1038/345147a0

Grossart, H. P., and G. Gust. 2009. Hydrostatic pressure affects physiology and community structure of marine bacteria during settling to 4000 m: An experimental approach. Marine Ecology Progress Series **390**: 97–104. doi:10.3354/meps08201

Grossart, H. P., S. Hietanen, and H. Ploug. 2003a. Microbial dynamics on diatom aggregates in Øresund, Denmark. Marine Ecology Progress Series **249**: 69–78. doi:10.3354/meps249069

Grossart, H. P., L. Riemann, and F. Azam. 2001. Bacterial motility in the sea and its ecological implications. Aquatic Microbial Ecology **25**: 247–258. doi:10.3354/ame025247

Grossart, H.-P. H.-P., T. Kiorboe, K. Tang, H. Ploug, T. KiÃ¯Â¿Â½rboe, K. Tang, and H. Ploug. 2003b. Bacterial Colonization of Particles: Growth and Interactions. Applied and Environmental Microbiology **69**: 3500–3509. doi:10.1128/AEM.69.6.3500-3509.2003

Grossart, H.-P., F. Levold, M. Allgaier, M. Simon, and T. Brinkhoff. 2005. Marine diatom species harbour distinct bacterial communities. Environmental Microbiology **7**: 860–873. doi:10.1111/j.1462-2920.2005.00759.x

Grossart, H.-P., and H. Ploug. 2001. Microbial degradation of organic carbon and nitrogen on diatom aggregates. Limnol. Oceanogr. **46**: 267–277. doi:10.4319/lo.2001.46.2.0267

Guidi, L., S. Chaffron, L. Bittner, and others. 2016. Plankton networks driving carbon export in the oligotrophic ocean. Nature **532**: 465–470. doi:10.1038/nature16942

Guidi, L., G. A. Jackson, L. Stemmann, J. C. Miquel, M. Picheral, and G. Gorsky. 2008. Relationship between particle size distribution and flux in the mesopelagic zone. Deep-Sea Research Part I: Oceanographic Research Papers **55**: 1364–1374. doi:10.1016/j.dsr.2008.05.014

Guidi, L., L. Legendre, G. Reygondeau, J. Uitz, L. Stemmann, and S. A. Henson. 2015. A new look at ocean carbon remineralization for estimating deepwater sequestration: OCEAN REMINERALIZATION AND SEQUESTRATION. Global Biogeochem. Cycles **29**: 1044–1059. doi:10.1002/2014GB005063

Guo, S., Y. Wu, M. Zhu, and X. Sun. 2022. Concentrations of transparent exopolymer particles (TEPs) and their role in the carbon export in the South China Sea and western tropical North Pacific. Marine Environmental Research **179**: 105699. doi:10.1016/J.MARENVRES.2022.105699

Hamamoto, Y., and D. Honda. 2019. Nutritional intake of Aplanochytrium (Labyrinthulea, Stramenopiles) from living diatoms revealed by culture experiments suggesting the new prey–predator interactions in the grazing food web of the marine ecosystem A. Ianora [ed.]. PLoS ONE **14**: e0208941. doi:10.1371/journal.pone.0208941

Hastings, J. W., and K. H. Nealson. 2003. BACTERIAL BIOLUMINESCENCE. https://doi.org/10.1146/annurev.mi.31.100177.003001 **31**: 549–595. doi:10.1146/ANNUREV.MI.31.100177.003001

He, C., J. Liu, R. Wang, and others. 2022. Metagenomic evidence for the microbial transformation of carboxyl-rich alicyclic molecules: A long-term macrocosm experiment. Water Research **216**: 118281. doi:10.1016/j.watres.2022.118281

Hedges, J. I., J. A. Baldock, Y. Gélinas, C. Lee, M. Peterson, and S. G. Wakeham. 2001. Evidence for non-selective preservation of organic matter in sinking marine particles. Nature **409**: 801–804. doi:10.1038/35057247

Henson, S. A., C. Laufkötter, S. Leung, S. L. C. Giering, H. I. Palevsky, and E. L. Cavan. 2022. Uncertain response of ocean biological carbon export in a changing world. Nature Geoscience **15**. doi:10.1038/s41561-022-00927-0

Henson, S. A., R. Sanders, and E. Madsen. 2012. Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. Global Biogeochemical Cycles **26**: 1–14. doi:10.1029/2011GB004099

Herlemann, D. P. R., S. Markert, C. Meeske, and others. 2019. Individual Physiological Adaptations Enable Selected Bacterial Taxa To Prevail during Long-Term Incubations. Applied and Environmental Microbiology **85**: e00825-19. doi:10.1128/AEM.00825-19

Herman, A. W., B. Beanlands, and E. F. Phillips. 2004. The next generation of Optical Plankton Counter: the Laser-OPC. Journal of Plankton Research **26**: 1135–1145. doi:10.1093/plankt/fbh095

Hernández-León, S., S. Putzeys, C. Almeida, P. Bécognée, A. Marrero-Díaz, J. Arístegui, and L. Yebra. 2019. Carbon export through zooplankton active flux in the Canary Current. Journal of Marine Systems **189**: 12–21. doi:10.1016/j.jmarsys.2018.09.002

Herren, C. M., A. L. Alldredge, and J. F. Case. 2004. Coastal bioluminescent marine snow: fine structure of bioluminescence distribution. Continental Shelf Research **24**: 413–429. doi:10.1016/j.csr.2003.10.008

Heussner, S., C. Ratti, and J. Carbonne. 1990. The PPS 3 time-series sediment trap and the trap sample processing techniques used during the ECOMARGE experiment. Continental Shelf Research **10**: 943–958. doi:10.1016/0278-4343(90)90069-X

Ho, C., and J. Marra. 1994. Early-spring export of phytoplankton production in the northeast Atlantic Ocean. Marine Ecology Progress Series **114**: 197–202.

Hoffman, C. L., S. L. Nicholas, D. C. Ohnemus, and others. 2018. Near-field iron and carbon chemistry of non-buoyant hydrothermal plume particles, Southern East Pacific Rise 15°S. Marine Chemistry **201**: 183–197. doi:10.1016/j.marchem.2018.01.011

Honjo, S., and K. W. Doherty. 1988. Large aperture time-series sediment traps; design objectives, construction and application. Deep Sea Research Part A. Oceanographic Research Papers **35**: 133–149. doi:10.1016/0198-0149(88)90062-3

Hwang, J., E. R. M. Druffel, and J. E. Bauer. 2006. Incorporation of aged dissolved organic carbon (DOC) by oceanic particulate organic carbon (POC): An experimental approach using natural carbon isotopes. Marine Chemistry **98**: 315–322. doi:10.1016/j.marchem.2005.10.008

Ionescu, D., M. Bizic-Ionescu, A. Khalili, R. Malekmohammadi, M. R. Morad, D. de Beer, and H.-P. Grossart. 2015. A new tool for long-term studies of POM-bacteria interactions: overcoming the century-old Bottle Effect. Sci Rep **5**: 14706. doi:10.1038/srep14706

Iversen, M. H., N. Nowald, H. Ploug, G. A. Jackson, and G. Fischer. 2010. High resolution profiles of vertical particulate organic matter export off Cape Blanc, Mauritania: Degradation processes and ballasting effects. Deep Sea Research Part I: Oceanographic Research Papers **57**: 771–784. doi:10.1016/j.dsr.2010.03.007

Iversen, M. H., and H. Ploug. 2010. Ballast minerals and the sinking carbon flux in the ocean: carbon-specific respiration rates and sinking velocity of marine snow aggregates. Biogeosciences **7**: 2613–2624. doi:10.5194/bg-7-2613-2010

Iversen, M. H., and H. Ploug. 2013. Temperature effects on carbon-specific respiration rate and sinking velocity of diatom aggregates – potential implications for deep ocean export processes. Biogeosciences **10**: 4073–4085. doi:10.5194/bg-10-4073-2013

Iversen, M., and L. Poulsen. 2007. Coprorhexy, coprophagy, and coprochaly in the copepods Calanus helgolandicus, Pseudocalanus elongatus, and Oithona similis. Marine Ecology Progress Series **350**: 79–89. doi:10.3354/meps07095

van der Jagt, H., I. Wiedmann, N. Hildebrandt, B. Niehoff, and M. H. Iversen. 2020. Aggregate Feeding by the Copepods Calanus and Pseudocalanus Controls Carbon Flux Attenuation in the Arctic Shelf Sea During the Productive Period. Frontiers in Marine Science **7**. doi:10.3389/fmars.2020.543124

Jain, R., S. Raghukumar, R. Tharanathan, and N. B. Bhosle. 2005. Extracellular Polysaccharide Production by Thraustochytrid Protists. Mar Biotechnol **7**: 184–192. doi:10.1007/s10126-004-4025-x

Jambeck, J. R., R. Geyer, C. Wilcox, T. R. Siegler, M. Perryman, A. Andrady, R. Narayan, and K. L. Law. 2015. Marine pollution. Plastic waste inputs from land into the ocean. Science (New York, N.Y.) **347**: 768–71. doi:10.1126/science.1260352

Jannasch, H. W., O. C. Zafiriou, and J. W. Farrington. 1980. A sequencing sediment trap for time-series studies of fragile particles1,2. Limnology and Oceanography **25**: 939–943. doi:10.4319/lo.1980.25.5.0939

de Jesus Mendes, P. A., L. Thomsen, B. Holscher, H. C. de Stigter, and G. Gust. 2007. Pressure effects on the biological degradation of organo-mineral aggregates in submarine canyons. Marine Geology **246**: 165–175. doi:10.1016/j.margeo.2007.05.012

Jiao, N., R. Cai, Q. Zheng, and others. 2018. Unveiling the enigma of refractory carbon in the ocean. National Science Review **5**: 459–463. doi:10.1093/nsr/nwy020

Jiao, N., G. J. Herndl, D. A. Hansell, and others. 2010. Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. Nature Reviews Microbiology **8**: 593–599. doi:10.1038/nrmicro2386

Joubin, L. 1930. La vie dans les grandes profondeurs de l'océan, *In* Vol. 60, No. 3, 1er DÉCEMBRE 1930 of Revue des Deux Mondes (1829-1971).

Karl, D. M., K. M. Björkman, M. J. Church, L. A. Fujieki, E. M. Grabowski, and R. M. Letelier. 2022. Temporal dynamics of total microbial biomass and particulate detritus at Station ALOHA. Progress in Oceanography **205**: 102803. doi:10.1016/j.pocean.2022.102803

Karl, D. M., G. A. Knauer, and J. H. Martin. 1988. Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. Nature **332**: 438–441. doi:10.1038/332438a0

Karl, D. M., G. A. Knauer, J. H. Martin, and B. B. Ward. 1984. Bacterial chemolithotrophy in the ocean is associated with sinking particles. Nature **309**: 54–56. doi:10.1038/309054a0

Karl, D. M., R. Letelier, D. V. Hebel, D. F. Bird, and C. D. Winn. 1992. TRICHODESMIUM BWOMS AND NEW NITROGEN IN THE NORTH PACIFIC GYRE, p. 219–237. *In*.

Karleskind, P., M. Lévy, and L. Mémery. 2011. Modifications of mode water properties by sub-mesoscales in a bio-physical model of the Northeast Atlantic. Ocean Modelling **39**: 47–60. doi:10.1016/j.ocemod.2010.12.003

Karthäuser, C., S. Ahmerkamp, H. K. Marchant, and others. 2021. Small sinking particles control anammox rates in the Peruvian oxygen minimum zone. Nature Communications **12**: 3235. doi:10.1038/s41467-021-23340-4

Kellogg, C. T. E., and J. W. Deming. 2014. Particle-associated extracellular enzyme activity and bacterial community composition across the Canadian Arctic Ocean. FEMS Microbiology Ecology **89**: 360–375. doi:10.1111/1574-6941.12330

Kharbush, J. J., H. G. Close, B. A. S. Van Mooy, and others. 2020. Particulate Organic Carbon Deconstructed: Molecular and Chemical Composition of Particulate Organic Carbon in the Ocean. Frontiers in Marine Science **7**: 518. doi:10.3389/fmars.2020.00518

Kiko, R., A. Biastoch, P. Brandt, and others. 2017. Biological and physical influences on marine snowfall at the equator. Nature Geoscience **10**. doi:10.1038/NGEO3042

Kiørboe, T. 2003. Marine snow microbial communities: scaling of abundances with aggregate size. Aquatic Microbial Ecology **33**: 67–75. doi:10.3354/ame033067

Kiørboe, T. 2007. The Sea Core Sampler: A simple water sampler that allows direct observations of undisturbed plankton. Journal of Plankton Research **29**: 545–552. doi:10.1093/plankt/fbm037

Kiørboe, T., K. P. Andersen, and H. G. Dam. 1990. Coagulation efficiency and aggregate formation in marine phytoplankton. Marine Biology **107**: 235–245. doi:10.1007/BF01319822

Kiørboe, T., and G. A. Jackson. 2001. Marine snow, organic solute plumes, and optimal chemosensory behavior of bacteria. Limnol. Oceanogr. **46**: 1309–1318. doi:10.4319/lo.2001.46.6.1309

Kiorboe, T., K. Tang, H.-P. Grossart, and H. Ploug. 2003. Dynamics of Microbial Communities on Marine Snow Aggregates: Colonization, Growth, Detachment, and Grazing Mortality of Attached Bacteria. Applied and Environmental Microbiology **69**: 3036–3047. doi:10.1128/AEM.69.6.3036-3047.2003

Kiørboe, T., P. Tiselius, B. Mitchell-Innes, J. L. S. Hansen, A. W. Visser, and X. Mari. 1998. Intensive aggregate formation with low vertical flux during an upwelling-induced diatom bloom. Limnology and Oceanography **43**: 104–116. doi:10.4319/lo.1998.43.1.0104

Kiørboe, T., and A. W. Visser. 1999. Predator and prey perception in copepods due to hydromechanical signals. Marine Ecology Progress Series **179**: 81–95. doi:10.3354/meps179081

Klaas, C., and D. E. Archer. 2002. Association of sinking organic matter with various types of mineral ballast in the deep sea: Implications for the rain ratio: OCEAN CARBON-MINERAL FLUX ASSOCIATION. Global Biogeochem. Cycles **16**: 63-1-63–14. doi:10.1029/2001GB001765

Knauer, G. A., J. H. Martin, and K. W. Bruland. 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. Deep Sea Research Part A. Oceanographic Research Papers **26**: 97–108. doi:10.1016/0198-0149(79)90089-X

Kooi, M., E. H. van Nes, M. Scheffer, and A. A. Koelmans. 2017. Ups and Downs in the Ocean: Effects of Biofouling on Vertical Transport of Microplastics. Environmental Science & Technology **51**: 7963–7971. doi:10.1021/acs.est.6b04702

De La Rocha, C. L., and U. Passow. 2007. Factors influencing the sinking of POC and the efficiency of the biological carbon pump. Deep Sea Research Part II: Topical Studies in Oceanography **54**: 639–658. doi:10.1016/j.dsr2.2007.01.004

Lam, P. J., and O. Marchal. 2015. Insights into Particle Cycling from Thorium and Particle Data. Annual Review of Marine Science **7**: 159–184. doi:10.1146/annurev-marine-010814-015623

Lamborg, C. H., K. O. Buesseler, J. Valdes, and others. 2008. The flux of bio- and lithogenic material associated with sinking particles in the mesopelagic “twilight zone” of the northwest and North Central Pacific Ocean. Deep Sea Research Part II: Topical Studies in Oceanography **55**: 1540–1563. doi:10.1016/j.dsr2.2008.04.011

Lampitt, R. S., B. Boorman, L. Brown, and others. 2008. Particle export from the euphotic zone: Estimates using a novel drifting sediment trap, 234Th and new production. Deep Sea Research Part I: Oceanographic Research Papers **55**: 1484–1502. doi:10.1016/j.dsr.2008.07.002

Lampitt, R. S., T. Noji, and B. von Bodungen. 1990. What happens to zooplankton faecal pellets? Implications for material flux. Mar. Biol. **104**: 15–23. doi:10.1007/BF01313152

Lampitt, R. S., K. F. Wishner, C. M. Turley, and M. V. Angel. 1993. Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Marine Biology: International Journal on Life in Oceans and Coastal Waters **116**: 689–702. doi:10.1007/BF00355486

Laurenceau-Cornec, E. C., T. W. Trull, D. M. Davies, C. L. De La Rocha, and S. Blain. 2015. Phytoplankton morphology controls on marine snow sinking velocity. Marine Ecology Progress Series **520**. doi:10.3354/meps11116

Le Moigne, F. A. C. 2019a. Pathways of organic carbon downward transport by the oceanic biological carbon pump. Frontiers in Marine Sciences **6**: 1–8. doi:10.3389/fmars.2019.00634

Le Moigne, F. A. C., C. Cisternas-Novoa, J. Piontek, M. Maßmig, and A. Engel. 2017. On the effect of low oxygen concentrations on bacterial degradation of sinking particles. Sci Rep **7**: 16722. doi:10.1038/s41598-017-16903-3

Le Moigne, F. a. C., M. Gallinari, E. Laurenceau, and C. L. De La Rocha. 2013. Enhanced rates of particulate organic matter remineralization by microzooplankton are diminished by added ballast minerals. Biogeosciences **10**: 5755–5765. doi:10.5194/bg-10-5755-2013

Le Moigne, F. A. C., S. A. Henson, E. Cavan, and others. 2016. What causes the inverse relationship between primary production and export efficiency in the Southern Ocean? Geophysical Research Letters **43**: 4457–4466. doi:10.1002/2016GL068480

Leblanc, K., B. Quéguiner, F. Diaz, and others. 2018. Nanoplanktonic diatoms are globally overlooked but play a role in spring blooms and carbon export. Nature Communications **9**: 1–12. doi:10.1038/s41467-018-03376-9

Lecleir, G. R., J. M. Debruyn, E. W. Maas, P. W. Boyd, and S. W. Wilhelm. 2014. Temporal changes in particle-associated microbial communities after interception by nonlethal sediment traps.doi:10.1111/1574-6941.12213

Lee, C., R. A. Armstrong, J. K. Cochran, and others. 2009. MedFlux: Investigations of particle flux in the Twilight Zone. Deep-Sea Research Part II: Topical Studies in Oceanography **56**: 1363–1368. doi:10.1016/j.dsr2.2008.12.003

Lee, C., S. Wakeham, and C. Arnosti. 2004. Particulate organic matter in the sea: The composition conundrum. Ambio **33**: 565–575. doi:10.1579/0044-7447-33.8.565

Lee, S., and J. A. Fuhrman. 1991. Spatial and temporal variation of natural bacterioplankton assemblages studied by total genomic DNA cross-hybridization. Limnology and Oceanography **36**: 1277–1287. doi:10.4319/lo.1991.36.7.1277

Leu, A. O., J. M. Eppley, A. Burger, and E. F. DeLong. 2022. Diverse Genomic Traits Differentiate Sinking-Particle-Associated versus Free-Living Microbes throughout the Oligotrophic Open Ocean Water Column. 19. doi:https://doi.org/10.1128/mbio.01569-22

Levy, M., L. Bopp, P. Karleskind, L. Resplandy, C. Ethe, and F. Pinsard. 2013. Physical pathways for carbon transfers between the surface mixed layer and the ocean interior. Global Biogeochemical Cycles **27**: 1001–1012. doi:10.1002/gbc.20092

Levy, M., P. Klein, and A.-M. Treguier. 2001. Impact of sub-mesoscale physics on production and subduction of phytoplankton in an oligotrophic regime. Journal of Marine Research **59**: 535–565.

Lin, Y.-S., J. Lee, L.-H. Lin, K.-H. Fu, C.-T. A. Chen, Y.-H. Wang, and I.-H. Lee. 2020. Biogeochemistry and dynamics of particulate organic matter in a shallow-water hydrothermal field (Kueishantao Islet, NE Taiwan). Marine Geology **422**: 106121. doi:10.1016/j.margeo.2020.106121

Liszka, C. M., C. Manno, G. Stowasser, C. Robinson, and G. A. Tarling. 2019. Mesozooplankton Community Composition Controls Fecal Pellet Flux and Remineralization Depth in the Southern Ocean. **6**: 1–14. doi:10.3389/fmars.2019.00230

Liu, R., L. Wang, Q. Liu, Z. Wang, Z. Li, J. Fang, L. Zhang, and M. Luo. 2018. Depth-Resolved Distribution of Particle-Attached and Free-Living Bacterial Communities in the Water Column of the New Britain Trench. Frontiers in Microbiology **9**: 1–12. doi:10.3389/fmicb.2018.00625

Liu, Y., M. Zeng, Z. Xie, D. Ning, J. Zhou, X. Yu, R. Liu, and L. Zhang. 2022. Microbial Community Structure and Ecological Networks during Simulation of Diatom Sinking. 1–20.

Lloyd, C. C., S. Brown, J. P. Balmonte, A. Hoarfrost, S. Ghobrial, and C. Arnosti. 2022. Particles act as 'specialty centers' with expanded enzymatic function throughout the water column in the western North Atlantic. Frontiers in Microbiology **13**.

Long, R., and F. Azam. 1996. Abundant Protein-Containing Particles in the Sea. Aquatic Microbial Ecology **10**: 213–221. doi:https://doi.org/10.3354/ame010213

Luo, E., A. O. Leu, J. M. Eppley, D. M. Karl, and E. F. DeLong. 2022. Diversity and origins of bacterial and archaeal viruses on sinking particles reaching the abyssal ocean. The ISME Journal 1–9. doi:10.1038/s41396-022-01202-1

Maas, A. E., S. Liu, L. M. Bolaños, B. Widner, R. Parsons, E. B. Kujawinski, L. Blanco-Bercial, and C. A. Carlson. 2020. Migratory Zooplankton Excreta and Its Influence on Prokaryotic Communities. Frontiers in Marine Science **7**: 1014. doi:10.3389/fmars.2020.573268

Maerz, J., K. D. Six, I. Stemmler, S. Ahmerkamp, and T. Ilyina. 2020. Microstructure and composition of marine aggregates as co-determinants for vertical particulate organic carbon transfer in the global ocean. Biogeosciences **17**: 1765–1803. doi:10.5194/bg-17-1765-2020

Maiti, K., C. R. Benitez-Nelson, and K. O. Buesseler. 2010. Insights into particle formation and remineralization using the short-lived radionuclide, Thoruim-234. Geophysical Research Letters **37**. doi:10.1029/2010GL044063

Mari, X., U. Passow, C. Migon, A. B. Burd, and L. Legendre. 2017. Transparent exopolymer particles: Effects on carbon cycling in the ocean. Progress in Oceanography **151**: 13–37. doi:10.1016/j.pocean.2016.11.002

Marsay, C. M., R. J. Sanders, S. A. Henson, K. Pabortsava, E. P. Achterberg, and R. S. Lampitt. 2015. Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean. Proceedings of the National Academy of Sciences **112**: 1089–1094. doi:10.1073/pnas.1415311112

Marshall, J. C., R. G. Williams, and A. J. G. Nurser. 1993. Inferring the Subduction Rate and Period over the North Atlantic. Journal of Physical Oceanography **23**: 1315–1329. doi:10.1175/1520-0485(1993)023<1315:ITSRAP>2.0.CO;2

Martin, J. H., G. A. Knauer, D. M. Karl, and W. W. Broenkow. 1987. VERTEX: carbon cycling in the northeast Pacific. Deep Sea Research Part A. Oceanographic Research Papers **34**: 267–285. doi:10.1016/0198-0149(87)90086-0

Martini, S., B. Al Ali, M. Garel, and others. 2013. Effects of Hydrostatic Pressure on Growth and Luminescence of a Moderately-Piezophilic Luminous Bacteria Photobacterium phosphoreum ANT-2200 A. Driks [ed.]. PLoS ONE **8**: e66580. doi:10.1371/journal.pone.0066580

Maruyama, A., N. Mita, and T. Higashihara. 1993. Particulate materials and microbial assemblages around the Izena black smoking vent in the Okinawa trough. Journal of Oceanography **49**: 353–367. doi:10.1007/BF02269570

Mayor, D. J., W. C. Gentleman, and T. R. Anderson. 2020. Ocean carbon sequestration: Particle fragmentation by copepods as a significant unrecognised factor? BioEssays **42**: 2000149. doi:10.1002/bies.202000149

Mayor, D. J., R. Sanders, S. L. C. Giering, and T. R. Anderson. 2014. Microbial gardening in the ocean's twilight zone: Detritivorous metazoans benefit from fragmenting, rather than ingesting, sinking detritus. BioEssays **36**: 1132–1137. doi:10.1002/bies.201400100

McCave, I. N. 1975. Vertical flux of particles in the ocean. Deep Sea Research and Oceanographic Abstracts **22**: 491–502. doi:10.1016/0011-7471(75)90022-4

McDonnell, A. M. P., P. W. Boyd, and K. O. Buesseler. 2015a. Effects of sinking velocities and microbial respiration rates on the attenuation of particulate carbon fluxes through the mesopelagic zone. Global Biogeochemical Cycles **29**: 175–193. doi:10.1002/2014GB004935

McDonnell, A. M. P., P. J. Lam, C. H. Lamborg, and others. 2015b. The oceanographic toolbox for the collection of sinking and suspended marine particles. Progress in Oceanography **133**: 17–31. doi:10.1016/j.pocean.2015.01.007

Mendes, P. A. de J., and L. Thomsen. 2012. Effects of Ocean Acidification on the Ballast of Surface Aggregates Sinking through the Twilight Zone. PLOS ONE **7**: e50865. doi:10.1371/journal.pone.0050865

Mestre, M., E. Borrull, M. M. Sala, and J. M. Gasol. 2017. Patterns of bacterial diversity in the marine planktonic particulate matter continuum. ISME J **11**: 999–1010. doi:10.1038/ismej.2016.166

Mestre, M., C. Ruiz-González, R. Logares, C. M. Duarte, J. M. Gasol, and M. M. Sala. 2018. Sinking particles promote vertical connectivity in the ocean microbiome. Proceedings of the National Academy of Sciences **115**: E6799–E6807. doi:10.1073/pnas.1802470115

Metfies, K., E. Bauerfeind, C. Wolf, P. Sprong, S. Frickenhaus, L. Kaleschke, A. Nicolaus, and E. M. Nöthig. 2017. Protist communities in moored long-term sediment traps (Fram Strait, Arctic)-preservation with mercury chloride allows for PCR-based molecular genetic analyses. Frontiers in Marine Science **4**. doi:10.3389/fmars.2017.00301

Michaud, C. A., C. L. Huffard, K. L. Smith Jr, and C. A. Durkin. 2022. Changes in phytoplankton and biomineral content of particles during episodic fluxes to abyssal depth. Limnology and Oceanography Letters **7**: 342–353. doi:10.1002/lol2.10255

Milici, M., Z.-L. Deng, J. Tomasch, and others. 2016a. Co-occurrence Analysis of Microbial Taxa in the Atlantic Ocean Reveals High Connectivity in the Free-Living Bacterioplankton. Frontiers in Microbiology **7**: 1–20. doi:10.3389/fmicb.2016.00649

Milici, M., J. Tomasch, M. L. Wos-Oxley, and others. 2016b. Bacterioplankton Biogeography of the Atlantic Ocean: A Case Study of the Distance-Decay Relationship. Frontiers in Microbiology **7**.

Milici, M., J. Tomasch, M. L. Wos-Oxley, and others. 2016c. Low diversity of planktonic bacteria in the tropical ocean. Sci Rep **6**: 19054. doi:10.1038/srep19054

Milici, M., M. Vital, J. Tomasch, and others. 2017. Diversity and community composition of particle-associated and free-living bacteria in mesopelagic and bathypelagic Southern Ocean water masses: Evidence of dispersal limitation in the Bransfield Strait. Limnology and Oceanography **62**: 1080–1095. doi:10.1002/lno.10487

Mina Bižić-Ionescu. 2014. Polyphasic comparison of limnic and marine particle-associated bacteria.

Mirza, J., Y. Oba, J. Mirza, and Y. Oba. 2021. Semi-Intrinsic Luminescence in Marine Organisms, IntechOpen.

Le Moigne, F. A. C. 2019b. Pathways of organic carbon downward transport by the oceanic biological carbon pump. Frontiers in Marine Sciences **6**: 1–8. doi:10.3389/fmars.2019.00634

Mullin, M. M., and P. M. Evans. 1974. The use of a deep tank in plankton ecology. 2. Efficiency of a planktonic food chain1: Planktonic food chain. Limnol. Oceanogr. **19**: 902–911. doi:10.4319/lo.1974.19.6.0902

Nagai, T., N. Gruber, H. Frenzel, Z. Lachkar, J. C. McWilliams, and G.-K. Plattner. 2015. Dominant role of eddies and filaments in the offshore transport of carbon and nutrients in the California Current System. Journal of Geophysical Research: Oceans **120**: 5318–5341. doi:10.1002/2015JC010889

Nagata, T., Y. Yamada, and H. Fukuda. 2021. Transparent Exopolymer Particles in Deep Oceans: Synthesis and Future Challenges. Gels **7**: 75. doi:10.3390/gels7030075

Nealson, K. H. 1977. Autoinduction of bacterial luciferase. Archives of Microbiology 1977 112:1 **112**: 73–79. doi:10.1007/BF00446657

Nealson, K. H., T. Platt, and J. W. Hastings. 1970. Cellular Control of the Synthesis and Activity of the Bacterial Luminescent System1. Journal of bacteriology **104**: 313–322.

Nguyen, T. T. H., E. J. Zakem, A. Ebrahimi, and others. 2022. Microbes contribute to setting the ocean carbon flux by altering the fate of sinking particulates. Nat Commun **13**: 1657. doi:10.1038/s41467-022-29297-2

Niewiadomska, K., H. Claustre, L. Prieur, and F. d'Ortenzio. 2008. Submesoscale physical-biogeochemical coupling across the Ligurian current (northwestern Mediterranean) using a bio-optical glider. Limnology and Oceanography **53**: 2210–2225. doi:10.4319/lo.2008.53.5_part_2.2210

Noji, T. T., K. W. Estep, F. Macintyre, and F. Norrbin. 1991. Image Analysis of Faecal Material Grazed Upon by Three Species Of Copepods: Evidence For Coprorhexy, Coprophagy and Coprochaly. Journal of the Marine Biological Association of the United Kingdom **71**: 465–480. doi:10.1017/S0025315400051717

Oberbeckmann, S., and M. Labrenz. 2020. Marine Microbial Assemblages on Microplastics: Diversity, Adaptation, and Role in Degradation. Annual Review of Marine Science **12**: 209–232. doi:10.1146/annurev-marine-010419-010633

Ofaim, S., S. Sulheim, E. Almaas, D. Sher, and D. Segrè. 2021. Dynamic Allocation of Carbon Storage and Nutrient-Dependent Exudation in a Revised Genome-Scale Model of Prochlorococcus. Frontiers in Genetics **12**.

Omand, M. M., E. A. D'Asaro, C. M. Lee, M. J. Perry, N. Briggs, I. Cetinić, and A. Mahadevan. 2015. Eddy-driven subduction exports particulate organic carbon from the spring bloom. Science **348**. doi:10.1126/science.1260062

Orzech, J. K., and K. H. Nealson. 1984. Bioluminescence Of Marine Snow: Its Effect On The Optical Properties Of The Sea. Ocean Optics VII **0489**: 100. doi:10.1117/12.943292

Pabortsava, K., and R. S. Lampitt. 2020. High concentrations of plastic hidden beneath the surface of the Atlantic Ocean. Nat Commun **11**: 4073. doi:10.1038/s41467-020-17932-9

Panagiotopoulos, C., and R. Sempéré. 2007. Sugar dynamics in large particles during in vitro incubation experiments. Mar. Ecol. Prog. Ser. **330**: 67–74. doi:10.3354/meps330067

Panagiotopoulos, C., R. Sempéré, I. Obernosterer, L. Striby, M. Goutx, F. Van Wambeke, S. Gautier, and R. Lafont. 2002. Bacterial degradation of large particles in the southern Indian Ocean using in vitro incubation experiments. Organic Geochemistry **33**: 985–1000. doi:10.1016/S0146-6380(02)00057-8

Parekh, P., S. Dutkiewicz, M. J. Follows, and T. Ito. 2006. Atmospheric carbon dioxide in a less dusty world. Geophysical Research Letters **33**: L03610. doi:10.1029/2005GL025098

Parker, D. S., W. J. Kaufman, and D. Jenkins. 1972. Floc Breakup in Turbulent Flocculation Processes. Journal of the Sanitary Engineering Division **98**: 79–99. doi:10.1061/JSEDAI.0001389

Passow, U. 2002. Transparent exopolymer particles (TEP) in aquatic environments. Progress in Oceanography **55**: 287–333. doi:10.1016/S0079-6611(02)00138-6

Passow, U., and C. L. De La Rocha. 2006. Accumulation of mineral ballast on organic aggregates. Global Biogeochemical Cycles **20**. doi:10.1029/2005GB002579

Passow, U., A. Engel, and H. Ploug. 2003. The role of aggregation for the dissolution of diatom frustules. FEMS Microbiology Ecology **46**: 247–255. doi:10.1016/S0168-6496(03)00199-5

Passow, U., R. F. Shipe, A. Murray, D. K. Pak, M. A. Brzezinski, and A. L. Alldredge. 2001. The origin of transparent exopolymer particles (TEP) and their role in the sedimentation of particulate matter. Continental Shelf Research **21**: 327–346. doi:10.1016/S0278-4343(00)00101-1

Pelve, E. A., K. M. Fontanez, and E. F. DeLong. 2017. Bacterial Succession on Sinking Particles in the Ocean's Interior. Frontiers in Microbiology **8**: 1–15. doi:10.3389/fmicb.2017.02269

Peoples, L. M., S. Donaldson, O. Osuntokun, and others. 2018. Vertically distinct microbial communities in the Mariana and Kermadec trenches H. Smidt [ed.]. PLOS ONE **13**: e0195102. doi:10.1371/journal.pone.0195102

Peterson, M. L., J. Fabres, S. G. Wakeham, C. Lee, I. J. Alonso, and J. C. Miquel. 2009. Sampling the vertical particle flux in the upper water column using a large diameter free-drifting NetTrap adapted to an Indented Rotating Sphere sediment trap. Deep Sea Research Part II: Topical Studies in Oceanography **56**: 1547–1557. doi:10.1016/j.dsr2.2008.12.020

Peterson, M. L., P. J. Hernes, D. S. Thoreson, J. I. Ifedges, C. Lee, and S. G. Wakeham. 1993. Field evaluation of a valved sediment trap. Limnology and Oceanography **38**: 1741–1761. doi:10.4319/lo.1993.38.8.1741

Peterson, M. L., S. G. Wakeham, C. Lee, M. A. Askea, and J. C. Miquel. 2005. Novel techniques for collection of sinking particles in the ocean and determining their settling rates. Limnology and Oceanography: Methods **3**: 520–532. doi:10.4319/lom.2005.3.520

Pettersson, H., F. Gross, and F. Koczy. 1939. Large-Scale Plankton Culture. Nature **144**: 332–333. doi:10.1038/144332c0

Picheral, M., C. Catalano, D. Brousseau, and others. 2022. THE UNDERWATER VISION PROFILER 6: AN IMAGING SENSOR OF PARTICLE SIZE SPECTRA AND PLANKTON, FOR AUTONOMOUS AND CABLED PLATFORMS. Limnology & Ocean Methods **20**: 115–129. doi:10.1002/lom3.10475

Picheral, M., L. Guidi, L. Stemmann, D. M. Karl, G. Iddaoud, and G. Gorsky. 2010. The underwater vision profiler 5: An advanced instrument for high spatial resolution studies of particle size spectra and zooplankton. Limnology and Oceanography: Methods **8**: 462–473. doi:10.4319/lom.2010.8.462

Pinti, J., A. W. Visser, C. Serra-Pompei, K. H. Andersen, M. D. Ohman, and T. Kiørboe. 2022. Fear and loathing in the pelagic: How the seascape of fear impacts the biological carbon pump. Limnology and Oceanography **67**: 1238–1256. doi:10.1002/lno.12073

Piontek, J., N. Händel, G. Langer, J. Wohlers, U. Riebesell, and A. Engel. 2009. Effects of rising temperature on the formation and microbial degradation of marine diatom aggregates. Aquat. Microb. Ecol. **54**: 305–318. doi:10.3354/ame01273

Piontek, J., M. Sperling, E.-M. Nöthig, and A. Engel. 2014. Regulation of bacterioplankton activity in Fram Strait (Arctic Ocean) during early summer: The role of organic matter supply and temperature. Journal of Marine Systems **132**: 83–94. doi:10.1016/j.jmarsys.2014.01.003

Planquette, H., and R. M. Sherrell. 2012. Sampling for particulate trace element determination using water sampling bottles: methodology and comparison to in situ pumps. Limnology and Oceanography: Methods **10**: 367–388. doi:10.4319/lom.2012.10.367

Ploug, H. 2001. Small-scale oxygen fluxes and remineralization in sinking aggregates. Limnology and Oceanography **46**: 1624–1631. doi:10.4319/lo.2001.46.7.1624

Ploug, H., and J. Bergkvist. 2015. Oxygen diffusion limitation and ammonium production within sinking diatom aggregates under hypoxic and anoxic conditions. Marine Chemistry **176**: 142–149. doi:10.1016/j.marchem.2015.08.012

Ploug, H., H. Grossart, F. Azam, and B. Jørgensen. 1999. Photosynthesis, respiration, and carbon turnover in sinking marine snow from surface waters of Southern California Bight:implications for the carbon cycle in the ocean. Mar. Ecol. Prog. Ser. **179**: 1–11. doi:10.3354/meps179001

Ploug, H., and H. P. Grossart. 1999. Bacterial production and respiration in aggregates - a matter of the incubation method. EPIC3Aquatic microbial ecology, 20(1), pp. 21-29. doi:hdl:10013/epic.24842

Ploug, H., and H.-P. Grossart. 2000. Bacterial growth and grazing on diatom aggregates: Respiratory carbon turnover as a function of aggregate size and sinking velocity. Limnology and Oceanography **45**: 1467–1475. doi:10.4319/lo.2000.45.7.1467

Ploug, H., M. H. Iversen, and G. Fischer. 2008. Ballast, sinking velocity, and apparent diffusivity within marine snow and zooplankton fecal pellets: Implications for substrate turnover by attached bacteria. Limnology and Oceanography **53**: 1878–1886. doi:10.4319/lo.2008.53.5.1878

Ploug, H., and B. Jørgensen. 1999. A net-jet flow system for mass transfer and microsensor studies of sinking aggregates. Marine Ecology Progress Series **176**: 279–290. doi:10.3354/meps176279

Poff, K. E., A. O. Leu, J. M. Eppley, D. M. Karl, and E. F. DeLong. 2021. Microbial dynamics of elevated carbon flux in the open ocean's abyss. Proceedings of the National Academy of Sciences **118**: e2018269118. doi:10.1073/pnas.2018269118

Pollard, R. T., and L. Regier. 1990. Large variations in potential vorticity at small spatial scales in the upper ocean. Nature **348**: 227–229. doi:10.1038/348227a0

Pomeroy, L. R., and D. Deibel. 1980. Aggregation of organic matter by pelagic tunicates1. Limnology and Oceanography **25**: 643–652. doi:10.4319/lo.1980.25.4.0643

Poulsen, L., and M. Iversen. 2008. Degradation of copepod fecal pellets: key role of protozooplankton. Marine Ecology Progress Series **367**: 1–13. doi:10.3354/meps07611

Poulsen, L., and T. Kiørboe. 2005. Coprophagy and coprorhexy in the copepods Acartia tonsa and Temora longicornis: clearance rates and feeding behaviour. Marine Ecology Progress Series **299**: 217–227. doi:10.3354/meps299217

Prairie, J. C., K. Ziervogel, R. Camassa, R. M. McLaughlin, B. L. White, C. Dewald, and C. Arnosti. 2015. Delayed settling of marine snow: Effects of density gradient and particle properties and implications for carbon cycling. Marine Chemistry **175**: 28–38. doi:10.1016/j.marchem.2015.04.006

Preston, C. M., C. A. Durkin, and K. M. Yamahara. 2020. DNA metabarcoding reveals organisms contributing to particulate matter flux to abyssal depths in the North East Pacific ocean. Deep Sea Research Part II: Topical Studies in Oceanography **173**: 104708. doi:10.1016/j.dsr2.2019.104708

Puigcorbé, V., C. Ruiz-González, P. Masqué, and J. M. Gasol. 2020. Sampling Device-Dependence of Prokaryotic Community Structure on Marine Particles: Higher Diversity Recovered by in situ Pumps Than by Oceanographic Bottles. Frontiers in Microbiology **11**: 1645. doi:10.3389/fmicb.2020.01645

Rath, J., K. Y. Wu, G. J. Herndl, and E. F. DeLong. 1998. High phylogenetic diversity in a marine-snow-associated bacterial assemblage. Aquatic Microbial Ecology **14**: 261–269. doi:10.3354/ame014261

Ratmeyer, V., and G. Wefer. 1996. A high resolution camera system (ParCa) for imaging particles in the ocean: System design and results from profiles and a three-month deployment. Journal of Marine Research **54**: 589–603. doi:10.1357/0022240963213565

Raven, M. R., R. G. Keil, and S. M. Webb. 2021. Microbial sulfate reduction and organic sulfur formation in sinking marine particles. Science **371**: 178–181. doi:10.1126/science.abc6035

Reed, D. C., J. A. Breier, H. Jiang, and others. 2015. Predicting the response of the deep-ocean microbiome to geochemical perturbations by hydrothermal vents. The ISME Journal **9**: 1857–1869. doi:10.1038/ismej.2015.4

Reinthaler, T., H. van Aken, C. Veth, J. Arístegui, C. Robinson, P. J. L. B. Williams, P. Lebaron, and G. J. Herndl. 2006. Prokaryotic respiration and production in the meso- and bathypelagic realm of the eastern and western North Atlantic basin. Limnology and Oceanography **51**: 1262–1273. doi:10.4319/lo.2006.51.3.1262

Rembauville, M., C. Manno, G. A. Tarling, S. Blain, and I. Salter. 2016. Strong contribution of diatom resting spores to deep-sea carbon transfer in naturally iron-fertilized waters downstream of South Georgia. Deep-Sea Research Part I: Oceanographic Research Papers **115**: 22–35. doi:10.1016/j.dsr.2016.05.002

Reynolds, R. A., D. Stramski, and G. Neukermans. 2016. Optical backscattering by particles in Arctic seawater and relationships to particle mass concentration, size distribution, and bulk composition. Limnology and Oceanography **61**: 1869–1890. doi:10.1002/lno.10341

Richardson, D. C., J. D. Newbold, A. K. Aufdenkampe, P. G. Taylor, and L. A. Kaplan. 2013. Measuring heterotrophic respiration rates of suspended particulate organic carbon from stream ecosystems: Measuring respiration rates of POC. Limnol. Oceanogr. Methods **11**: 247–261. doi:10.4319/lom.2013.11.247

Riebesell, U. 1992. The formation of large marine snow and its sustained residence in surface waters. Limnology and Oceanography **37**: 63–76. doi:10.4319/lo.1992.37.1.0063

Riebesell, U., J. Czerny, K. von Bröckel, and others. 2013. Technical Note: A mobile sea-going mesocosm system – new opportunities for ocean change research. Biogeosciences **10**: 1835–1847. doi:10.5194/bg-10-1835-2013

Rieck, A., D. P. R. Herlemann, K. Jürgens, and H.-P. Grossart. 2015. Particle-Associated Differ from Free-Living Bacteria in Surface Waters of the Baltic Sea. Frontiers in Microbiology **6**. doi:10.3389/fmicb.2015.01297

Riley, J. S., R. Sanders, C. Marsay, F. A. C. Le Moigne, E. P. Achterberg, and A. J. Poulton. 2012. The relative contribution of fast and slow sinking particles to ocean carbon export. Global Biogeochemical Cycles **26**: 1–10. doi:10.1029/2011GB004085

Rinaldi, A., R. A. Vollenweider, G. Montanari, C. R. Ferrari, and A. Ghetti. 1995. Mucilages in Italian seas: the Adriatic and Tyrrhenian Seas, 1988–1991. Science of The Total Environment **165**: 165–183. doi:10.1016/0048-9697(95)04550-K

Riou, V., J. Para, M. Garel, and others. 2018. Biodegradation of Emiliania huxleyi aggregates by a natural Mediterranean prokaryotic community under increasing hydrostatic pressure. Progress in Oceanography **163**: 271–281. doi:10.1016/j.pocean.2017.01.005

Robinson, C., D. Wallace, J.-H. Hyun, and others. 2018. An implementation strategy to quantify the marine microbial carbon pump and its sensitivity to global change. National Science Review **5**: 474–480. doi:10.1093/nsr/nwy070

Robison, B. H., and T. M. Lancraft. 1984. An upward transport mechanism from the benthos. Naturwissenschaften **71**: 322–324. doi:10.1007/BF00396618

Rohr, T., A. Richardson, A. Lenton, M. Chamberlain, and E. Shadwick. 2022. Marine carbon cycling and sequestration is extremely sensitive to zooplankton grazing in biogeochemical models. preprint In Review.

Romera-Castillo, C., M. Pinto, T. M. Langer, X. A. Álvarez-Salgado, and G. J. Herndl. 2018. Dissolved organic carbon leaching from plastics stimulates microbial activity in the ocean. Nature Communications **9**: 1430. doi:10.1038/s41467-018-03798-5

Roth Rosenberg, D., M. Haber, J. Goldford, and others. 2021. Particle-associated and free-living bacterial communities in an oligotrophic sea are affected by different environmental factors. Environmental Microbiology **23**: 4295–4308. doi:10.1111/1462-2920.15611

Roth, S. E., and J. Dymond. 1989. Transport and settling of organic material in a deep-sea hydrothermal plume: evidence from particle flux measurements. Deep Sea Research Part A. Oceanographic Research Papers **36**: 1237–1254. doi:10.1016/0198-0149(89)90103-9

Ruiz-González, C., M. Mestre, M. Estrada, and others. 2020. Major imprint of surface plankton on deep ocean prokaryotic structure and activity. Mol Ecol **29**: 1820–1838. doi:10.1111/mec.15454

Saba, G. K., A. B. Burd, J. P. Dunne, and others. 2021. Toward a better understanding of fish-based contribution to ocean carbon flux. Limnology and Oceanography **66**: 1639–1664. doi:10.1002/lno.11709

Saifuddin, M., J. M. Bhatnagar, D. Segrè, and A. C. Finzi. 2019. Microbial carbon use efficiency predicted from genome-scale metabolic models. Nat Commun **10**: 3568. doi:10.1038/s41467-019-11488-z

Salazar, G., F. M. Cornejo-Castillo, V. Benítez-Barrios, E. Fraile-Nuez, X. A. Álvarez-Salgado, C. M. Duarte, J. M. Gasol, and S. G. Acinas. 2016. Global diversity and biogeography of deep-sea pelagic prokaryotes. The ISME Journal **10**: 596–608. doi:10.1038/ismej.2015.137

Samson, S., L. Langebrake, J. Patten, and C. Lembke. 2004. Shadowed Image Particle Profiling and Evaluation Recorder. 15.

Sanders, R. J., S. A. Henson, A. P. Martin, and others. 2016. Controls over ocean mesopelagic interior carbon storage (COMICS): Fieldwork, synthesis, and modeling efforts. Frontiers in Marine Science **3**. doi:10.3389/fmars.2016.00136

Santschi, P. H., C.-C. Hung, G. Schultz, N. Alvarado-Quiroz, L. Guo, J. Pinckney, and I. Walsh. 2003. Control of acid polysaccharide production and 234 Th and POC export fluxes by marine organisms. Geophysical Research Letters **30**: 2–5. doi:10.1029/2002GL016046

Schmid, M. S., C. Aubry, J. Grigor, and L. Fortier. 2016. The LOKI underwater imaging system and an automatic identification model for the detection of zooplankton taxa in the Arctic Ocean. Methods in Oceanography **15–16**: 129–160. doi:10.1016/j.mio.2016.03.003

Schneider, B., A. Engel, and R. Schlitzer. 2004. Effects of depth- and CO2-dependent C:N ratios of particulate organic matter (POM) on the marine carbon cycle. Global Biogeochemical Cycles **18**. doi:10.1029/2003GB002184

Scholten, J. C., J. Fietzke, S. Vogler, and others. 2001. Trapping efficiencies of sediment traps from the deep Eastern North Atlantic: Deep Sea Research Part II: Topical Studies in Oceanography **48**: 2383–2408. doi:10.1016/S0967-0645(00)00176-4

Sempéré, R., S. Yoro, F. Van Wambeke, and B. Charrière. 2000. Microbial decomposition of large organic particles in the northwestern Mediterranean Sea:an experimental approach. Mar. Ecol. Prog. Ser. **198**: 61–72. doi:10.3354/meps198061

Serra-Pompei, C., B. A. Ward, J. Pinti, A. W. Visser, T. Kiørboe, and K. H. Andersen. 2022. Linking Plankton Size Spectra and Community Composition to Carbon Export and Its Efficiency. Global Biogeochemical Cycles **36**: e2021GB007275. doi:10.1029/2021GB007275

Shanks, A., and M. Reeder. 1993. Reducing microzones and sulfide production in marine snow. Mar. Ecol. Prog. Ser. **96**: 43–47. doi:10.3354/meps096043

Shen, M., S. Ye, G. Zeng, Y. Zhang, L. Xing, W. Tang, X. Wen, and S. Liu. 2020. Can microplastics pose a threat to ocean carbon sequestration? Marine Pollution Bulletin **150**: 110712. doi:10.1016/j.marpolbul.2019.110712

Siegel, D. A., K. O. Buesseler, M. J. Behrenfeld, and others. 2016. Prediction of the Export and Fate of Global Ocean Net Primary Production: The EXPORTS Science Plan. Frontiers in Marine Science **3**: 22. doi:10.3389/fmars.2016.00022

Simon, M., H. Grossart, B. Schweitzer, and H. Ploug. 2002. Microbial ecology of organic aggregates in aquatic ecosystems. Aquatic Microbial Ecology **28**: 175–211. doi:10.3354/ame028175

Simoneit, B. R. T., J. O. Grimait, K. Fischer, and J. Dymond. 1986. Upward and downward flux of particulate organic material in abyssal waters of the Pacific Ocean. Naturwissenschaften **73**: 322–325. doi:10.1007/BF00451479

Smith, D. C., M. Simon, A. L. Alldredge, and F. Azam. 1992. Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. Nature **359**: 139–142. doi:10.1038/359139a0

Smith, K. L., P. M. Williams, and E. R. M. Druffel. 1989. Upward fluxes of particulate organic matter in the deep North Pacific. Nature **337**: 724–726. doi:10.1038/337724a0

Song, Y., and M. J. Rau. 2022. A novel method to study the fragmentation behavior of marine snow aggregates in controlled shear flow. Limnology and Oceanography: Methods **20**: 618–632. doi:10.1002/lom3.10509

Steinberg, D. K., and M. R. Landry. 2017. Zooplankton and the Ocean Carbon Cycle. http://dx.doi.org/10.1146/annurev-marine-010814-015924 **9**: 413–444. doi:10.1146/ANNUREV-MARINE-010814-015924

Steinberg, D. K., B. A. S. Van Mooy, K. O. Buesseler, P. W. Boyd, T. Kobari, and D. M. Karl. 2008. Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. Limnology and Oceanography **53**: 1327–1338. doi:10.4319/lo.2008.53.4.1327

Steiner, P. A., J. Geijo, E. Fadeev, A. Obiol, E. Sintes, T. Rattei, and G. J. Herndl. 2020. Functional Seasonality of Free-Living and Particle-Associated Prokaryotic Communities in the Coastal Adriatic Sea. Frontiers in Microbiology **11**: 1–18. doi:10.3389/fmicb.2020.584222

Stief, P., M. Elvert, and R. N. Glud. 2021. Respiration by "marine snow" at high hydrostatic pressure: Insights from continuous oxygen measurements in a rotating pressure tank. Limnology and Oceanography **66**: 2797–2809. doi:10.1002/LNO.11791

Stoderegger, K., and G. Herndl. 1999. Production of exopolymer particles by marine bacterioplankton under contrasting turbulence conditions. Marine Ecology Progress Series **189**: 9–16. doi:10.3354/meps189009

Strickland, J. D. H., O. Holm-Hansen, R. W. Eppley, and R. J. Linn. 1969. THE USE OF A DEEP TANK IN PLANKTON ECOLOGY. I. STUDIES OF THE GROWTH AND COMPOSITION OF PHYTOPLANKTON CROPS AT LOW NUTRIENT LEVELS1: DEEP-TANK CULTURE OF PHYTOPLANKTON. Limnol. Oceanogr. **14**: 23–34. doi:10.4319/lo.1969.14.1.0023

Stukel, M. R., L. I. Aluwihare, K. A. Barbeau, and others. 2017. Mesoscale ocean fronts enhance carbon export due to gravitational sinking and subduction. Proceedings of the National Academy of Sciences of the United States of America **114**: 1252–1257. doi:10.1073/pnas.1609435114

Stukel, M. R., M. Décima, and M. R. Landry. 2022. Quantifying biological carbon pump pathways with a data-constrained mechanistic model ensemble approach.

Styles, K. M., A. T. Brown, and A. P. Sagona. 2021. A Review of Using Mathematical Modeling to Improve Our Understanding of Bacteriophage, Bacteria, and Eukaryotic Interactions. Frontiers in Microbiology **12**: 1–17. doi:10.3389/fmicb.2021.724767

Sun, C.-C., M. Sperling, and A. Engel. 2018. Effect of wind speed on the size distribution of gel particles in the sea surface microlayer: insights from a wind–wave channel experiment. Biogeosciences **15**: 3577–3589. doi:10.5194/bg-15-3577-2018

Suzuki, N., and K. Kato. 1953. Studies on suspended materials marine snow in the sea：part Ⅰ. Sources of marine snow. **4**: 132–137.

Svensen, C., N. Morata, and M. Reigstad. 2014. Increased degradation of copepod faecal pellets by co-acting dinoflagellates and Centropages hamatus. Marine Ecology Progress Series **516**: 61–70. doi:10.3354/meps10976

Szabo, R. E., S. Pontrelli, J. Grilli, J. A. Schwartzman, S. Pollak, U. Sauer, and O. X. Cordero. 2021. Ecological stochasticity and phage induction diversify bacterioplankton communities at the microscale. bioRxiv 2021.09.27.461956.

Szabo, R. E., S. Pontrelli, J. Grilli, J. A. Schwartzman, S. Pollak, U. Sauer, and O. X. Cordero. 2022. Historical contingencies and phage induction diversify bacterioplankton communities at the microscale. Proceedings of the National Academy of Sciences **119**: e2117748119. doi:10.1073/pnas.2117748119

Tamburini, C., M. Boutrif, M. Garel, R. R. Colwell, and J. D. Deming. 2013a. Prokaryotic responses to hydrostatic pressure in the ocean–a review. Environmental microbiology reports **15**: 1262–1274.

Tamburini, C., M. Canals, X. D. de Madron, and others. 2013b. Deep-Sea Bioluminescence Blooms after Dense Water Formation at the Ocean Surface. PLOS ONE **8**: e67523. doi:10.1371/journal.pone.0067523

Tamburini, C., J. Garcin, G. Grégori, K. Leblanc, P. Rimmelin, and D. L. Kirchman. 2006. Pressure effects on surface Mediterranean prokaryotes and biogenic silica dissolution during a diatom sinking experiment. Aquatic Microbial Ecology **43**: 267–276. doi:10.3354/ame043267

Tamburini, C., M. Garel, A. Barani, and others. 2021. Increasing Hydrostatic Pressure Impacts the Prokaryotic Diversity during Emiliania huxleyi Aggregates Degradation. Water **13**: 2616. doi:10.3390/w13192616

Tamburini, C., M. Goutx, C. Guigue, and others. 2009. Effects of hydrostatic pressure on microbial alteration of sinking fecal pellets. Deep Sea Research Part II: Topical Studies in Oceanography **56**: 1533–1546. doi:10.1016/j.dsr2.2008.12.035

Tanet, L., S. Martini, L. Casalot, and C. Tamburini. 2020. Reviews and syntheses: Bacterial bioluminescence – ecology and impact in the biological carbon pump. Biogeosciences **17**: 3757–3778. doi:10.5194/bg-17-3757-2020

Tanet, L., C. Tamburini, C. Baumas, M. Garel, G. Simon, and L. Casalot. 2019. Bacterial Bioluminescence: Light Emission in Photobacterium phosphoreum is Not Under Quorum-Sensing Control. Frontiers in Microbiology **10**: 365. doi:10.3389/FMICB.2019.00365

Taucher, J., L. T. Bach, U. Riebesell, and A. Oschlies. 2014. The viscosity effect on marine particle flux: A climate relevant feedback mechanism. Global Biogeochemical Cycles **28**: 415–422. doi:10.1002/2013GB004728

Taucher, J., P. Stange, M. Alguero-Muniz, L. T. Bach, A. Nauendorf, R. Kolzenburg, J. Budenbender, and U. Riebesell. 2018. In situ camera observations reveal major role of zooplankton in modulating marine snow formation during an upwelling-induced plankton bloom. Progress in Oceanography **164**: 75–88. doi:10.1016/j.pocean.2018.01.004

Taylor, J. D., S. D. Cottingham, J. Billinge, and M. Cunliffe. 2014. Seasonal microbial community dynamics correlate with phytoplankton-derived polysaccharides in surface coastal waters. The ISME Journal **8**: 245–248. doi:10.1038/ismej.2013.178

Thiele, S., B. M. Fuchs, R. Amann, and M. H. Iversen. 2015. Colonization in the Photic Zone and Subsequent Changes during Sinking Determine Bacterial Community Composition in Marine Snow K.E. Wommack [ed.]. Applied and Environmental Microbiology **81**: 1463–1471. doi:10.1128/AEM.02570-14

Thornton, D. C. O. 2002. Diatom aggregation in the sea: mechanisms and ecological implications. Euro. J. Phycol. **37**: 149–161. doi:10.1017/S0967026202003657

Thornton, D. C. O. 2018. Coomassie Stainable Particles (CSP): Protein Containing Exopolymer Particles in the Ocean. Frontiers in Marine Science **5**. doi:10.3389/fmars.2018.00206

Thornton, D. C. O., S. D. Brooks, and J. Chen. 2016. Protein and Carbohydrate Exopolymer Particles in the Sea Surface Microlayer (SML). Frontiers in Marine Science **3**: 1–14. doi:10.3389/fmars.2016.00135

Toner, B. M., S. C. Fakra, S. J. Manganini, and others. 2009. Preservation of iron(II) by carbon-rich matrices in a hydrothermal plume. Nature Geoscience **2**: 197–201. doi:10.1038/ngeo433

Trull, T. W., S. G. Bray, K. O. Buesseler, C. H. Lamborg, S. Manganini, C. Moy, and J. Valdes. 2008. In situ measurement of mesopelagic particle sinking rates and the control of carbon transfer to the ocean interior during the Vertical Flux in the Global Ocean (VERTIGO) voyages in the North Pacific. Deep Sea Research Part II: Topical Studies in Oceanography **55**: 1684–1695. doi:10.1016/j.dsr2.2008.04.021

Turley, C., and P. Mackie. 1994. Biogeochemical significance of attached and free-living bacteria and the flux of particles in the NE Atlantic Ocean. Marine Ecology Progress Series **115**: 191–203. doi:10.3354/meps115191

Turner, J. 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquatic Microbial Ecology **27**: 57–102. doi:10.3354/ame027057

Turner, J. T. 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. Progress in Oceanography **130**: 205–248. doi:10.1016/j.pocean.2014.08.005

Vaksmaa, A., M. Egger, C. Lüke, P. D. Martins, R. Rosselli, A. A. Asbun, and H. Niemann. 2022. Microbial communities on plastic particles in surface waters differ from subsurface waters of the North Pacific Subtropical Gyre. Marine Pollution Bulletin **182**: 113949. doi:10.1016/j.marpolbul.2022.113949

Valdes, J. R., and J. F. Price. 2000. A Neutrally Buoyant, Upper Ocean Sediment Trap. Journal of Atmospheric and Oceanic Technology **17**: 62–68. doi:10.1175/1520-0426(2000)017<0062:ANBUOS>2.0.CO;2

Valencia, B., M. R. Stukel, A. E. Allen, J. P. McCrow, A. Rabines, and M. R. Landry. 2022. Microbial communities associated with sinking particles across an environmental gradient from coastal upwelling to the oligotrophic ocean. Deep Sea Research Part I: Oceanographic Research Papers **179**: 103668. doi:10.1016/j.dsr.2021.103668

Verdugo, P. 2012. Marine Microgels. Annual Review of Marine Science **4**: 375–400. doi:10.1146/annurev-marine-120709-142759

Verdugo, P., A. L. Alldredge, F. Azam, D. L. Kirchman, U. Passow, and P. H. Santschi. 2004. The oceanic gel phase: a bridge in the DOM–POM continuum. Marine Chemistry **92**: 67–85. doi:10.1016/j.marchem.2004.06.017

Volkman, J. K., and E. Tanoue. 2002. Chemical and biological studies of particulate organic matter in the ocean. Journal of Oceanography **58**: 265–279. doi:10.1023/A:1015809708632

Wakeham, S. G., C. Lee, J. I. Hedges, P. J. Hernes, and M. J. Peterson. 1997. Molecular indicators of diagenetic status in marine organic matter. Geochimica et Cosmochimica Acta **61**: 5363–5369. doi:10.1016/S0016-7037(97)00312-8

Weber, T., J. A. Cram, S. W. Leung, T. DeVries, and C. Deutsch. 2016. Deep ocean nutrients imply large latitudinal variation in particle transfer efficiency. Proceedings of the National Academy of Sciences **113**: 8606–8611. doi:10.1073/pnas.1604414113

Wenley, J., K. Currie, S. Lockwood, B. Thomson, F. Baltar, and S. E. Morales. 2021. Seasonal Prokaryotic Community Linkages Between Surface and Deep Ocean Water. Frontiers in Marine Science **8**: 1–10. doi:10.3389/fmars.2021.659641

Wieczorek, A. M., P. L. Croot, F. Lombard, J. N. Sheahan, and T. K. Doyle. 2019. Microplastic Ingestion by Gelatinous Zooplankton May Lower Efficiency of the Biological Pump. Environmental Science & Technology **53**: 5387–5395. doi:10.1021/acs.est.8b07174

Wilson, J. D., O. Andrews, A. Katavouta, and others. 2022. The biological carbon pump in CMIP6 models: 21st century trends and uncertainties. Proceedings of the National Academy of Sciences **119**: e2204369119. doi:10.1073/pnas.2204369119

Wilson, J. D., S. Barker, and A. Ridgwell. 2012. Assessment of the spatial variability in particulate organic matter and mineral sinking fluxes in the ocean interior: Implications for the ballast hypothesis. Global Biogeochemical Cycles **26**. doi:10.1029/2012GB004398

Woebken, D., B. M. Fuchs, M. M. M. Kuypers, and R. Amann. 2007. Potential Interactions of Particle-Associated Anammox Bacteria with Bacterial and Archaeal Partners in the Namibian Upwelling System. Appl Environ Microbiol **73**: 4648–4657. doi:10.1128/AEM.02774-06

Wright, R. J., G. Erni-Cassola, V. Zadjelovic, M. Latva, and J. A. Christie-Oleza. 2020. Marine Plastic Debris: A New Surface for Microbial Colonization. Environmental Science & Technology **54**: 11657–11672. doi:10.1021/acs.est.0c02305

Xie, N., M. Bai, L. Liu, and others. 2022. Patchy Blooms and Multifarious Ecotypes of Labyrinthulomycetes Protists and Their Implication in Vertical Carbon Export in the Pelagic Eastern Indian Ocean A.L. Dos Santos [ed.]. Microbiol Spectr **10**: e00144-22. doi:10.1128/spectrum.00144-22

Yamada, N., H. Fukuda, H. Ogawa, H. Saito, and M. Suzumura. 2012. Heterotrophic bacterial production and extracellular enzymatic activity in sinking particulate matter in the western North Pacific Ocean. Frontiers in Microbiology **3**: 1–13. doi:10.3389/fmicb.2012.00379

Yamada, Y., T. Yokokawa, M. Uchimiya, S. Nishino, H. Fukuda, H. Ogawa, and T. Nagata. 2017. Transparent exopolymer particles (TEP) in the deep ocean: full-depth distribution patterns and contribution to the organic carbon pool. Marine Ecology Progress Series **583**: 81–93. doi:10.3354/meps12339

Yayanos, A. A., and J. C. Nevenzel. 1978. Rising-particle hypothesis: Rapid ascent of matter from the deep ocean. Naturwissenschaften **65**: 255–256. doi:10.1007/BF00368567

Yoshida-Takashima, Y., T. Nunoura, H. Kazama, and others. 2012. Spatial Distribution of Viruses Associated with Planktonic and Attached Microbial Communities in Hydrothermal Environments. Applied and Environmental Microbiology **78**: 1311–1320. doi:10.1128/AEM.06491-11

Yuan, H., T. Li, H. Li, C. Wang, L. Li, X. Lin, and S. Lin. 2021. Diversity Distribution, Driving Factors and Assembly Mechanisms of Free-Living and Particle-Associated Bacterial Communities at a Subtropical Marginal Sea. Microorganisms **9**: 2445. doi:10.3390/microorganisms9122445

Zamanillo, M., E. Ortega-Retuerta, S. Nunes, and others. 2019. Distribution of transparent exopolymer particles (TEP) in distinct regions of the Southern Ocean. Science of The Total Environment **691**: 736–748. doi:10.1016/j.scitotenv.2019.06.524

Zäncker, B., A. Engel, and M. Cunliffe. 2019a. Bacterial communities associated with individual transparent exopolymer particles (TEP). Journal of Plankton Research **41**: 561–565. doi:10.1093/plankt/fbz022

Zäncker, B., A. Engel, and M. Cunliffe. 2019b. Bacterial communities associated with individual transparent exopolymer particles (TEP). Journal of Plankton Research **41**: 561–565. doi:10.1093/plankt/fbz022

Zarubin, M., S. Belkin, M. Ionescu, and A. Genin. 2012. Bacterial bioluminescence as a lure for marine zooplankton and fish. Proceedings of the National Academy of Sciences **109**: 853–857. doi:10.1073/pnas.1116683109

Zettler, E. R., T. J. Mincer, and L. A. Amaral-Zettler. 2013. Life in the “Plastisphere”: Microbial Communities on Plastic Marine Debris. Environmental Science & Technology **47**: 7137–7146. doi:10.1021/es401288x

Zhang, L., M. Chen, X. Chen, and others. 2021. Nitrifiers drive successions of particulate organic matter and microbial community composition in a starved macrocosm. Environment International **157**: 106776. doi:10.1016/j.envint.2021.106776

Zhao, Z., F. Baltar, and G. J. Herndl. 2020. Linking extracellular enzymes to phylogeny indicates a predominantly particle-associated lifestyle of deep-sea prokaryotes. Science Advances **6**: eaaz4354. doi:10.1126/sciadv.aaz4354

Zorrilla, F., F. Buric, K. R. Patil, and A. Zelezniak. 2021. metaGEM: reconstruction of genome scale metabolic models directly from metagenomes. Nucleic Acids Research **49**: e126. doi:10.1093/nar/gkab815

Zorz, J., C. Willis, A. M. Comeau, M. G. I. Langille, C. L. Johnson, W. K. W. Li, and J. LaRoche. 2019. Drivers of Regional Bacterial Community Structure and Diversity in the Northwest Atlantic Ocean. Frontiers in Microbiology **10**.