Biogeosciences Discuss., https://doi.org/10.5194/bg-2017-362
Manuscript under review for journal Biogeosciences
Discussion started: 29 August 2017

Reviews and Synthesis: To the bottom of carbon processing at the seafloor

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** Invited contribution by Jack J. Middelburg, recipient of the EGU Vladimir Vernadsky Medal 2016*

Abstract

Organic carbon processing at the seafloor is studied by geologists to better understand the sedimentary record, by biogeochemists to quantify burial and respiration, by organic geochemists to elucidate compositional changes and by ecologists to follow carbon transfers within food webs. Here I review these disciplinary approaches and discuss where they agree and disagree. It shown that the biogeochemical approach (ignoring the identity of organisms) and the ecological approach (focussing on growth and biomass of organisms) are consistent on longer time scales. It is hypothesized that secondary production by microbes and animals might impact the composition of sedimentary organic matter eventually buried. Animals impact sediment organic carbon processing by microbes in multiple ways: by governing organic carbon supply to sediments and by mixing labile organic matter to deeper layers. An inverted microbial loop is presented in which microbes profit from bioturbation rather than animals profiting from microbial processing of otherwise lost dissolved organic resources. Sediments devoid of fauna therefore function differently and are less efficient in processing organic matter with the consequence that more organic matter is buried and transferred from Vernadsky's biosphere to the geosphere.

1 Introduction

The seawater-sediment interface represents one of the largest interfaces on earth and our knowledge of processes at and fluxes through this dynamic and understudied interface is rather limited. This interface extends a few cm-dm upwards into the water column, i.e. benthic boundary layer (Boudreau and Jørgensen, 1992), as well as few cm-dm into the sediments, i.e. the bioturbated, active surface layer (Berner, 1980; Meysman et al., 2006; Aller, 2013). It serves as a habitat for organisms, governs the partitioning of material being buried or recycled and acts as a filter for the paleorecord (Rhoads, 1974). Processes in the surface sediment layer determine whether carbon is recycled within the biosphere (short-term cycle) or transferred to the geosphere (long-term cycle) and as such it functions as a key interface in the System Earth.

This pivotal role of the seafloor in processing material deposited has been studied by scientists from various disciplines with their own interests, techniques and paradigms (Figure 1). Marine geologists and paleoceanographers

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study sediments with the primary aim to extract information on past environmental conditions using down-core measurements of substances delivered to the seafloor and that have survived the processing at the seafloor (Burdige, 2006; Bender, 2013). Biogeochemists quantify the fate of material delivered, in particular how much of the material is eventually buried or processed, and determine when and in what form the remaining part is recycled to the water column, because recycling of key nutrients (e.g. N, P, Si, Fe) sustains primary production (Berner, 1980; Aller, 1980, 2001, 2013; Soetaert et al., 2000). Organic geochemists investigate how organic matter delivered to the seafloor is degraded, transformed or preserved using changes in the composition at the molecular level (Hedges and Keil, 1995; Dauwe et al, 1999; Burdige, 2006; Bianchi and Canuel, 2011). Ecologists focus on the organisms, i.e. the actors consuming, producing and transporting the material deposited (Gage and Tyler, 1992; Gray and Elliot, 2009; Herman et al., 1999; Krumins et al., 2013).

Although these disciplines often study the same topic, e.g. organic matter delivered to the seafloor, they focus on different aspects and usually ignore key concepts, findings and approaches from other disciplines. For example, ecologists and biogeochemist studying carbon flows at the seafloor normally ignore detailed molecular information available from organic geochemistry. Bioturbation, particle transport and mixing by animals at the seafloor , is often ignored by paleoceanographers, and biogeochemists have developed advanced transport-reaction models in which the actors, the animals, mix the particles but do so without consuming organic matter, their food.

Here I present the existing views on organic carbon processing at the seafloor, discuss where they agree and disagree and aim to arrive at an integrated view of carbon processing at the seafloor that is consistent with recent views within the organic geochemical, sediment geochemical, ecological and microbiological research communities. This overview is necessarily and admittedly incomplete but rather covers personal interests and presents new concepts on this topic. It is a concise version of the Vernadsky Medal Lecture presented at the 2017 EGU meeting.

2 Geochemists focus on quantification of burial and mineralization.

Organic matter delivered to marine sediments eventually is either mineralized and the metabolites (carbon dioxide and nutrients) accumulate in pore-waters and exchange with the overlying water, or it is not consumed and then buried through the steady accumulation of particles (Fig. 2). This geochemical view is highly simplified, but for that reason also quantitative and instructive (Berner, 1980; Boudreau, 1997; Aller, 2013). The percentage of organic matter buried varies from less than one % to a few tens % and is closely related with total sediment accumulation rate (Canfield, 1989, 1994; Middelburg et al., 1993). Since sediment accumulation rates are much higher in vegetated, coastal, deltaic, shelf and ocean-margin settings, the majority of organic matter burial occurs there, with organic carbon burial in deep-sea sediments accounting for <5 % (Berner, 1982; Duarte et al., 2005; Burdige, 2007). In the deep sea and other ~~low burial efficiency settings~~, almost all organic matter is degraded to inorganic carbon and organic matter degradation rates provide an excellent proxy for organic matter deposition (Jørgensen, 1982; Cai and Reimers, 1995;

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Glud, 2008). Organic matter degradation can be quantified via the consumption of oxygen, the production of dissolved inorganic carbon and through the use of pore-water data and diagenetic models (i.e. reaction-transport models for sediments). At steady state sediment oxygen consumption provides an accurate measure for total sediment organic matter degradation, independent whether organic matter is degraded aerobically (i.e. with oxygen) or anaerobically (with alternative electron acceptors such as nitrate, metal oxides, sulphate), because almost all reduced metabolites released (ammonium, manganese (II), iron(II), hydrogen sulfide and methane) are re-oxidized (Jørgensen, 1977, 2006; Berner and Westrich, 1985; Aller and Rude, 1988; Soetaert et al., 1996; Boetius et al., 2000; Strous and Jetten, 2004; Raghoebarsing et al., 2006; Middelburg and Levin, 2009).

Geochemists have adopted a transport-reaction modeling approach to accurately quantify organic matter processing (Berner, 1980; Boudreau, 1997; Burdige, 2006). The basic premise of these diagenetic models is that both particles and solutes are subject to transport and reaction, making them distinct from for instance groundwater transport-reaction models in which normally only solutes and gas phases are mobile. Transport of solutes is due to molecular diffusion, pore-water advection and biologically mediated processes~~;~~ enhanced diffusion due to interstitial fauna (Aller and Aller, 1992) and bio-irrigation due tube and burrow construction and flushing by macrofauna (Aller, 1980, 1984; 2001). Particle transport is not only due to steady particle deposition but also due to animal activities (bioturbation, Boudreau, 1997; Aller, 1994, 2013; Rice, 1986; Meysman et al., 2003, 2006, 2010). The reaction terms in these diagenetic models are normally limited to microbial and chemical reactions and described using zero, first, second order or Monod/Michaelis-Menten type kinetics (Bouldin, 1968; Berner, 1980; Soetaert et al., 1996; Boudreau, 1997). There is a major inconsistency in the basic conceptual model underlying the (numerical) diagenetic models: animals dominate transport processes via pore-water irrigation and particle mixing, but without consuming any organic matter. This ~~is~~ has not received much attention because the ruling paradigm within the microbial ecological and geochemical research communities is that animals contribute very little to total carbon processing. Multiple recent studies involving use of ^{13}C as deliberate tracers show that this premise does not hold on the short term (days to weeks; Blair et al., 1996; Moodley et al., 2002, 2005a; Woulds et al., 2009, 2016). Another reason for continuing with the simple approach is that our understanding of particle mixing due to animals is very limited (Meysman et al., 2006; 2010), that particle movement may require little energy because of fracturing (Dorgan et al., 2005) and that diagenetic models can very accurately reproduce most observations (Soetaert et al., 1996; Berg et al., 2003).

~~These~~ models combined with solid-phase and pore-water concentration vs. depth profiles, sediment-water exchange fluxes and rate measurement have resulted in a consistent picture of organic matter degradation pathways in marine sediments (Berner, 1980; Boudreau, 1997; Aller, 2013). These models can predict where, when and why organic matter oxidation occurs aerobically or involves nitrate, metal oxides or sulphate as oxidants (Rabouille and Gaillard, 2001; Boudreau, 1996; Soetaert et al., 1996; Middelburg et al. 1996; van Cappellen and Wang, 1996; Archer et al., 2002; Meysman et al., 2003; Berg et al., 2003). They also resolve the re-oxidation of reduced products such as ammonium, manganese(II), iron (II), sulfide and methane (Fig. 2) and as such define the scope for aerobic and anaerobic organisms and the distribution and activity of chemoautotrophs. Chemoautotrophs in sediments produce about 0.4 Tg C y^{-1}, similar to the riverine delivery of organic carbon to the ocean (Middelburg, 2011). ~~However, these~~ diagenetic models cannot predict organic carbon burial rates, nor do they provide much insight why organic matter is buried or why it is labile (reactive) or ~~rather~~ refractory. For this we need to have a detailed look at the organic geochemistry of sediment organic carbon.

3 Organic geochemists focus on the composition of organic matter preserved

Organic matter delivered to the seafloor is predominantly produced in the surface sunlit layer of the ocean (Fig. 3). This organic matter is rich in proteins, carbohydrates and lipids and follows Redfield stoichiometry (Bianchi and Canuel, 2011). Organic matter processing leads to preferential degradation of the more labile components with the result that organic matter becomes less reactive (Middelburg, 1989; Arndt et al., 2013) and organic matter composition changes (Fig. 1; Wakeham et al. 1997; Dauwe et al., 1999; Lee et al., 2000). The proportion of organic matter that can be characterized molecularly decreases with progressive degradation, i.e. with water depth or depth downcore (Wakeham et al., 1997; Hedges et al., 2000; Middelburg et al., 1999; Nierop et al., 2017). This molecularly uncharacterizable material increases to more than 70% in deep-sea organic matter. The organic geochemical approach to study organic matter processing is limited not only by our inabilities to characterize the majority of the sedimentary organic matter, but also by the simple fact that the degraded fraction cannot be studied and we have to base our knowledge on the small fraction of extensively processed organic material remaining.

The changes in organic matter composition due to organic matter processing have been utilized to estimate the lability-digestability or its reverse the refractory nature of organic matter with various proxies such as chlorophyll to bulk organic matter, fraction of nitrogen present as amino acid, and the contribution of proteins and carbohydrates to total organic matter (Cowie et al., 1992; Dell'Anno et al., 2000; Danovaro et al., 2001; Koho et al., 2013). The amino-acid based degradation index (Dauwe and Middelburg, 1998) is one of the most commonly used proxies to quantify the extent of degradation or the quality of the remaining particulate organic matter (Dauwe et al., 1999; Keil et al., 2000).

The compositional changes have also been used to infer transformation of organic matter by bacteria (production of bacterial transformation products; accumulation of D-amino acids; Cowie and Hedges, 1994; Dauwe et al., 1999; Grutters et al., 2001; Vandewiele et al., 2009; Lomstein et al., 2006, 2012), extent of degradation under oxic and anoxic conditions (Sinninghe Damsté et al., 2002; Huguet et al, 2008; Nierop et al., 2017) and the relative importance of bacterial and faunal pathways of organic matter degradation pathways (Sun et al., 1999; Woulds et al., 2012, 2014). Although some organic geochemical studies hint at the importance of secondary production (new organic matter produced by microbes and animals and other heterotrophs; Cowie and Hedges, 1994; Grutters et al., 2001; Lomstein et al., 2006, 2012), this aspect has received little attention in organic geochemistry, yet is one of the main objectives within the ecological approach.

4 Ecologists focus on the dynamics of organisms using organic matter

Benthic communities are usually partitioned into different size classes (e.g. macrofauna, meiofauna, microbes; Gage and Tyler, 1992; Gray and Elliot, 2009; Herman et al., 1999), which are often studied by different research communities having distinct objectives, approaches and tools. Organic matter delivered to the seafloor fuels benthic food webs: i.e. it represents food for the animals and the energy substrate for heterotrophic microbes. Microbial ecologists study the growth of microbes on delivered organic matter (e.g. bacterial production) and subsequent microbial loss processes, including predation and viral lysis (Kemp, 1988; 1990; Danovaro et al., 2008, 2011, 2016). Microbial ecologists also study in detail the identities and activities or organisms involved in (an)aerobic respiration pathways and the re-oxidation of reduced metabolites produced during anaerobic organic matter degradation (Canfield et al., 2005). Animal ecologists focus on the response of fauna to food delivery, the diet and growth of animals and transfer of carbon up the food chain to top consumers (Krumins et al., 2013; Fig. 3). Interactions among food-web members are considered key to understand carbon flows (Pimm et al., 1991; van Oevelen et al., 2010).

During the last two decades, isotopically labeled phytodetritus addition experiments have been performed to identify the organisms involved in the immediate processing of organic matter delivered to the seafloor (Middelburg, 2014). These studies often covered all size classes (animals and microbes) and could show that respiration was the major fate and that all size classes directly profited from recently deposited organic matter (Moodley et al., 2002, 2005a; Woulds et al., 2007, 2009, 2016; Witte et al., 2003). In other words, heterotrophic microbes and small and big animals compete for the same food. The relative share of organisms in the processing of organic matter was in some systems and for some consumers proportional to the biomass of the benthic size class, but not always (Moodley et al., 2005a; Woulds et al, 2009, 2016). For instance, foraminifera, amoebid protozoa, sometimes contribute disproportionally to short-term carbon processing reflecting high turn-over of an active community (Moodley et al., 2002; Woulds et al., 2007). The spatial distribution of resources is also a key factor governing the relative use of phytodetritus by bacteria vs. animals (van Nugteren et al., 2009b).

5 Towards a synthesis

The above discussion on conceptual views within different research disciplines highlights a few discrepancies and gaps in our knowledge. Secondary production by animals and microbes is not included in the geochemical view that focuses on preservation versus mineralization. It is also largely absent from the organic geochemical literature. Consumption of organic matter is restricted to microbes in the geochemical view, while the non-fed animals move organic matter, microbes and particles around by bioturbation and enhance solute transfer by bio-irrigation activities. The consumption of organic matter eventually results in compositional changes of the organic matter remaining but there is little information that the identity of the organism processing the organic carbon matters much. Whole ecosystem labeling experiments revealed direct flow from detritus to most benthic consumers and to the dissolved inorganic carbon pool, but these short-term experimental results cannot directly be compared to the long-term natural processing of deposited organic matter because long-term transfers in the food web and eventual carbon preservation cannot be resolved experimentally.

5.1 On the consistency of food-web carbon processing and the geochemical burial-respiration partitioning

Food webs describe the exchange of matter (e.g. carbon or energy) among different compartments (organisms) within an ecosystem (Pimm et al., 1991; de Ruiter et al., 1995) and thus formalize the ecological view on carbon processing (Cole et al., 2006; van Oevelen et al, 2010). The emphasis is on interaction among organisms and respiration losses are normally lumped into a single carbon dioxide loss term (Fig. 3 left). Experimental studies using ^{13}C labelled phytodetritus as a tracer of sediment carbon processing showed that animals and microbes both can assimilate labile carbon directly and confirmed that respiration is the largest sink (Moodley et al, 2005a; Buhring et al., 2006; Andersson et al. 2008; Woulds et al. 2009, 2016). The geochemical budgeting approach basically distinguishes only between (refractory) carbon preserved and buried versus labile organic carbon that is respired to carbon dioxide (Glud, 2008; Aller, 2013; Fig. 3 right). These ecological and geochemical concepts are consistent when the typical timescale of interest is considered. On the time scale of days to month deposited carbon is processed by the benthic organisms, a small part is assimilated and the majority is respired. On longer time scales and when considering steady-state conditions, i.e. constant faunal and microbial biomass, there is no net transfer from the detritus pool to the living biomass pool and all labile carbon is eventually respired because organisms only represent a (temporary) carbon sink when their biomass is building up or when remains of secondary producers are buried.

5.2 Secondary production and the formation of molecularly uncharacterizable organic matter.

The mere presence of living organisms in sediments clearly indicates that secondary production is omnipresent. Microbes usually dominate living biomass, but not always, and living biomass typically contributes a few % at most to the standing stock of total organic carbon in sediments (Herman et al., 1999). Various types of experimental evidence have shown that carbon flow through living compartment is much higher than through the non-living sediment organic matter pool. Short-term, in situ experiments using ^{13}C and/or ^{15}N labelled organic matter (e.g. phytodetritus) revealed rapid incorporation of ^{13}C/^{15}N in physically separated organisms (macro- and meiofauna and foraminifera) and microbes, the latter via incorporation of tracers in biomarkers specific for certain microbial groups (Middelburg et al., 2000; Boschker and Middelburg, 2002;

Veuger et al., 2007; Oakes et al., 2012;, Woulds et al., 2007, 2016) Similarly, ammonium isotope dilution studies have shown that net ammonification is only a small fraction of the total ammonium regeneration because most of the ammonium liberated is re-assimilated by the microbial community (Blackburn and Henriksen, 1983). Clearly the microbes and animals living in sediment assimilate carbon and synthesize new tissues. How can this be reconciled with the geochemical and organic geochemical views in which organic matter is either preferentially degraded to carbon dioxide or selective preserved (Fig. 1, 3). These two apparently inconsistent views are consistent if all of the newly produced organic matter is eventually degraded.

Detailed investigations of organic matter composition might in principle resolve this issue as microbial and animal processing of organic matter results in the formation of distinct compounds (Bradshaw et al., 1990; Sun et al., 1999; Thomas and Blair, 2002; Woulds et al., 2012, 2014). There are few issues with this approach: (1) most sedimentary organic matter is molecularly uncharacterizable and the origin (imported from the water column vs. newly produced within the sediment) can thus not be investigated, (2) microbes living within (the guts) of animals may mask the animal signatures (Woulds et al., 2012, 2014) and (3) different analytical windows (amino acids vs. lipids) may result in different inferences. On the one hand, the accumulation of bacterial derived non-protein amino acids and peptidoglycan derived D amino acids are clear signs that extensively modified organic matter contains a major fraction that is derived from (heterotophic) bacteria (Cowie and Hedges, 1994; Dauwe et al., 1999; Grutters et al., 2001; Lomstein et al., 2006; Keil and Fogel, 2001; Keil et al., 2000). On the other hand, using a combined lipid-isotope approach Hartgers et al. (1994) reported only a minor contribution of bacteria to sedimentary organic carbon pools. However, Gong and Hollander (1997) used fatty acids and identified a substantial microbial contribution to sedimentary organic matter.

Secondary production has potentially major consequences for the interpretation of sedimentary records. If microbial reworking of deposited organic matter represents a major carbon processing flow and part of the material is preserved then one would expect that bulk organic matter properties such as C, N, P elemental ratios and nitrogen isotopes would reflect this. Degradation of organic matter usually results in the preferential release of nitrogen and phosphor relative to carbon. Microbes normally have lower C/N ratios than their substrate, implying that secondary production and accumulation of microbial derived organic matter ~~results~~ in a net decrease of sediment C/N ratios (Müller, 1977). In contrast, the C/P ratio of heterotrophic microbes is rather variable because P demands depends on the growth rate (Sterner and Elser, 2002) and slowly growing benthic microbes may have high C:P ratios (Steenbergh et al., 2013). Moreover, microbial P storage also depends on redox conditions with the consequences that sedimentary C:P ratios are highly variable (Algeo and Ingall, 2007). Sediment δ^{15}N values often show a post-depositional shift towards heavier values in alternating oxic/anoxic settings (Moodley et al., 2005b). Such a shift is to be expected because regenerated ammonium is either transformed into nitrite/nitrate (nitrification) or re-assimilated by the microbial community. During oxic conditions nitrification occurs with preference for ^{14}N and the remaining ammonium available for re-assimilation by microbes will be relatively rich in ^{15}N, while during anoxic conditions oxidation of ammonium is less important or absent, and the ammonium re-assimilated will have similar $\delta^{15}N$ values as that regenerated. Secondary production of microbial biomarkers within sediment may also impact the interpretation of paleorecords (Schouten et al., 2010).

To reconcile the strong experimental evidence for preferential degradation (Middelburg, 1989), selective preservation (Tegelaar et al., 1989) and formation of new compounds by secondary producers (Lomstein et al, 2012; Braun et al, 2017) we present a new integral concept (Fig. 4). Phytodetritus delivered to sediments is preferentially degraded with the result that new biomass is formed and that some compounds are selectively preserved. The newly formed biomass is after death of the organism added to the pool of degraded detritus and subject to further microbial processing. After multiple cycles of processing by benthic heterotrophs most of the remaining organic matter becomes molecularly uncharacterizable. This conceptual model is consistent with the ruling paradigms of preferential degradation and selective preservation as well as with the occurrence of secondary production and formation of molecular uncharacterizable organic matter, but the next step is to quantify this conceptual view. One approach would be to use proxies for organic matter degradation state such as fraction of total nitrogen present as amino acid, non-protein amino acids accumulation and the degradation index (Cowie and Hedges, 1994; Dauwe and Middelburg, 1998; Dauwe et al., 1999). Lomstein et al. (2012) and Braun et al. (2017) used amino acid racemization to quantify turnover of living microbial biomass as well as of bacterially derived organic matter (necromass) in the deep biosphere. Veuger et al. (2012) executed a $^{13}C/^{15}N$ tracer experiment and followed the isotope labels into carbohydrates, amino acids and lipids and basically showed that most of the deliberately added heavy isotopes were recovered from the molecularly uncharacterizable pool within a few weeks and remained in that pool till the end of the experiment (> 1year). Their study provided direct evidence for rapid formation of new microbial biomass and subsequent transfer of microbial biomass to the pool of molecular uncharacterizable organic matter. Moreover, the efficient retention of label was indicative of recycling of molecules (or parts thereof) by microbes rather than de novo synthesis, consistent with findings in soil science (Dippold and Kuzyakov, 2016).

5.3 Animals and carbon supply to sediments

Marine sediments are often considered donor-controlled systems, i.e. organic matter is delivered via settling of organic matter produced in the sunlit upper part of the ocean (Fig. 3) and the consuming sediment communities have no control on its carbon delivery (Fig. 5). It is only on the time-scale of ocean bottom-water renewal (10-100 years) that nutrient regenerated by benthic organisms may impact primary producer in the sunlit upper part of the ocean (Soetaert et al., 2000). This is obviously different for sediments in the photic zone that make up about 1/3 of the coastal ocean (Gattuso et al, 1996) because animals can directly graze and consume the benthic primary producers at the sediment surface (Middelburg et al., 2000; Evrard et al., 2010, 2012; Oakes et al., 2012; Fig. 5). Donor and consumer controlled food webs have intrinsic different dynamics.

Animals living in sediments below the photic zone can in multiple ways impact carbon processing within marine sediments (Fig. 5). Deposit-feeding animals mix particles (and thus particulate organic carbon) as a consequence of their activities. In the case of constant organic carbon delivery (donor-control) bioturbation stimulates organic carbon processing at depth (Herman et al., 1999). In coastal systems, organic matter delivery is more complex because of multiple deposition-resuspension events and lateral transport pathways. Rice and Rhoads (1989) showed that in this case (with constant organic carbon concentration in the top layer) more bioturbation will increase the organic matter flux into the sediment. Moreover, organic carbon gradients with depth are steeper for high-quality than low-quality material and bioturbation thus results in transfer of high-quality organic matter to (micro-)organisms living at depth. Animals living in permeable sediment can via surface sediment topography (bioroughness) induce pore-water flows resulting in the trapping of phytoplankton (Huettel et al., 2014).

Tropical and cold-water corals, coastal and deep-sea sponges, suspension feeding bivalves and other marine forests communities utilize particulate organic matter suspended in the water (Herman et al., 1999; Roberts et al., 2006; Rossi et al., 2017). This organic carbon is used for maintenance respiration and growth, but part is excreted as faeces or pseudofaeces and becomes then available for consumers in the sediments. This can result in local hotspots of biodiversity and microbial activity in the sediments (Herman et al., 1999; Gutierrez et al., 2003; Cathalot et al., 2015). Moreover, the physical structures build by these ecosystem engineers impact hydrodynamics with consequences for local and distant carbon deposition rates. Soetaert et al. (2016) reported elevated carbon deposition to ocean margin sediments due to cold-water corals reefs at very large distances.

Some sponges have the capability to take up dissolved organic carbon and transform it into sponge tissue (de Goeij et al., 2013; Fiore et al., 2017; Hoer et al., 2017). This sponge tissue and in particular its detritus can be consumed by benthic organisms. This sponge loop (de Goeij et al., 2013; Rix et al., 2016) is another example how animals can manipulate the transfer of organic carbon from the water-column to the sediments (Fig. 5).

5.4 Animal stimulation of microbes: An inverted microbial loop?

The microbial loop is a key concept in ocean biogeochemistry (Pomeroy, 1974; Azam et al., 1983). Dissolved organic matter released by phytoplankton, zooplankton or viral lysis of bacteria, archaea and algae is consumed by heterotrophic microbes. These heterotrophs are in turn consumed by flagellates, ciliates and other small consumers that are predated upon by zooplankton (Azam et al., 1983; Jumars et al. 1989). Energy shunted into the large, heterogeneous dissolved organic matter pool is in this way made available again for animals (Fig. 6).

After discovery of this loop in the surface ocean water, research has been executed to identify and quantify it in sediments (Kemp, 1988, 1990). This required substantial investment in developing new methods: these studies basically revealed that predation on sedimentary bacteria was not that important (Kemp, 1990; Hondeveld et al., 1992; Hamels et al., 2001; Guilini et al., 2009). Van Oevelen et al., (2006) made a detailed study on the fate of bacterial production using in situ ^{13}C labelling of bacteria. They observed that 8% was lost by physical processes, 27% was consumed by animal predation, while bacterial mortality accounted for 65%. Viruses are the most important loss term for sedimentary microbes (Danovaro et al, 2009, 2011, 2016) and the viral lysis products (dissolved organic matter) are consumed by microbes. This results in a dissolved organic carbon-microbes cycle (Fig. 6). This benthic microbial cycle represents a dead end in terms of food web topology, because there is little transfer to higher trophic levels and most carbon is eventually respired as needed for mass-balance closure on the long term (Fig. 3).

In fact, the benthic microbial cycle represents more an *inverted microbial loop*: rather that animals profit from the microbial loop sensu Azam et al. (1983), it appears that benthic microbes profit from animals mixing labile organic matter downwards into the sediments (Fig. 6). Labile organic matter delivered to the sediment surface is mixed by animals inhabiting the sediments (Fig. 5). The transfer of high quality organic matter to deeper sediment layer may prime sediment microbial communities and in this way stimulate degradation of indigenous organic matter (van Nugteren et al, 2009a, Bianchi, 2011; Hannadis & Aller, 2017). This inverted microbial loop is a prime example how animals as ecosystem engineers impact sediment carbon processing (Meysman et al., 2006).

5.5 Imagine a world without animals.

An ocean floor inhabited solely by microbes and without animals was likely the reference state during the first four billion of years of Earth's history (Canfield, 2014; Lenton and Watson, 2011). Moreover, in modern systems with anoxic bottom waters benthic animals are absent (Rhoads and Morse, 1971; Diaz and Rosenberg, 1995, 2008; Levin, 2003; Levin et al, 2009). In these systems, organic matter degradation pathways are different not only because of a lack of oxygen and use of alternative electron acceptors, but also because bio-irrigation and bioturbation are absent (Aller and Aller, 1998; Levin et al., 2009; Middelburg and Levin, 2009). Consequently, microbe-fauna interactions (enhanced carbon delivery, Fig. 5; animal stimulation of microbes, Fig. 6) are impeded. This likely is the reason why more organic carbon is buried in sediments underlying anoxic bottom waters (Hartnett et al., 1998; Hartnett and Devol, 2003; Middelburg and Levin, 2009; Jessen et al., 2017). Moreover, the organic matter buried in hypoxic and anoxic settings is usually less degraded (Cowie, 2005, Cowie et al., 2009; Vandewiele et al., 2009; Koho et al., 2013; Jessen et al., 2017). This presence of animals and all their interactions with organic matter and microbes has consequences for organic carbon processing in marine sediments and thus the global carbon cycle. It is obvious for any terrestrial microbiologist that a world with trees and other macrophytes would be different than one without. Moreover, biological oceanographers and limnologists agree that zooplankton and other metazoan consumers contribute to biogeochemical cycles (Vanni, 2002; Vanni and McIntyre, 2016), and I hope that colleagues studying marine sediments are aware that BIO in sediment biogeochemistry is more than just microbiology.

Acknowledgement

This paper presents my acceptance lecture for the Vladimir Ivanovich Vernadsky Medal 2017 of the European Geosciences Union. I thank the colleagues that nominated me for this award and the many colleagues, students and postdoctoral fellows with which I have had the pleasure to interact and collaborate over the years. In particular, the late Carlo Heip who was instrumental for getting the BIO into my biogeochemistry and my long-term collaborators in modelling benthic ecosystems (Karline Soetaert, Peter Herman, Filip Meysman and Bernie Boudreau), in food-web studies (Dick van Oevelen, Leon Moodley), in organic geochemistry (Jaap Sinninghe Damsté and Stefan Schouten) and in coastal biogeochemistry (Jean-Pierre Gattuso and Carlos Duarte). Ton Marcus is thanked for graphic support. This is a contribution to the Netherlands Earth System Science Centre supported by the Dutch ministry of Education and Science.

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Figure 1. Different views, approaches and interests on carbon processing in marine sediments. Paleoceanographers focus on the sedimentary record, biogeochemists quantify carbon burial and recycling, organic geochemists study alteration of organic matter and ecologists focus on carbon as food for organisms living in the sediment

Figure 2. Conceptual model of organic matter (OM) degradation and re-oxidation pathways (based on Middelburg and Levin, 2009).

Figure 3. Carbon processing in marine sediments on the short-term (left) and the long-term (right). Organic matter produced in the sunlit layer of the ocean and delivered to the sediments is either consumed by organisms or buried. The organic matter consumed by organisms is used to synthesize biomass or metabolized to carbon dioxide and nutrients. On the long-term or at steady-state, i.e. the biomass of benthic organisms does not change, the benthic community can be considered a black box diverting organic matter either into metabolites or into the geosphere (burial).

Figure 4. Conceptual diagram showing the relationships between molecular uncharacterizable organics, deposited phytodetritus and secondary production. Phytodetritus is degraded preferentially and new biomass is formed, which after death of the organisms is added to the pool of detritus and subject to degradation. Multiple cycles of organic matter processing eventually results in the formation of molecular uncharacterizable organic matter.

Figure 5. Organic matter supply to sediments. 1. The traditional view of organic matter settling passively from the water column (donor control). 2. Sediments in the photic zone are inhabited by benthic microalgae that produce new organic matter in situ and grazing animals can impact the growth of these organisms. 3. Bioturbating animals transfer labile carbon from the sediment surface layer to deeper layers in the sediments. 4. Suspension feeding organisms enhance the transfer of suspended particulate matter from the water column to the sediments (biodeposition). 5. Sponge consume dissolved organic carbon and produce cellular debris that can be consumed by benthic organisms (i.e. the sponge loop).

Figure 6. The microbial and inverted microbial loop. In the water column dissolved organic carbon derived from phytoplankton, zooplankton or microbes (via viral loop) is consumed by heterotrophic microbes, which in turn are consumed by protists and small animals with the consequence that carbon flowing through dissolved organic carbon pools eventually can be used by larger animals (microbial loop). In sediments, the dissolved organic carbon (from viral lysis and other sources) is also consumed by heterotrophic microbes but this carbon is inefficiently transferred to animals. The engineering activities of animals are key in delivering labile organic matter (phytodetritus) to microbes living in the subsurface (inverted microbial loop).

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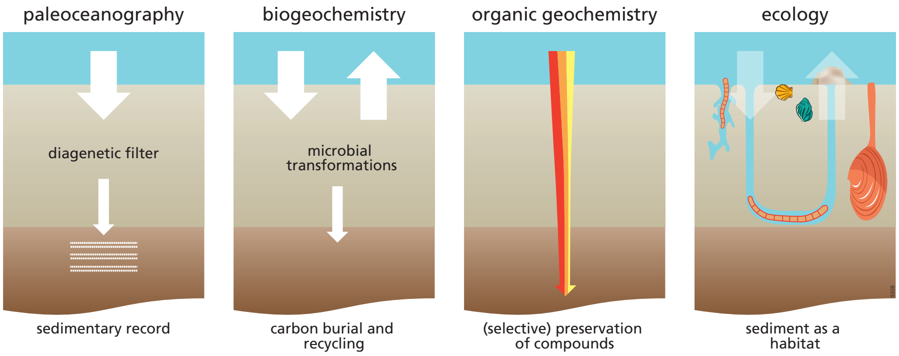

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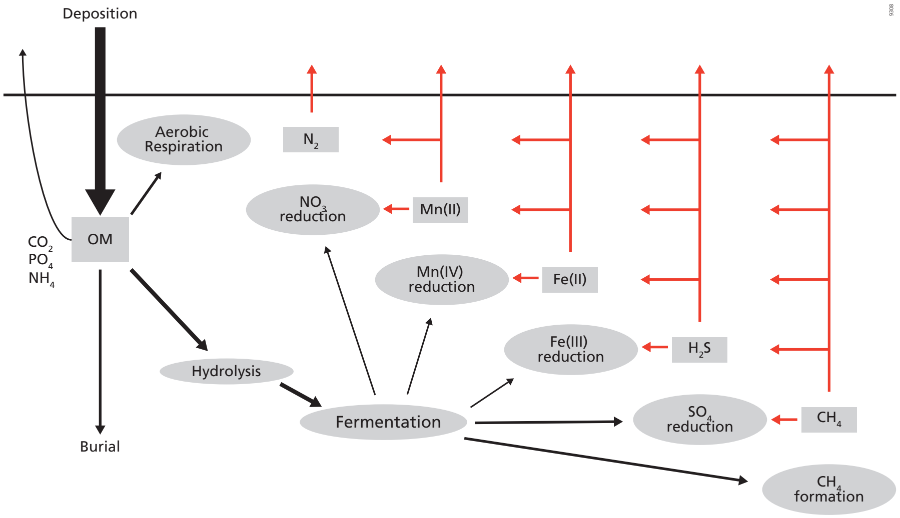

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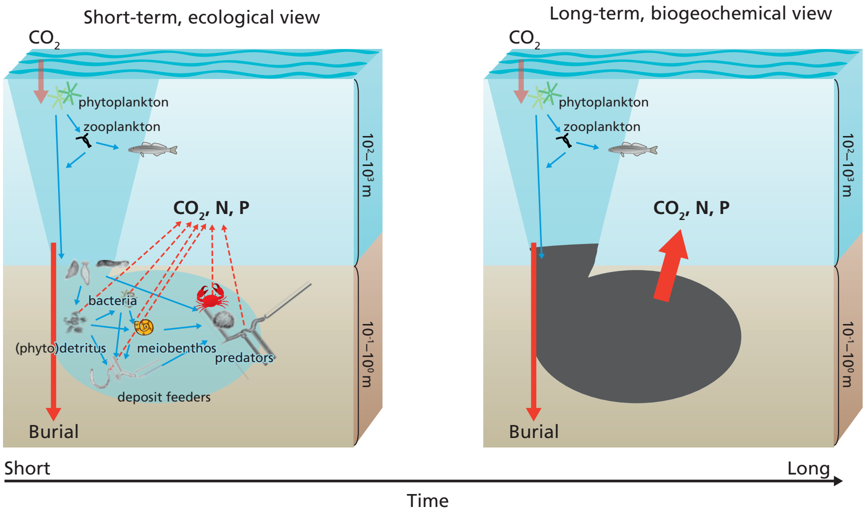

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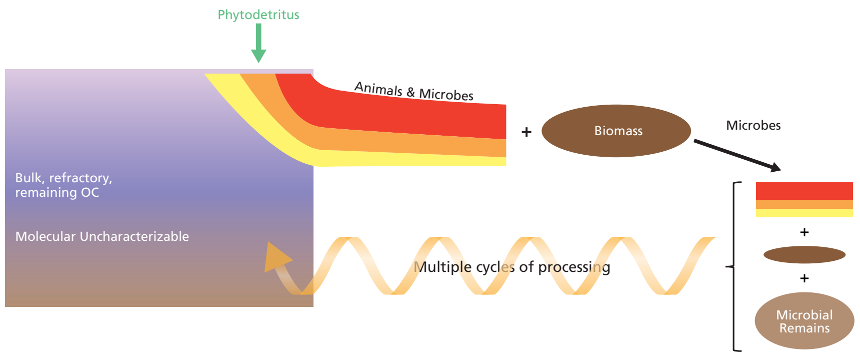

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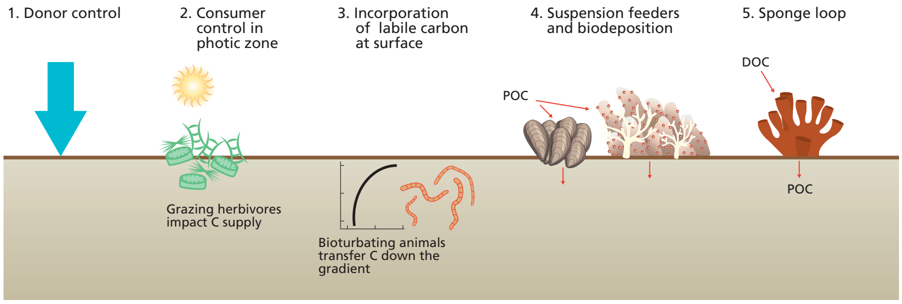

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