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Carbon Export in the Ocean: A Biologist's Perspective

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Abstract

Understanding the nature of organic matter flux in the ocean remains a major goal of oceanography because it impacts some of the most important processes in the ocean. Sinking particles are important for carbon dioxide removal from the atmosphere and its movement to the deep ocean. They also feed life below the ocean's productive surface and sustain life in the deep sea, in addition to depositing organic matter on the seafloor. However, the magnitude of all of these processes is dependent on the transformation of sinking particles during their journey through the water column. This review focuses on the movement of organic matter from the surface ocean to the deep sea via the biological carbon pump and examines the processes that prevent this downward movement—namely, attenuation via microbial colonization and zooplankton feeding. It also discusses how the depth-specific interactions among microbes, zooplankton, and aggregates determine carbon export as well as nutrient recycling, which in turn impact ocean production and Earth's climate.

Particulate organic carbon (POC): the particulate fraction of organic carbon, operationally defined as organic carbon that is retained by a 0.45-µm pore size

Biological carbon pump (BCP): the suite of biological processes that mediate transport of carbon from the surface ocean

Marine snow: macroscopic organic aggregates with diameters larger than 0.5 mm

Zooplankton fecal pellet: egested material that remains after zooplankton ingestion and subsequent dissolution and assimilation in the gut

Efficiency of the BCP: the proportion of the flux at the base of the euphotic zone that sinks to a greater discrete depth (typically 100 m below the base of the euphotic zone)

Magnitude of the BCP: the amount of POC that sinks out of the euphotic zone, also referred to as the export flux or the strength of the BCP

Dissolved inorganic carbon (DIC): the total amount of dissolved CO_2, bicarbonate, and calcium carbonate in seawater

1. INTRODUCTION

Typically, works that focus on the export of particulate organic carbon (POC) to the deep ocean introduce the biological carbon pump (BCP) as the suite of complex processes that produce and transport organic carbon from the surface ocean to depth via settling organic aggregates—that is, marine snow (phytoplankton aggregates) and zooplankton fecal pellets. This suite of complex processes is then converted to simple metrics that we can measure and compare seasonally and regionally, such as the efficiency and magnitude of the BCP. These metrics are essential as they allow us to parameterize how much of the organic carbon produced in the surface ocean may end up being exported to the deep sea and seafloor. Yet the processes that are responsible for the export and transformation of organic matter are treated as a black box. In other words, we tend to focus on the carbon, since it is the component of the export flux that is most relevant for climate change, and forget to pay attention to the biological processes that attenuate and transform organic matter as it sinks through the water column.

The aim of this review is to provide a biologist's perspective on the processes that determine the export, attenuation, and transformation of organic matter from the surface ocean to the deep sea. I first go through vertical processes that determine the export, attenuation, and transformation of settling organic matter. I also present mechanisms that export suspended and slow-sinking organic matter from the surface ocean to its interior. Finally, I discuss how the biologically driven attenuation processes impact nutrient recycling and, as a result, fertilize production in the upper, sunlit part of the water column.

2. THE OCEANIC CARBON PUMP

The oceans contain approximately 38,000 Pg of carbon (Sarmiento & Gruber 2006), 60 times the amount held in the atmosphere. Furthermore, and perhaps more importantly, the oceans are also a carbon sink, associated with a net removal of 2–2.5 Pg of carbon annually from the atmosphere, although the gross fluxes are much higher. Clearly, therefore, it is essential that we understand how carbon is pumped into the oceans and stored and the potential for these processes to mitigate climate change.

The processes controlling the uptake of CO_2 and its storage in the ocean interior are referred to as the oceanic carbon pumps (Broecker & Peng 1982, Sarmiento & Gruber 2006). These pumps are often divided into the physical carbon pump (also known as the solubility pump) and the BCP (Sarmiento & Gruber 2006, Volk & Hoffert 1985, Yamanaka & Tajika 1996). The physical carbon pump refers to the dissolution of CO_2 into cold polar and subpolar waters, mainly in the Atlantic, and the sinking of CO_2-laden water to depth as part of the ocean's overturning circulation. The BCP comprises the organic carbon pump (soft-tissue pump) and the carbonate pump (hard-tissue pump) (Volk & Hoffert 1985, Yamanaka & Tajika 1996). Both of these pumps refer to the lowering of surface dissolved inorganic carbon (DIC) concentration via phytoplankton, which convert CO_2 to dissolved organic carbon (DOC), POC (soft-tissue pump), or particulate inorganic carbon (calcium carbonate via the hard-tissue pump) that can subsequently be exported out of the surface ocean. Both fixation of CO_2 to organic matter in the soft-tissue pump and the production of calcium carbonate in the hard-tissue pump increase the difference in the partial pressure of CO_2 between the surface ocean and the atmosphere; however, the soft-tissue pump is much more efficient than the hard-tissue pump. The physical carbon pump and the BCP are connected, however, since the uptake of CO_2 from the atmosphere via the physical carbon pump is driven by the difference in the partial pressure of CO_2 between the surface ocean and the atmosphere, which is increased by the BCP.

All three carbon pumps contribute to the vertical transport of carbon from the surface ocean to the deep sea, which leads to a vertical gradient of DIC in the ocean. As a global average, in the preindustrial era DIC increased by approximately 300 μmol DIC kg^{-1} between the surface and the deep ocean (Sarmiento & Gruber 2006, Volk & Hoffert 1985). This gradient is maintained only because the oceanic carbon pumps counteract the continuous long-term physical mixing that erodes the gradient. By separating out the relative importance of the three pumps in maintaining the surface-ocean-to-deep-sea DIC gradient, Sarmiento & Gruber (2006) estimated that the soft-tissue pump was responsible for 70%, while the hard-tissue pump and the solubility pump made up only 20% and 10%, respectively (see figure 9.14 in Sarmiento & Gruber 2006). This suggests that the soft-tissue pump is the dominating factor that controls the distribution of DIC in the water column. Therefore, while the solubility pump is responsible for most of the oceans' net carbon uptake, the soft-tissue pump has the potential to remove large amounts of CO_2 from contact with the atmosphere on short timescales. Furthermore, without the storage of CO_2 in the oceans by the soft-tissue pump, the atmospheric CO_2 concentration would be 50% higher than it is today, which is equivalent to 200–300 ppm of atmospheric CO_2 (Heinze et al. 2015, Parekh et al. 2005).

Typically, when referring to the BCP, we consider only the soft-tissue pump, meaning the processes that produce and transport organic carbon from the surface ocean to depth via settling organic aggregates, that is, marine snow (phytoplankton aggregates) and zooplankton fecal pellets (Volk & Hoffert 1985) (see the sidebar titled Aggregate Formation). In this review, therefore, I also use the term BCP to refer to the soft-tissue pump and do not go into further detail concerning the hard-tissue pump or other BCPs, such as the microbial carbon pump, lipid pump, or whale pump. It should be noted, however, that calcium carbonate does play a role in the soft-tissue pump due to the ballasting effect of the settling aggregates (see the sidebar titled Aggregate Ballasting). The general view of the BCP is that phytoplankton take up CO_2 in the sunlit epipelagic zone and fix organic carbon via photosynthesis. The organic matter may be converted into dissolved organic matter, respired to CO_2, or channeled through the food web as biomass, or it may form settling aggregates. It is primarily the fraction of the organic matter that forms settling aggregates that escapes remineralization in the upper 100 m of the water column and is exported to depths below 100 m (i.e., the mesopelagic) (**Figure 1**). To date, however, the modeled global estimates

Dissolved organic carbon (DOC): the fraction of organic carbon that is dissolved in water, operationally define as organic carbon that passes through a 0.45-μm pore size

Remineralization: conversion of organic matter (both particulate and dissolved) into inorganic elements and molecules, typically referred to as inorganic nutrients

AGGREGATE FORMATION

Alexander Agassiz (1888) first postulated that a "rain of detritus" connected biological production in the surface ocean to the deep-sea communities. This rain of detritus was later documented as marine snow in the logbooks of the *Challenger* expedition in 1899. This term became common only after William Beebe made direct observations from his Bathysphere in the 1930s and when it was first published by Rachel Carson in *The Sea Around Us* (Carson 1951). While the majority of marine snow forms via physical coagulation when individual particles encounter each other and stick together, marine snow can also form biologically from, for example, discarded appendicularian houses and fragments from feeding nets produced by pteropods and polychaetes. Marine snow consists of aggregates with diameters greater than 0.5 mm. Another aggregate type is zooplankton fecal pellets, which are produced when zooplankton egest the leftovers of ingested food. Typically, fecal pellets are surrounded by a peritrophic mucous membrane that makes them very compact and dense. Marine snow and fecal pellets are denser that the surrounding water, causing them to sink. Their sinking velocities range from tens to hundreds of meters per day, though large salp fecal pellets can sink with velocities up to 1 km per day.

AGGREGATE BALLASTING

Observations have shown that fluxes of ballast minerals (e.g., calcium carbonate, silicate, and cryogenic and lithogenic material) correlate with organic carbon flux in the deep sea. This has led to the hypothesis that organic carbon export is determined by the presence of ballast minerals within settling aggregates (e.g., Armstrong et al. 2002). However, it was long unclear whether this correlation was caused by a protection of the organic matter due to association with ballast minerals or by increased densities from the ballast minerals that resulted in fast settling velocities of ballasted aggregate and thus less degradation. Several direct measurements have shown no significant differences in microbial degradation between ballasted and nonballasted aggregates (Iversen & Robert 2015; Iversen et al. 2010; Ploug et al. 2008a,b). Therefore, the main effect of mineral ballasting of settling aggregates appears to be an increase in excess density, which increases the size-specific settling velocities of the ballasted aggregates. This reduces the retention time of ballasted versus nonballasted aggregates within a certain water depth layer and thereby allows less degradation of the ballasted aggregates (i.e., less flux attenuation). However, some studies have found that incorporation of ballast minerals into marine snow causes them to disaggregate (i.e., become smaller) (Engel et al. 2009, Hamm 2002, Passow & De La Rocha 2006). Though this still increases the size-specific settling velocities of the aggregates (Iversen & Ploug 2010), it may result in an overall lower average settling velocity across all aggregate sizes, thus decreasing the efficiency of the BCP.

of annual carbon export into the mesopelagic via the BCP vary between 4 and 12 Pg (DeVries & Weber 2017, Henson et al. 2011). This large uncertainty stems from a lack in our understanding of how physical, chemical, and biological processes interact and function in the BCP.

There are differing views as to the role of biology in the oceanic uptake of anthropogenic CO_2. Though it is clear that the biological component of the BCP is responsible for a large fraction of the surface-to-deep gradient in DIC, it has long been assumed that the downward transport of organic matter is in steady state with the upward transport of DIC (Broecker 1991). In this view, the BCP is a closed loop, where deep water that is brought to the surface contains an excess of DIC and nutrients relative to the surface water. Due to slow exchange of CO_2 with the atmosphere (~10 months for a 50-m mixed layer; Broecker & Peng 1974), the biological processes are fast enough to fix both nutrients and the excess CO_2 into organic matter in most regions (Sarmiento & Gruber 2006). In some regions, however (i.e., the Southern Ocean, the equatorial Pacific, and the North Pacific), nutrients and excess CO_2 are not exhausted by biology, and excess CO_2 escapes into the atmosphere (Murnane et al. 1999). However, on a global scale, the loss of CO_2 to the atmosphere is compensated by a net uptake of CO_2 at midlatitudes, seemingly rendering the role of the BCP in anthropogenic CO_2 uptake negligible (Sarmiento & Sundquist 1992). The fact that atmospheric CO_2 levels have been stable during the past 3,000 years (Etheridge et al. 1996, Indermühle et al. 1999) supports the idea that the BCP is in a balanced and closed loop. However, past records suggest that changes in the BCP caused drastic fluctuations in atmospheric CO_2 between glacial and interglacial periods (Boyle 1988, Broecker 1982, Martin 1990, Sarmiento & Toggweiler 1984, Siegenthaler & Wenk 1984). It therefore seems clear that we cannot assume that the BCP will remain in steady state during future climate change. Yamamoto et al. (2018) suggested that circulation change and lower nutrient supply to the surface ocean will reduce the efficiency of the BCP and be the main driver for reduced future oceanic CO_2 uptake. Furthermore, recent discoveries of overlooked biological pumps (see Boyd et al. 2019, Jiao & Zheng 2011, Legendre et al. 2015) show that there are still considerable gaps in our understanding of the biological processes in the BCPs and even larger gaps in how we model these processes.

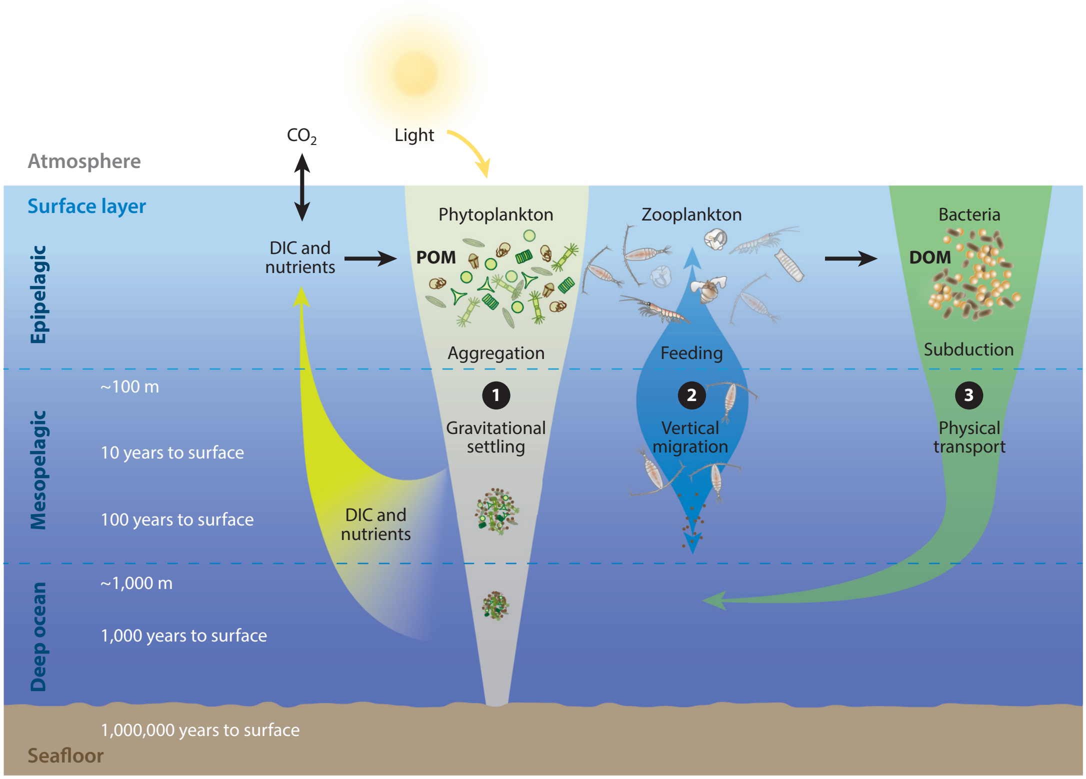


Figure 1

Overview of the BCP. Phytoplankton fix CO$_2$ into POM via photosynthesis in the euphotic zone. The main export processes within the BCP are (❶) aggregation and gravitational settling, (❷) grazing in the surface and fecal pellet production at depth by vertically migrating zooplankton, and (❸) subduction of DOM via physical transport. Organic matter is converted to DIC and nutrients by bacterial remineralization during sinking. The depth of remineralization determines how long the carbon is removed from the atmosphere. Abbreviations: BCP, biological carbon pump; DIC, dissolved inorganic carbon; DOM, dissolved organic matter; POM, particulate organic matter.

3. MECHANISMS OF CARBON EXPORT IN THE BIOLOGICAL CARBON PUMP

To a large extent, the gaps in our understanding of the BCP stem from the traditional biogeochemical approach of extrapolating one-dimensional particle fluxes using large-scale models and remote sensing (e.g., Siegel et al. 2014). This one-dimensional view cannot capture complex biological processes that vary temporally and spatially. Furthermore, many approaches, such as the use of sediment traps, are designed to capture and quantify particles that sink gravitationally, as for many years, it has been assumed that sinking particles are the main vectors of carbon export within the BCP. Yet there is a growing awareness that gravitational settling is not the only mechanism by which carbon is exported to depth.

Boyd et al. (2019) recently defined five additional particle injection pumps and estimated that, combined, they may contribute carbon fluxes comparable to those associated with gravitationally settling particles—the biological gravitational pump. The injection pumps can be separated into three physical subduction processes (Dall'Olmo et al. 2016, Levy et al. 2013, Omand et al. 2015,

Carbon flux attenuation: loss of POC from the pool of settling aggregates through the water column, resulting in a decrease in total POC flux with increasing depth

Net primary production: the difference between organic carbon produced and respired by primary producers per area and time

Sequestration flux: POC export that is removed from exchange with the atmosphere on a long timescale, typically to depths below 1,000 m

Stukel et al. 2017) and two biological pumps related to zooplankton migration (Bianchi et al. 2013, Steinberg & Landry 2017). The physical subduction pumps are separated according to the depth that they export carbon to and therefore the timescale that they sequester carbon for. These pumps are (*a*) the mixed-layer pump, which refers to the subduction of organic matter associated with the shallowing of the mixed layer, which transports carbon tens of meters and therefore sequesters it only on short timescales; (*b*) the eddy-subduction pump, which occur on scales of up to 100 km and hundreds of years; and (*c*) the large-scale subduction pump, which is related to the ocean circulation and operates on scales of up to 1,000 km and 1,000 years (see Boyd et al. 2019, Dall'Olmo et al. 2016, Levy et al. 2013, Omand et al. 2015, Stukel et al. 2017). The two biological pumps are (*a*) the mesopelagic-migrant pump, which refers to the diurnal vertical migration of zooplankton that feed at the surface during night and migrate to depth during the day, where they egest and respire part of the material ingested at the surface, and (*b*) the seasonal lipid pump, which refers to zooplankton that perform seasonal hibernation at depth during winter at high latitudes and survive by catabolizing carbon-rich lipids that were accumulating in the surface ocean during summer (Boyd et al. 2019, Jónasdóttir et al. 2015, Steinberg & Landry 2017, Steinberg et al. 2008).

The most important of the five particle injection pumps in terms of carbon export is the mesopelagic-migrant pump, which alone may globally store additional carbon at levels equivalent to 60% of that what is stored by the biological gravitational pump. Still, subduction processes can be locally very important, and Swoboda et al. (S. Swoboda, H. Marchant, S. Ahmerkamp, J.-H. Hehemann, H. Buck-Wiese, et al., manuscript in review) found that lateral advection and subduction of slow-settling aggregates from the shallow shelf contributed up to 80% of the open ocean carbon export at 2,000-m depth in the upwelling region off Cape Blanc, northwest Africa. Taking the additional carbon sequestered by the particle injection pumps into account might make it possible to resolve the mismatch between export fluxes derived from biogeochemical tracers (settling and suspended organic particles at depth), which are often two- to threefold larger than those measured with sediment traps (only gravitational settling particles) (e.g., Emerson 2014).

4. CARBON FLUX ATTENUATION

Globally, phytoplankton fix approximately 50 Pg of carbon per year in the oceans (Carr et al. 2006, Kulk et al. 2020); however, the vast majority of the carbon is remineralized as it sinks through the water column. Spatial and temporal differences in this so-called carbon flux attenuation are a key topic in BCP research, as on average, if carbon is remineralized in the upper 1,000 m of the ocean, we assume that it can be readily exchanged with the atmosphere (although this may differ for DOC that is transformed by the microbial carbon pump, which is not covered here; see Jiao & Zheng 2011, Legendre et al. 2015). By contrast, when carbon is remineralized below 1,000 m, it is sequestered for hundreds of years (Bopp et al. 2001, Kwon et al. 2009, Passow & Carlson 2012, Primeau 2005). Typically, only 5–25% of the net primary production sinks to depths below the euphotic zone (>100 m) (De La Rocha & Passow 2007). Organic matter that sinks out of the euphotic zone is generally termed the export flux. However, only 10% of the export flux reaches bathypelagic depths (>1,000 m), meaning that less than 3% of the net primary production is exported to 1,000-m depth, while more than 97% of the organic matter is hydrolyzed, remineralized, and utilized in the water column by bacteria, microzooplankton, and mesozooplankton. The fraction of carbon export that sinks below 1,000 m is considered sequestration flux. Finally, less than 1% of the net primary production eventually reaches the deep seafloor, where it can be sequestered for millennia (Ducklow et al. 2001). Carbon flux attenuation and its spatial distribution also have another important impact: When organic matter is remineralized, nutrients are also released. The depth at which nutrients are released influences elemental distributions in the oceans and as a result impacts other biogeochemical cycles, and furthermore determines upper limits for primary production in the following growth season (Passow & Carlson 2012).

While it is possible to describe carbon flux attenuation in the open ocean with broad strokes (i.e., attenuation is highest at the surface and decreases with increasing depth; e.g., Buesseler et al. 2008, Martin et al. 1987), there is still extensive discussion as to which mathematical function best describes the vertical shape of the carbon flux profile (Armstrong et al. 2002, Banse 1990, Cael & Bisson 2018, Kriest & Oschlies 2008, Lauderdale & Cael 2021, Lutz et al. 2002, Martin et al. 1987, Middelburg 1989, Suess 1980, Wotton 1994). Common to all suggested remineralization profiles is that they are derived from assumed particle settling velocities and degradation rates. The most famous of these remineralization profiles is the so-called Martin curve described in 1987, which is a power-law function that assumes that slow-settling and/or labile particles are degraded in the upper water column (Martin et al. 1987). This causes higher attenuation at shallow depths compared with greater depths. Many studies have since aimed to constrain the flux attenuation coefficient (the exponent *b*) in the Martin curve to identify one globally optimal *b* value. However, *b* tends to have large regional and seasonal variations and even substantial global variability (Gloege et al. 2017, Kriest et al. 2012, Kwon & Primeau 2008, Kwon et al. 2009). This is perhaps unsurprising, since *b* in effect represents the biological processes that lead to attenuation as organic matter sinks through the water column. Therefore, in order to represent the BCP in Earth system models, we need to understand the complex biological processes that determine *b*.

Remineralization profile: a mathematical function to describe carbon flux attenuation

Earth system model: a model that includes all components of the Earth system, including physical, chemical, and biological processes in all habitats

4.1. Modeling Carbon Flux Attenuation

Cael & Bisson (2018) compared seven models that have been used to describe POC flux over depth and found that all of them were within the variabilities of in situ measurements; hence, there was not one model that was significantly better than another. However, they suggested that the exponential (Banse 1990) and power-law (Martin et al. 1987) models could be used as lower and upper bounds for functional extrapolation of depth-corrected POC flux, respectively. The exponential model considers POC flux attenuation to be a remineralization length scale [L (m)]—that is, the ratio of remineralization rate [r (d^{-1})] to sinking velocity [w (m d^{-1})], representing the vertical distance a particle settles before it is completely degraded:

$$L = \frac{w}{r}. \qquad 1.$$

The power-law model considers POC flux attenuation to be a time-dependent (i.e., depth-dependent for settling aggregates) decrease in the remineralization rate. This means that the unitless *b* in the Martin curve is the remineralization rate [r (d^{-1})] multiplied by the ratio of the vertical sinking distance [z (m)] to the settling velocity [w (m d^{-1})]—that is, *b* is the remineralization rate of the POC flux after one day of degradation and settling:

$$b = r \cdot \frac{z}{w}. \qquad 2.$$

The power-law function, or the Martin curve, is

$$F_z = F_{z_{\mathrm{eu}}} \cdot \left(\frac{z}{z_{\mathrm{eu}}}\right)^{-b}, \qquad 3.$$

where F_z is the fraction of the POC flux from the base of the euphotic zone that sinks through the depth horizon z; $F_{z_{eu}}$ and z_{eu} are the POC flux and depth at the base of the euphotic zone, respectively; and b is the nondimensional exponent that controls for how F_z decreases with increasing depth (Equation 2). Martin et al. (1987) found b to be 0.858, but as mentioned above, other studies have found large variations in b depending on region (Guidi et al. 2015, Henson et al. 2012, Pavia et al. 2019), temperature (Marsay et al. 2015), microbial community composition (Boyd & Newton 1999), particle composition (Armstrong et al. 2002, Wiedmann et al. 2020), oxygen concentration (Devol & Hartnett 2001), particle aggregation (Gehlen et al. 2006, Niemeyer et al. 2019, Schwinger et al. 2016), or mineral ballasting (Gehlen et al. 2006, Pabortsava et al. 2017).

The most obvious difference between the exponential and power-law models is that the exponential model does not have changing attenuation with increasing depth, while the power-law model has decreasing attenuation with increasing depth (Cael & Bisson 2018). It therefore seems that the power-law model represents in situ biological processes better than the exponential model, and here I focus only on the power-law model (i.e., the Martin curve).

4.2. Estimating Carbon-Specific Degradation from Flux Profiles

Independent of the actual function used to model the POC flux profile, it is clear that there is high attenuation in the upper few hundred meters of the ocean and less attenuation in the deep ocean. Therefore, by examining the rate of change of POC flux over depth, we can gain insights into the processes taking place at different depth layers. As an example, **Figure 2*a*** plots the open ocean POC flux estimates provided by Martin et al. (1987). It seems that the POC flux profile has four depth layers with different attenuation rates: (*a*) rapid attenuation in the upper water

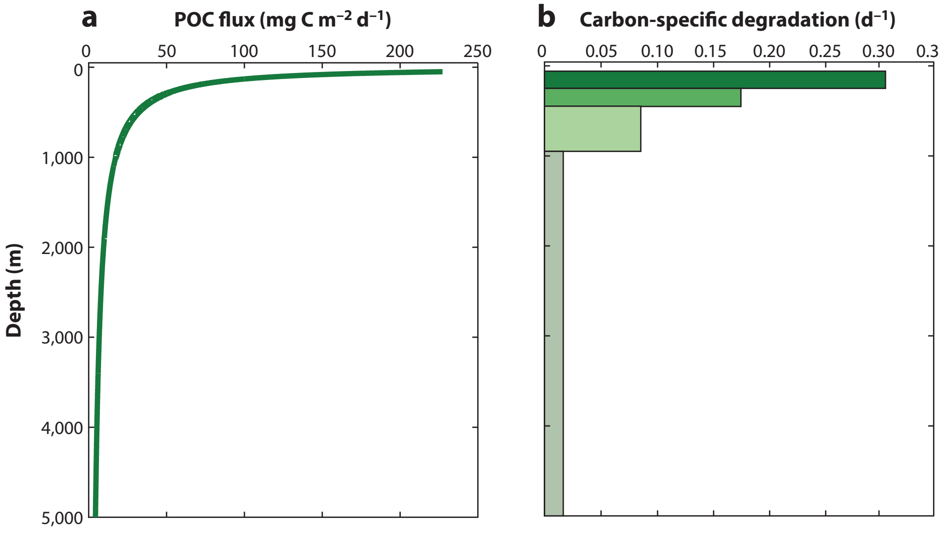


Figure 2

(*a*) Vertical POC flux plotted over depth, replotted from Martin et al. (1987). (*b*) Carbon-specific degradation rates (C_{spec}) calculated (using Equation 6) for the depth intervals 50–300 m, 300–500 m, 500–1,000 m, and 1,000–5,000 m. The resulting rates were 0.31, 0.18, 0.09, and 0.02 d^{-1} for these four depth layers, respectively. Abbreviation: POC, particulate organic carbon.

column, especially at the depths of the interface between the epi- and mesopelagic (between 50 and 300 m), suggesting that the upper mesopelagic depth layer has high biological activity (Iversen et al. 2010, Jackson & Checkley 2011, Stemmann et al. 2004); (*b*) intermediate attenuation in the mid-mesopelagic, between 300 and 500 m; (*c*) a second intermediate attenuation in the lower mesopelagic, between 500 and 1,000 m, with less attenuation than the mid-mesopelagic layer; and (*d*) low, quasi-constant attenuation in the deep bathypelagic, at depths greater than 1,000 m. If we assume a constant average particle settling velocity for particles at all depths [w_{av} (m d^{-1})], similar to direct in situ measurements of aggregate settling velocities (Alldredge & Gotschalk 1988, Diercks & Asper 1997, Iversen & Lampitt 2020, Nowald et al. 2009, Pilskaln et al. 1998), we can use the POC flux profiles to estimate the carbon-specific degradation rate for the four depth layers. By assuming a constant average settling velocity of 100 m d^{-1}, we can estimate the POC concentration [POC_{conc} (g m^{-3})] of the settling aggregates at the top of each depth layer:

$$POC_{\mathrm{conc}} = \frac{w_{\mathrm{av}}}{F_{\mathrm{top}}}, \tag{4.}$$

where F_{top} is the POC flux (g m^{-2} d^{-1}) at the top of each depth layer. We can use the slope between depth and POC flux through each depth layer to estimate the loss rate of POC per volume water [POC_{loss} (g m^{-3} d^{-1})] in the depth layer:

$$POC_{\mathrm{loss}} = -1 \cdot \frac{\Delta F}{\Delta z}, \tag{5.}$$

where ΔF and Δz are the differences in POC flux (g m^{-2} d^{-1}) and depth (m) between the upper and lower bounds of the depth layer, respectively, which are equivalent to the average losses of carbon per cubic meter (the multiplication by -1 is to give the loss rate as a positive value). By normalizing POC_{loss} by the concentration of settling POC [POC_{conc} (g m^{-3})] at the top of the depth layer, we can estimate the carbon-specific degradation rate for each depth layer [C_{spec} (d^{-1})]:

$$C_{\mathrm{spec}} = \frac{POC_{\mathrm{loss}}}{POC_{\mathrm{conc}}}. \tag{6.}$$

Calculating the C_{spec} for the different depth layers gives rates of 0.31, 0.18, 0.09, and 0.02 d^{-1} for the upper mesopelagic, mid-mesopelagic, lower mesopelagic, and bathypelagic, respectively (**Figure 2*b***). We can then dissect which processes might be responsible for this attenuation. At temperatures typical for the upper mesopelagic and mid-mesopelagic (~15°C) at the low to mid-latitudes where Martin et al. (1987) measured POC flux, the microbial C_{spec} values of settling aggregates vary between 0.08 and 0.20 d^{-1} (Grossart & Ploug 2001, Iversen & Ploug 2013, Iversen & Robert 2015, Iversen et al. 2010, Ploug & Grossart 1999). This suggests that the C_{spec} of 0.31 d^{-1} in the upper mesopelagic cannot be explained by microbial degradation alone, while the C_{spec} in the mid-mesopelagic and lower mesopelagic can. Therefore, as flux attenuation in the upper few hundred meters of the water column exceeds measured microbial remineralization rates, this indicates that both zooplankton and microorganisms are responsible for the high flux attenuations in the upper mesopelagic (Iversen et al. 2010, 2017; Jackson & Checkley 2011; Pauli et al. 2021; Stemmann et al. 2004; van der Jagt et al. 2020). As direct measurements have shown that the microbial C_{spec} values of marine snow and zooplankton fecal pellets do not vary significantly with particle size, type, age, or composition (Grossart & Ploug 2001, Iversen & Ploug 2010, Iversen & Robert 2015, Ploug & Grossart 1999), it is also logical to conclude that POC flux variability in the upper mesopelagic is driven largely by the presence of zooplankton that intercept and graze on

Coprophagous zooplankton: zooplankton that feed on fecal pellets; coprophagy has been observed for copepods and dinoflagellates

and/or fragment the settling aggregates (e.g., Briggs et al. 2020, Buesseler et al. 2007, Steinberg et al. 2008, Wilson et al. 2008). Due to decreasing zooplankton abundances with increasing depth, microbial degradation becomes the main attenuation process below the upper mesopelagic (e.g., Stemmann et al. 2004). The low C_{spec} in the bathypelagic suggests that the microbial degradation is limited, possibly by increasing pressure and decreasing temperatures with increasing depth (Grossart & Gust 2009, Iversen & Ploug 2013, Nagata et al. 2010, Tamburini et al. 2002). It is also possible that changes in the organic matter composition limit specific metabolic processes (e.g., Datta et al. 2016). The following sections detail the important biological processes for flux attenuation in the various depth layers.

5. THE ROLE OF ZOOPLANKTON AS GATEKEEPERS FOR PARTICULATE ORGANIC CARBON FLUX

After aggregates are formed and sink out of the epipelagic, there generally seems to be a sharp decrease in POC flux with increasing depth at the boundary between the epi- and mesopelagic layers (Buesseler et al. 2008, Iversen et al. 2010, Martin et al. 1987). This strong flux attenuation has been associated with intense biological turnover of the settling aggregates at the base of the euphotic zone (e.g., Iversen et al. 2010, Jackson & Checkley 2011, Lampitt et al. 1993, Olli et al. 2001, Stemmann et al. 2004, Wassmann et al. 2003). Since zooplankton abundances often correlate with the depths of high flux attenuation, it seems that zooplankton feeding on settling aggregates in the upper mesopelagic is responsible for a substantial fraction of the attenuation (Christiansen et al. 2018, Forest et al. 2011, Jackson & Checkley 2011, Möller et al. 2012, Napp et al. 1988, van der Jagt et al. 2020, Whitmore & Ohman 2021). In this way, zooplankton have been defined as gatekeepers for POC flux at the base of the euphotic zone (Jackson & Checkley 2011). This idea has been confirmed by laboratory experiments in which several zooplankton species fed directly on marine snow and fecal pellets (e.g., Cavan et al. 2021, Dilling & Brzezinski 2004, Green & Dagg 1997, Iversen & Poulsen 2007, Koski et al. 2005, Lampitt et al. 1990, Lombard et al. 2013, Noji et al. 1991, Poulsen & Kiørboe 2005, Steinberg 1995, Steinberg et al. 1994).

However, it has proven difficult to quantify the importance of zooplankton feeding on aggregates in situ, and zooplankton-mediated attenuation ranges from 8% to 70% of the total POC flux attenuation in the upper water column (Mayor et al. 2014, Steinberg et al. 2008, van der Jagt et al. 2020). Such a large range is not surprising since zooplankton can impact POC flux and flux attenuation in several ways: (*a*) Filter-feeding zooplankton can regulate the concentration of phytoplankton and, as a result, net primary production, which will decrease POC flux via a top-down control (e.g., Hernández-Leon & Ikeda 2005); (*b*) zooplankton can ingest small, slow-sinking cells and turn them into large, fast-settling fecal pellets, which may increase POC flux (Dubischar & Bathmann 2002, Ducklow et al. 2001, Fortier et al. 2002); (*c*) zooplankton can fragment large, fast-settling aggregates into smaller and slower-sinking particles, reducing the efficiency of the BCP (Briggs et al. 2020, Cavan et al. 2021, Dilling & Brzezinski 2004, Dilling et al. 1998, Goldthwait et al. 2005, Iversen & Poulsen 2007); (*d*) zooplankton can increase export via vertical migration, which increases POC flux in the middle and lower mesopelagic but increases the attenuation in the upper mesopelagic, where they ingest and fragment settling aggregates (e.g., Steinberg et al. 2008); and (*e*) flux feeders, such as pteropods and polychaetes, may expand feeding nets below the maximum particle concentration and intercept and capture the settling aggregates (Christiansen et al. 2018, Jackson 1993, Silver & Bruland 1981). In general, then, the importance of the various types of zooplankton–aggregate interactions can also be described over depth, with aggregate feeding occurring at the flux maxima, flux feeding occurring below the flux maxima, and coprophagous zooplankton and protozooplankton, such as copepods and dinoflagellates, occurring in the

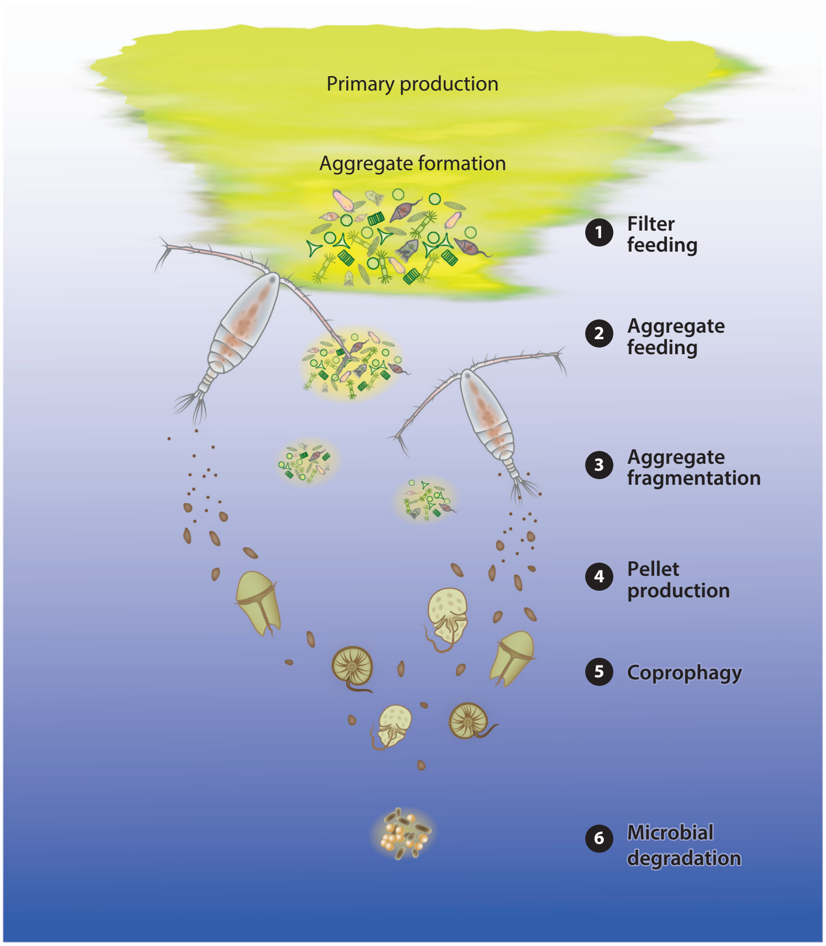


Figure 3

Vertical perspective on zooplankton–aggregate interactions. After primary production and aggregate formation in the surface ocean, zooplankton can impact the POC flux and flux attenuation in several ways: (❶) zooplankton filter feeding packages single cells into fecal pellets in the chlorophyll maximum; (❷) zooplankton ingestion of settling aggregates decreases the POC flux by removing carbon via ingestion, respiration, and assimilation; (❸) zooplankton can encounter and fragment large, fast-settling aggregates, which reduces the size and settling velocity of the aggregates; (❹) zooplankton produce fecal pellets, which themselves are settling organic aggregates; (❺) coprophagous zooplankton, such as dinoflagellates, feed on settling fecal pellets; and (❻) the aggregates that escape ingestion and fragmentation by zooplankton are further degraded by microbes in deeper waters. Abbreviation: POC, particulate organic carbon.

mid-mesopelagic, below the depth of pellet producers (Iversen & Poulsen 2007, Lampitt et al. 1990, Poulsen & Iversen 2008, Poulsen et al. 2011, Svensen et al. 2012) (**Figure 3**).

6. MICROBIALLY MEDIATED FLUX ATTENUATION

The aggregates that escape the intense transformation and turnover by microbes and zooplankton in the upper mesopelagic are exposed to microbial degradation primarily in the mid-mesopelagic. Typically, concentrations of aggregate-associated microbes exceed those in the ambient water by

VERTICAL CONNECTIVITY

Until the last decade, little was known about the microbial community composition and dynamics associated with marine snow below the depths that could be reached by scuba divers. It was apparent, however, that aggregates seemed to harbor diverse microbial communities (Azam 1998). This led to a debate about where these communities came from: Were they primarily seeded in the upper water column, or did prokaryotes and eukaryotes continue to hop on and off during sinking (Kiørboe et al. 2003)? With the advent of next-generation sequencing technologies and improved in situ collection tools such as the Marine Snow Catcher, we have started to be able to answer such questions. In fact, it seems as though particles are colonized largely when they form in the mixed layer, after which an ecological succession of taxa occurs in response to heterotrophic degradation, internal competition, predation, and changes in temperature and pressure (Bachmann et al. 2018, Cram et al. 2014, Fadeev et al. 2021, Grossart & Gust 2009, Iversen & Ploug 2010, Iversen et al. 2010, Mestre et al. 2018, Tamburini et al. 2009, Thiele et al. 2015). As such, sinking aggregates act as vehicles that transport microorganisms from the surface to the deep sea, enhancing oceanic microbial connectivity.

one to several orders of magnitude (Alldredge & Silver 1988, Azam 1998, Thiele et al. 2015), making settling aggregates such as marine snow and fecal pellets hot spots for microbial activity in the deep ocean (Azam 1998). It is important to note that aggregate-associated microbes include not only prokaryotes but also heterotrophic nanoflagellates and ciliates (Alldredge et al. 1986, Iversen & Robert 2015, Kiørboe 2001, Silver et al. 1978, Turley & Mackie 1994). Thus, each settling aggregate contains a whole microcosm comprising more than one trophic level where microbes interact, compete, and predate (**Supplemental Video 1**).

Supplemental Material >

As aggregates sink deeper in the water column, the C_{spec} calculations show that the degradation decreases from 0.18 to 0.02 d^{-1} from the mid-mesopelagic to the bathypelagic (**Figure 2*b***). This decrease is hypothesized to be due to the response of the aggregate-associated microbial community to increasing pressure, decreasing temperature, and changing carbon and nutrient sources within aggregates with increasing depth (Datta et al. 2016, Grossart & Gust 2009, Iversen & Ploug 2013, Nagata et al. 2010, Tamburini et al. 2009). This response is in turn hypothesized to occur because the majority of bacteria within deep-ocean aggregates seem to originate from bacterial communities in the surface ocean (Bachmann et al. 2018, Cram et al. 2014, Fadeev et al. 2021, Mestre et al. 2018, Thiele et al. 2015) (see the sidebar titled Vertical Connectivity). Upon sinking out of the surface ocean, only some microbes have physiological pressure adaptations that allow them to maintain their metabolic and respiratory activity with increasing depth (Grossart & Gust 2009, Nagata et al. 2010, Tamburini et al. 2009). Hence, depending on the bacterial community composition within aggregates, this could cause a decrease in the microbial degradation with increasing depth. Additionally, when aggregate-associated microbes adapted to surface waters with temperatures of 15°C were exposed to deep-ocean temperatures of 4°C, C_{spec} decreased 3.3-fold (Iversen & Ploug 2013), which is similar to the observed C_{spec} decrease between the mid-mesopelagic and the bathypelagic (**Figure 2*b***).

Furthermore, by considering only the temperature effects on C_{spec}, Iversen & Ploug (2013) found that the predicted POC flux to the deep ocean matched POC flux measurements from globally deployed sediment traps. This finding suggests a strong temperature dependence in C_{spec} in the deep ocean, resulting from aggregate-associated bacteria that originated from shallower and warmer waters. It is unclear whether organic matter in aging aggregates can limit degradation by becoming refractory or protected by mineral structures in the aggregates (Armstrong et al. 2002; Iversen & Ploug 2010; Ploug et al. 2008a,b; van Mooy et al. 2002). However, a study by

AGGREGATE SETTLING

Since the settling velocity of organic matter determines the time available for degradation in the upper ocean, it is a key goal of oceanography to identify the controlling mechanisms for aggregate settling. For a long time, aggregate size was considered a key predictor of settling velocity, and Stokes's law was generally used to estimate aggregate settling velocities (see Passow & De La Rocha 2006). However, when comparing different types of aggregates, it is clear that aggregate size is less important for sinking velocity than excess density (e.g., Diercks & Asper 1997, Iversen & Lampitt 2020, Iversen & Ploug 2010). Hence, our previous view of a positive relationship between aggregate size and sinking velocity stems from past laboratory studies where aggregates had similar composition (e.g., Iversen & Ploug 2013; Ploug et al. 2008a,b). However, this positive size-to-settling relationship falls apart when viewed across a pool of heterogeneous aggregates in situ (e.g., Alldredge & Gotschalk 1988, Diercks & Asper 1997, Iversen & Lampitt 2020, Nowald et al. 2009). It therefore seems that size-specific settling velocities are controlled by their excess densities, rather than aggregate size, and without direct measurements it is difficult to predict in situ settling velocities.

Datta et al. (2016) suggested that successions and interactions between prokaryotic primary and secondary consumers within settling aggregates may cause community-wide metabolic shifts that could limit microbial degradation rates in aging aggregates.

7. OTHER BIOLOGICAL PROCESSES THAT IMPACT FLUX ATTENUATION

The example above used a very simplified system with an average settling velocity of 100 m d^{-1}. Of course, this does not mean that all particles were sinking with the same velocity; rather, the pool of particles on average sank at 100 m d^{-1} (see the sidebar titled Aggregate Settling). While this simplification allows us to estimate C_{spec} for different depth layers, there are still many other particle-associated factors that impact export and attenuation, including size-, density-, and type-specific settling velocities, which are again dependent on the aggregate composition and its ballasting, temperature-dependent degradation rates, and aggregation and disaggregation at depth (e.g., production of fecal pellets and fragmentation of aggregates by zooplankton). Furthermore, while at first it seems that zooplankton have the most influence in shallow water, it should be noted that they not only are important for attenuation, but also can contribute to flux by feeding in surface waters at night and descending to depths during the day, where they then defecate (Schnetzer & Steinberg 2002; Steinberg et al. 2002, 2008). The active flux can account for 0–70% of the total POC flux (see Turner 2015). However, the significant mismatches between mesopelagic carbon demand and POC attenuation indicate that we do not understand the drivers of spatial and temporal variability in organic matter production, transformation, export, and attenuation or their relationship to food web structure (Anderson & Tang 2010, Burd et al. 2010, Reinthaler et al. 2006, Steinberg et al. 2008).

Active flux: direct transport of organic matter from the surface to the deep ocean via vertically migrating zooplankton

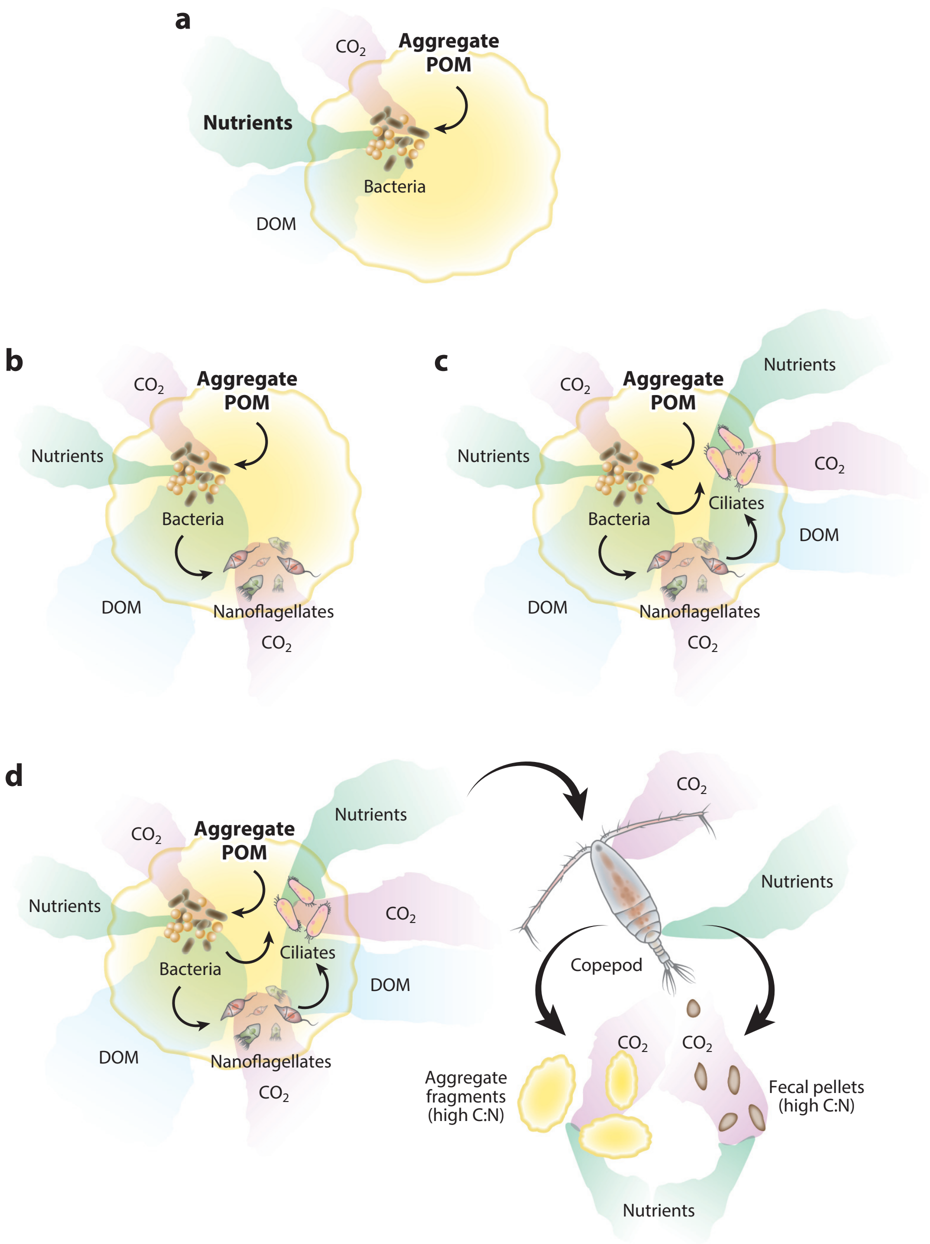
8. ORGANIC MATTER TRANSFORMATION IN SETTLING AGGREGATES

Organic matter is transported through the water column in many forms, including single phytoplankton cells, small aggregates, marine snow, fecal pellets, and dead animals (see Turner 2015). Though there has been a traditional focus on large, fast-settling aggregates in BCP research, there is increasing acknowledgment that slow-sinking aggregates and single cells can be the dominant vector for carbon flux seasonally and regionally (Puigcorbé et al. 2015, Richardson & Jackson 2007). An important contributing mechanism to the production of slow-settling aggregates is aggregate fragmentation by zooplankton (Briggs et al. 2020, Iversen & Poulsen 2007, Iversen et al. 2017, Lampitt et al. 1990), which causes the smaller aggregate fragments to sink more slowly than the original aggregates, thereby increasing their residence time in a depth layer. Fragmentation of aggregates by zooplankton is most frequent at the interface between the epi- and mesopelagic, where both aggregates and zooplankton have high abundances (**Figure 3**). The extended retention time of the aggregate fragments at the base of the euphotic zone has been suggested to encourage microbial colonization and thereby the microbial food web within aggregate fragments (Cavan et al. 2021, Giering et al. 2014, Mayor et al. 2014). In this way, there is a trophic upgrading of the aggregated organic matter, where it is transformed from detritus to a range of labile unsaturated fatty acids via de novo synthesis by bacteria and heterotrophic protists (Mayor et al. 2014). This hypothesis is supported by observations of more labile compounds on small, slow-settling aggregates compared with large, fast-settling aggregates (Alldredge & Silver 1988, Alonso-González et al. 2010, van Mooy et al. 2002). The older and more transformed, or trophic-upgraded, aggregates thereby become a better food source for zooplankton compared with younger aggregates that are composed primarily of phytoplankton detritus, a process called microbial gardening (Mayor et al. 2014). Mayor et al. (2014) further pointed out that aggregate fragmentation and subsequent increased microbial activity in the upper water column ultimately causes a reduction in the amount of exported carbon, that is, a reduction in the efficiency of the BCP.

9. STOICHIOMETRIC TRANSFORMATION OF SETTLING AGGREGATES

Research on the BCP tends to focus on the mechanisms that control how much carbon escapes the upper ocean, and very little emphasis is placed on the fate and form of the organic matter that is recycled in the surface ocean. Generally, it is assumed that since remineralization reduces the magnitude of carbon export, it decreases the efficiency of the BCP. Yet remineralization results in higher carbon-to-nutrient ratios of the degraded aggregates, due to preferential recycling of nutrients over carbon by bacteria (Grossart & Ploug 2001, Hach et al. 2020). Studies have shown that microbial remineralization is often associated with high nutrient release from aggregates (Cabanes et al. 2017, Karthäuser et al. 2021, Sabatini & Kiørboe 1994) and that such released nutrients can fertilize primary production, greatly extending the productive bloom period (Böckmann et al. 2021, Sarthou et al. 2008, Schmidt et al. 2011). These findings offer a new perspective on the role of heterotrophic activity in the efficiency of the BCP: When viewed over a whole season, aggregate fragmentation and heterotrophic activity at the base of the euphotic zone may increase the overall efficiency of the BCP by promoting export of carbon-rich aggregates, while nutrients are retained and fertilize the surface ocean, and thus extend the period of primary production.

From the few existing studies, it seems that zooplankton in particular may govern a preferential export of carbon-rich aggregates, since their fecal pellets tend to have severalfold-higher carbon-to-nitrogen ratios than phytoplankton and marine snow (Daly et al. 1999, Gerber & Gerber 1979). Furthermore, zooplankton fecal pellets tend to be small and compact, and they may contain similar amounts of carbon and sink with similar velocities as marine snow aggregates that are several times larger than the fecal pellets (e.g., Iversen & Ploug 2010). This means that a preferential export of zooplankton fecal pellets will increase the amount of carbon that is exported per unit nitrogen compared with a situation when single phytoplankton cells or marine snow dominate the export flux (**Figure 4**), which could explain observations of drastically increasing carbon-to-nitrogen ratios in exported organic matter with increasing depth (Fischer et al. 2019, Martin et al. 1987, Tamelander 2013). Currently, however, this mechanism is generally not included in biogeochemical models that use nitrogen as their currency and convert nitrogen into carbon via the Redfield ratio (i.e., 6.6 mol carbon per 1 mol nitrogen). This continuous recycling of nutrients in the surface ocean while carbon is preferentially exported to depth may fertilize the surface ocean and support extended periods of primary production, which allow more CO_2 uptake from the atmosphere (**Figure 5**). Continuous nutrient recycling and upper-ocean fertilization may increase in a warmer future ocean where higher temperatures increase biological



(Caption appears on following page)

Figure 4 (*Figure appears on preceding page*)

Organic matter transformation within aggregates. (*a*) When a settling aggregate is degraded only by bacteria, nutrients are released into the surrounding water, which may prolong primary production if it takes place in the euphotic zone. As the aggregate is degraded, its carbon-to-nitrogen ratios increase; hence, a substantial amount of carbon is exported per unit nitrogen, resulting in an efficient BCP. (*b*) When a predator, such as a nanoflagellate, feeds on the bacteria, there will be a trophic transfer of organic matter from bacteria to the nanoflagellate, with a substantial carbon loss via respiration. Furthermore, less nutrients are released and less carbon is exported per unit nitrogen, leading to a less efficient BCP. (*c*) When a second predator, such as a ciliate, is present, the food chain becomes even longer, and more carbon is lost through respiration. Furthermore, if the ciliate predates the nanoflagellates, it reduces the pressure on the bacteria, and hence the bacteria remineralize more organic nitrogen. However, if the ciliate feeds on the bacteria, then less organic nitrogen is remineralized by the bacteria. (*d*) When zooplankton feed on aggregates, they can either fragment them or ingest them and package the organic matter into fecal pellets. Both aggregate fragments and fecal pellets have higher carbon-to-nitrogen ratios than the original aggregate; hence, more carbon is exported per unit nitrogen, leading to a more efficient BCP. Abbreviations: BCP, biological carbon pump; DOM, dissolved organic matter; POM, particulate organic matter.

activity (e.g., Cavicchioli et al. 2019) and make for more efficient nutrient recycling and higher rates of primary production. However, future oceans may also shift toward higher stratification and less ballasted aggregates (e.g., Hofmann & Schellnhuber 2009), which could hamper POC export in general and make the BCP very ineffective.

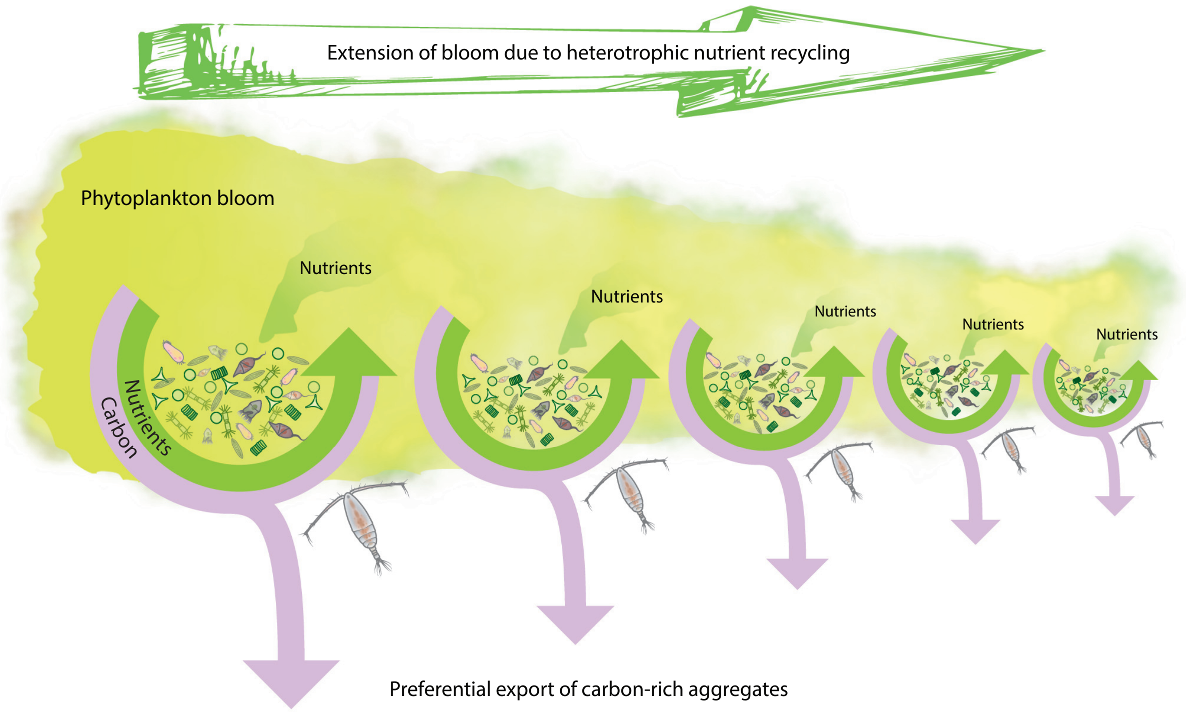


Figure 5

Preferential nutrient recycling. Continuous recycling of nutrients in the surface ocean while carbon is preferentially exported to depth may fertilize the surface ocean and support extended periods of primary production, which allows more CO_2 uptake from the atmosphere.

SUMMARY POINTS

1. The biological carbon pump (BCP) seems to have been in steady state for at least 3,000 years but is not guaranteed to remain so in response to global change.
2. Particle injection pumps other than gravitational settling may provide an additional particulate organic carbon export flux of similar magnitude to the gravitational settling of organic matter, but these pumps are still understudied.
3. Different mechanisms are responsible for flux attenuation over depth; zooplankton are gatekeepers of carbon flux out of the upper mesopelagic, whereas microbes dominate flux attenuation in deeper waters.
4. Microbial flux attenuation decreases with increasing depth as the communities that colonize aggregates in the upper water column respond to changes in temperature and pressure and transformations in the organic composition of settling aggregates.
5. While much attention has been paid to the mechanisms that control how much carbon escapes the upper ocean, we still lack an understanding of the fate and form of the organic matter that is recycled in the surface ocean.
6. Fragmentation of aggregates by zooplankton at the base of the euphotic zone increases the retention time of the fragmented aggregates, allowing more time for microbial colonization and growth. This may cause a trophic upgrading from detritus to labile fatty acids within the aggregates as the decaying phytoplankton is converted to microbial biomass, which in turn upgrades the quality of the aggregated organic matter, making the aggregates a more suitable food source for zooplankton.
7. Preferential nutrient recycling by heterotrophic organisms may retain nutrients in the surface ocean, where they fertilize further primary production, while carbon-rich aggregates are exported. This suggests that grazing, degradation, and remineralization at the base of the euphotic zone increase the efficiency of the BCP.

FUTURE ISSUES

1. We still do not understand flux attenuation processes well enough to predict how the biological pump will change in response to ocean warming, acidification, and stratification. As pointed out by Jackson & Checkley (2011), this stems from a disciplinary separation of the ocean, where biogeochemists tend to start measuring below the euphotic zone, while biologists stop measuring at that depth. In this way, the processes of production and flux have been separated not only spatially but also across disciplines. Closing knowledge gaps will require an interdisciplinary view of the full water column in order to gain a higher-resolution picture of upper-ocean attenuation.
2. The preferential uptake or release of nutrients within the BCP likely has important consequences for production and the efficiency of the BCP. However, more measurements of C:N:P:Fe:Si ratios of sinking particles are required and should be linked both to direct rate measurements and to modeling frameworks such as geometrical stoichiometry (Anderson et al. 2020). This will allow us to expand from a carbon-centric view and follow the export and transformations of the full elemental spectra of the organic matter.

3. We need to examine how microbial upgrading of aggregated organic matter and subsequent zooplankton grazing alter the biochemical and stoichiometric composition of the organic matter that sinks to the deep ocean and seafloor and subsequently impacts the efficiency of the BCP.
4. Implementation of long-term instrumentation to follow exported organic matter through the water column via direct measurements of aggregate types, composition, and sinking velocities will enable us to link surface processes to the biochemical and biogeochemical composition of exported organic matter.

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Errata

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