1

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

Jack J. Middelburg*

Earth Sciences, Utrecht University, PO Box 80 021, 3508 TA Utrecht, The Netherlands

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Abstract

Organic carbon processing at the seafloor is studied 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 will be 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. Secondary production by microbes and animals is identified to potentially impact the composition of sedimentary organic matter. Animals impact sediment organic carbon processing by microbes in multiple ways: by governing organic carbon supply to sediments, by aeration via bio-irrigation and by mixing labile organic matter to deeper layers. I will present an inverted microbial loop 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 remains from organisms (organic matter, biogenic silica) are 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 study sediments with the primary aim to extract information on past environmental conditions using down-core measurements of substances that have survived the processing at the seafloor (Burdige, 2006; Bender, 2013). Biogeochemists quantify the fate of material delivered, in particular how much of that is eventually buried or processed, and determine when and in what form the remaining part is recycled as key nutrients to sustain primary production in the water column (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 underappreciate or do not incorporate 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 (Berner, 1980; Glud, 2008). Bioturbation, biological reworking of sediments (Meysman et al., 2006), is often ignored by paleoceanographers, and biogeochemists (Berner, 1980; Boudreau, 1997) have developed advanced transport-reaction models in which the actors, the animals, mix the sediment but do so without consuming organic matter.

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, biogeochemical and ecological 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 Biogeochemists focus on quantification of burial and mineralization.

Organic matter delivered to marine sediments is either mineralized and the metabolites (carbon dioxide and nutrients) accumulate in pore-waters and exchange with the overlying water, or buried through the steady accumulation of particles (Fig. 2). This biogeochemical view (Berner, 1980; Boudreau, 1997; Aller, 2013) is highly simplified, but for that reason also quantitative and I believe instructive. The percentage of organic matter buried varies from less than one % to a few tens % and is closely and positively related with total sediment accumulation rate (Canfield, 1989, 1994; Middelburg et al., 1993). Since sediment accumulation rates are high 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 % of the total buried (Berner, 1982; Duarte et al., 2005; Burdige, 2007). In the deep sea and other settings with low burial efficiency, almost all organic matter is degraded to inorganic carbon at rates that provide an excellent approximation

99   for organic matter deposition (Jørgensen, 1982; Cai and Reimers, 1995; Glud,
100   2008). Organic matter degradation can be quantified via the consumption of
101   oxygen, the production of dissolved inorganic carbon and through the use of
102   pore-water data and diagenetic models (i.e. reaction-transport models for
103   sediments). At steady state, sediment oxygen consumption provides an accurate
104   measure for total sediment organic matter degradation, independent whether
105   organic matter is degraded aerobically (i.e. with oxygen) or anaerobically (with
106   alternative electron acceptors such as nitrate, metal oxides, sulphate), because
107   almost all reduced metabolites released (ammonium, manganese (II), iron(II),
108   hydrogen sulfide and methane) are re-oxidized (Jørgensen, 1977, 2006; Berner
109   and Westrich, 1985; Aller and Rude, 1988; Soetaert et al., 1996; Boetius et al.,
110   2000; Strous and Jetten, 2004; Raghoebarsing et al., 2006; Middelburg and Levin,
111   2009).
112   Biogeochemists have adopted a transport-reaction modeling approach to
113   accurately quantify organic matter processing (Berner, 1980; Boudreau, 1997;
114   Burdige, 2006). The basic premise of these diagenetic models is that both
115   particles and solutes are subject to transport and reaction, making them distinct
116   from for instance groundwater transport-reaction models in which normally
117   only solutes and gas phases are mobile (Lichtner, 1996; Appelo, 1996).
118   Transport of solutes is due to molecular diffusion, pore-water advection and
119   biologically mediated processes such as enhanced diffusion due to interstitial
120   fauna (Aller and Aller, 1992) and bio-irrigation due to tube and burrow
121   construction and flushing by macrofauna (Aller, 1980, 1984; 2001; Volkenborn
122   et al., 2010; 2016; Kristensen et al., 2012). Particle transport is not only due to
123   steady particle deposition but also due to sediment reworking by animals
124   (bioturbation, Boudreau, 1997; Aller, 1994, 2013; Rice, 1986; Meysman et al.,
125   2003, 2006, 2010). The reaction terms in these diagenetic models are normally
126   limited to microbial and chemical reactions and are described using zero, first,
127   second order kinetic relationships or Monod/Michaelis-Menten type kinetics
128   (Bouldin, 1968; Berner, 1980; Soetaert et al., 1996; Boudreau, 1997). There is a
129   major inconsistency in the basic conceptual model underlying the (numerical)
130   diagenetic models: animals dominate transport processes via pore-water
131   irrigation and particle mixing, but without consuming any organic matter. This
132   inconsistency has not received much attention because the ruling paradigm
133   within the biogeochemical research community is that animals contribute very
134   little to total carbon processing. Multiple recent studies involving use of ^{13}C as
135   deliberate tracers show that this premise does not hold on the short term (days
136   to weeks; Blair et al., 1996; Moodley et al., 2002, 2005a; Woulds et al., 2009,
137   2016). Moreover, detailed studies of oxygen consumption have revealed that
138   animals contribute substantially to total sediment oxygen uptake; directly via
139   their respiration as well as indirectly via particle and solute mixing (Glud, 2008).
140   Nevertheless, diagenetic models can very accurately reproduce most
141   observations (Soetaert et al., 1996; Berg et al., 2003).
142   Diagenetic models combined with solid-phase and pore-water depth
143   profiles, sediment-water exchange fluxes and rate measurement have resulted in
144   a consistent picture of organic matter degradation pathways in marine
145   sediments (Berner, 1980; Boudreau, 1997; Aller, 2013). These models can
146   predict where, when and why organic matter oxidation occurs aerobically or
147   involves nitrate, metal oxides or sulphate as oxidants (Rabouille and Gaillard,

148 2001; Boudreau, 1996; Soetaert et al., 1996; Middelburg et al. 1996; van
149 Cappellen and Wang, 1996; Archer et al., 2002; Meysman et al., 2003; Berg et al.,
150 2003). They also resolve the re-oxidation of reduced products such as
151 ammonium, manganese(II), iron (II), sulfide and methane (Fig. 2) and as such
152 define the scope for aerobic and anaerobic organisms, including the distribution
153 and activity of chemoautotrophs (Middelburg, 2011). Despite these advances,
154 diagenetic models cannot predict organic carbon burial rates, nor do they
155 provide much insight into why organic matter is buried, or why it is either labile
156 (reactive) or refractory. For this we need to have a detailed look at the organic
157 geochemistry of sediment organic carbon.
158
159 **3 Organic geochemists focus on the composition of organic matter**
160 **preserved**
161
162   Organic matter delivered to the seafloor is predominantly produced in the
163 surface sunlit layer of the ocean (Fig. 3). This organic matter is rich in proteins,
164 carbohydrates and lipids and generally follows Redfield stoichiometry (Sterner
165 and Elser, 2002; Bianchi and Canuel, 2011). Organic matter processing leads to
166 preferential degradation of the more labile components with the result that
167 organic matter becomes less reactive (Jørgensen, 1979; Westrich and Berner,
168 1984; Middelburg, 1989; Arndt et al., 2013) and organic matter composition
169 changes (Fig. 1; Wakeham et al. 1997; Dauwe et al., 1999; Lee et al., 2000). The
170 proportion of organic matter that can be characterized molecularly decreases
171 with progressive degradation, i.e. with water depth or depth downcore
172 (Wakeham et al., 1997; Hedges et al., 2000; Middelburg et al., 1999; Nierop et al.,
173 2017). This molecularly uncharacterizable material increases to more than 70%
174 of the total in deep-sea sediment organic matter. The organic geochemical
175 approach to study organic matter processing is limited not only by our inabilities
176 to characterize the majority of the sedimentary organic matter, but also by the
177 simple fact that the degraded fraction cannot be easily studied and we have to
178 base our knowledge on the small fraction of extensively processed organic
179 material remaining.
180   The changes in organic matter composition due to organic matter
181 processing have been utilized to estimate the lability-digestability or the
182 refractory nature of organic matter with various proxies such as chlorophyll to
183 bulk organic matter, fraction of nitrogen present as amino acids, and the
184 contribution of proteins and carbohydrates to total organic matter (Cowie et al.,
185 1992; Dell'Anno et al., 2000; Danovaro et al., 2001; Koho et al., 2013). The amino-
186 acid based degradation index (Dauwe and Middelburg, 1998) is one of the most
187 commonly used proxies to quantify the extent of degradation or the quality of
188 the remaining particulate organic matter and is based on subtle changes in the
189 amino acid composition due to organic matter processing (Dauwe et al., 1999;
190 Keil et al., 2000).
191   The compositional changes have also been used to infer transformation of
192 organic matter by bacteria (Cowie and Hedges, 1994; Dauwe et al., 1999;
193 Grutters et al., 2001; Vandewiele et al., 2009; Lomstein et al., 2006, 2012), extent
194 of degradation under oxic and anoxic conditions (Sinninghe Damsté et al., 2002;
195 Huguet et al, 2008; Nierop et al., 2017) and the relative importance of bacteria
196 and fauna for organic matter degradation (Sun et al., 1999; Woulds et al., 2012,

197   2014). Although some organic geochemical studies hint at the importance of
198   secondary production (Hayes et al., 1989; Cowie and Hedges, 1994; Grutters et
199   al., 2001; Lomstein et al., 2006, 2012), this aspect has received little attention in
200   organic geochemistry, yet it is one of the main objectives within the ecological
201   approach.
202
203   **4 Ecologists focus on the dynamics of organisms using organic matter**
204
205   Benthic communities are usually partitioned into different size classes
206   (e.g. macrofauna, meiofauna and microbes; Gage and Tyler, 1992; Gray and Elliot,
207   2009; Herman et al., 1999), which are often studied by different research
208   communities having distinct objectives, approaches and tools. Organic matter
209   delivered to the seafloor fuels benthic food webs: i.e. it represents food for the
210   animals and the energy substrate for heterotrophic microbes. Microbial
211   ecologists study the growth of microbes on delivered organic matter (e.g.
212   bacterial production) and subsequent microbial loss processes, including
213   predation and viral lysis (Kemp, 1988; 1990; Danovaro et al., 2008, 2011, 2016).
214   Microbial ecologists also study in detail the identities and activities or organisms
215   involved in (an)aerobic respiration pathways and the re-oxidation of reduced
216   metabolites produced during anaerobic organic matter degradation (Canfield et
217   al., 2005). Animal ecologists focus on the response of fauna to food delivery, the
218   diet and growth of animals and transfer of carbon up the food chain to top
219   consumers (Krumins et al., 2013; Fig. 3). Interactions among food-web members
220   are considered the key to understand carbon flows (Pimm et al., 1991; van
221   Oevelen et al., 2010).
222   During the last two decades, ^{13}C-labeled phytodetritus addition
223   experiments have been performed to identify the organisms involved in the
224   immediate processing of organic matter delivered to the seafloor (Middelburg,
225   2014). These studies often covered all size classes (animals and microbes) and
226   could show that respiration was the major fate of added phytodetritus and that
227   all size classes directly profited from recently deposited organic matter (Blair et
228   al., 1996; Moodley et al., 2002, 2005a; Woulds et al., 2007, 2009, 2016; Witte et
229   al., 2003; Nomaki et al., 2005; Sweetman and Witte, 2008). In other words,
230   heterotrophic microbes and small and big animals compete for the same food.
231   Van Nugteren et al. (2009b) have shown that the spatial distribution of resources
232   is a key factor governing the relative use of phytodetritus by bacteria vs. animals.
233   Moreover, the relative share of organisms in the processing of organic matter
234   was in some systems and for some consumers proportional to the biomass of the
235   benthic size class, but not always (Moodley et al., 2005a; Woulds et al, 2009,
236   2016). For instance, foraminifera and amoebid protozoa, sometimes contribute
237   disproportionally to short-term carbon processing reflecting high turn-over of an
238   active community (Moodley et al., 2002; Woulds et al., 2007).
239
240
241   **5 Towards a synthesis**
242
243   The above discussion on conceptual views within different research disciplines
244   highlights a few discrepancies and gaps in our knowledge. Secondary production
245   by animals and microbes is often not included in the biogeochemical view that

246 focuses on preservation versus mineralization. It is also largely absent from the
247 organic geochemical literature. Consumption of organic matter is restricted to
248 microbes in the biogeochemical view, while the non-fed animals move organic
249 matter, microbes and particles around and enhance solute transfer by bio-
250 irrigation activities. The consumption of organic matter eventually results in
251 compositional changes of the organic matter remaining but there is little
252 information that the identity of the organism matters much. Whole ecosystem
253 labeling experiments revealed direct flow from detritus to most benthic
254 consumers and to the dissolved inorganic carbon pool, but these short-term
255 experimental results cannot directly be compared to the long-term natural
256 processing of deposited organic matter because long-term transfers within the
257 food web and eventual carbon preservation cannot be resolved experimentally.
258
5.1 On the consistency of food-web carbon processing and the biogeochemical burial-respiration partitioning

262 Food-web models describe the exchange of matter (e.g. carbon or energy) among
263 different compartments (organisms) within an ecosystem (Pimm et al., 1991; de
264 Ruiter et al., 1995) and usually lump respiration losses (Cole et al., 2006; van
265 Oevelen et al, 2010; Fig. 3 left). Experimental studies using ^{13}C labelled
266 phytodetritus as a tracer of sediment carbon processing showed that animals
267 and microbes both can assimilate labile carbon directly and confirmed that
268 respiration is the largest sink (Moodley et al, 2005a; Buhring et al., 2006;
269 Andersson et al. 2008; Woulds et al. 2009, 2016). The biogeochemical budgeting
270 approach basically distinguishes only between (refractory) carbon preserved
271 and buried versus labile organic carbon that is respired to carbon dioxide (Aller,
272 2013; Fig. 3 right). These ecological and biogeochemical concepts can be
273 consistent depending on the timescale considered. On the time scale of days to
274 month deposited carbon is processed by the benthic organisms, a small part is
275 assimilated and the majority is respired. On longer time scales and when
276 considering steady-state conditions, i.e. constant faunal and microbial biomass,
277 there is transfer from the detritus pool to the living biomass pool, but these
278 secondary producers die and their remains are returned to the detritus pool for
279 another cycle with the result that eventually all labile organic matter is respired.
280
5.2 Secondary production and the formation of molecularly uncharacterizable organic matter.

284 The mere presence of living organisms in sediments clearly indicates that
285 secondary production is omnipresent. Microbes usually dominate living biomass,
286 but not always, and living biomass typically contributes a few % to the standing
287 stock of total organic carbon in coastal sediments (Herman et al., 1999). The
288 importance of microbial biomass relative to total biomass increases with
289 increasing water depth (Rex et al., 2006; Danovaro et al., 2014, 2015). Moreover,
290 living biomass may contribute substantially to total carbon stocks in coarse-
291 grained sandy sediments with low background organic carbon contents (Herman
292 et al., 1999; Evrard et al., 2012). Various types of experimental evidence have
293 shown that carbon flow through the living compartment is much higher than
294 through the non-living sediment organic matter pool. Short-term, in situ

295   experiments using ^{13}C and/or ^{15}N labelled organic matter (e.g. phytodetritus)
296   revealed rapid incorporation of ^{13}C/^{15}N in physically separated organisms
297   (macro- and meiofauna and foraminifera) and microbes, the latter via
298   incorporation of tracers in biomarkers specific for certain microbial groups
299   (Middelburg et al., 2000; Boschker and Middelburg, 2002; Veuger et al., 2007;
300   Oakes et al., 2012;, Woulds et al., 2007, 2016) Similarly, ammonium isotope
301   dilution studies have shown that net ammonification (ammonium release) is
302   only a fraction of the total ammonium regeneration because a substantial part of
303   the ammonium liberated is re-assimilated by the microbial community
304   (Blackburn and Henriksen, 1983). Clearly the microbes and animals living in
305   sediment assimilate carbon and synthesize new biomass (Veuger et al., 2012).
306   How can this be reconciled with the biogeochemical and organic geochemical
307   views in which organic matter is either preferentially degraded to carbon dioxide
308   or selectively preserved (Fig. 1, 3). These two apparently inconsistent views are
309   consistent if most of the newly produced organic matter is eventually degraded.
310   Detailed investigations of organic matter composition might in principle
311   resolve this issue as microbial and animal processing of organic matter results in
312   the formation of distinct compounds (Bradshaw et al., 1990; Sun et al., 1999;
313   Thomas and Blair, 2002; Woulds et al., 2012, 2014). There are few issues with
314   this approach: (1) most sedimentary organic matter is molecularly
315   uncharacterizable and the origin (imported from the water column vs. newly
316   produced within the sediment) can thus not directly be investigated, (2)
317   microbes living within (the guts) of animals may mask the animal signatures
318   (Woulds et al., 2012, 2014) and (3) different analytical windows (amino acids vs.
319   lipids) may result in different inferences. On one hand, the accumulation of
320   bacterial derived non-protein amino acids and peptidoglycan derived D amino
321   acids are clear signs that extensively modified organic matter contains a major
322   fraction that is derived from (heterotophic) bacteria (Cowie and Hedges, 1994;
323   Dauwe et al., 1999; Grutters et al., 2001; Lomstein et al., 2006; Keil and Fogel,
324   2001; Keil et al., 2000). Using fatty acids, Gong and Hollander (1997) also
325   identified a substantial microbial contribution to sedimentary organic matter. On
326   the other hand, using a combined lipid-isotope approach Hartgers et al. (1994)
327   reported only a minor contribution of bacteria to sedimentary organic carbon
328   pools.
329   Secondary production has potentially major consequences for the
330   interpretation of sedimentary records. If microbial reworking of deposited
331   organic matter represents a major carbon flow and part of the material is
332   preserved, then one would expect that bulk organic matter properties such as C,
333   N, P elemental ratios and nitrogen and carbon isotopes would reflect this.
334   Degradation of organic matter initially results in the preferential release of
335   nitrogen and phosphorus relative to carbon. Microbes normally have lower C:N
336   ratios than their substrate (Sterner and Elser, 2002) implying that secondary
337   production and accumulation of microbial derived organic matter should
338   eventually result in a net decrease of sediment C:N ratios (Müller, 1977). In
339   contrast, the C:P ratio of heterotrophic microbes is rather variable because P
340   demands depends on the growth rate (Sterner and Elser, 2002) and slowly
341   growing benthic microbes may have high C:P ratios (Steenbergh et al., 2013).
342   Moreover, microbial P storage also depends on redox conditions with the
343   consequences that sedimentary C:P ratios are highly variable (Algeo and Ingall,

344   2007). Sediment $\delta^{15}N$ values often show a post-depositional shift towards
345   heavier values in alternating oxic/anoxic settings (Moodley et al., 2005b). Such a
346   shift is to be expected because regenerated ammonium is either transformed
347   into nitrite/nitrate (nitrification) or re-assimilated by the microbial community.
348   During oxic conditions nitrification occurs with preference for ^{14}N and the
349   remaining ammonium available for re-assimilation by microbes will be relatively
350   rich in ^{15}N, while during anoxic conditions oxidation of ammonium is less
351   important or absent, and the ammonium re-assimilated will have similar $\delta^{15}N$
352   values as that regenerated. Secondary production within sediment may also
353   impact the interpretation of bulk stable carbon isotope records (Hayes et al.,
354   1998) and paleorecords of microbial biomarkers (Schouten et al., 2010).
355   To reconcile the strong experimental evidence for preferential
356   degradation (Middelburg, 1989), selective preservation (Tegelaar et al., 1989)
357   and formation of new compounds by secondary producers (Lomstein et al, 2012;
358   Braun et al, 2017) I present a new integral concept (Fig. 4). Phytodetritus
359   delivered to sediments is preferentially degraded with the result that new
360   biomass is formed and that some compounds are selectively preserved. The
361   newly formed biomass is after death of the organism added to the pool of
362   degraded detritus and subject to further microbial processing. After multiple
363   cycles of processing by benthic heterotrophs most of the remaining organic
364   matter becomes molecularly uncharacterizable. This conceptual model is
365   consistent with the ruling paradigms of preferential degradation and selective
366   preservation as well as with the occurrence of secondary production and
367   formation of molecular uncharacterizable organic matter, but the next step is to
368   quantify this conceptual view. One approach would be to use proxies for organic
369   matter degradation state such as fraction of total nitrogen present as amino acid,
370   non-protein amino acids accumulation and the degradation index (Cowie and
371   Hedges, 1994; Dauwe and Middelburg, 1998; Dauwe et al., 1999). Lomstein et al.
372   (2012) and Braun et al. (2017) used amino acid racemization to quantify
373   turnover of living microbial biomass as well as of bacterially derived organic
374   matter (necromass) in the deep biosphere. Veuger et al. (2012) executed a
375    $^{13}C/^{15}N$ tracer experiment and followed the isotope labels into carbohydrates,
376   amino acids and lipids and basically showed that most of the deliberately added
377   heavy isotopes were recovered from the molecularly uncharacterizable pool
378   within a few weeks and remained in that pool till the end of the experiment (> 1
379   year). Their study provided direct evidence for rapid formation of new microbial
380   biomass and subsequent transfer of microbial biomass to the pool of molecular
381   uncharacterizable organic matter. Moreover, the efficient retention of label was
382   indicative of recycling of molecules (or parts thereof) by microbes rather than de
383   novo synthesis, consistent with findings for archaeal lipids in marine sediments
384   (Takano et al., 2010, Lipsewers et al., 2017) and bacteria in soils (Dippold and
385   Kuzyakov, 2016).
386
387

5.3 Animals and carbon supply to sediments

390   Marine sediments are often considered donor-controlled systems, i.e. organic
391   matter is delivered via settling of organic matter produced in the sunlit upper
392   part of the ocean (Fig. 3) and the consuming sediment communities have no

393 control on its carbon delivery (Fig. 5). It is only on the time-scale of ocean
394 bottom-water renewal (100-1000 years) that nutrient regenerated by benthic
395 organisms may impact primary producers in the sunlit upper part of the ocean
396 (Soetaert et al., 2000). This is obviously different for sediments in the photic
397 zone that make up about 1/3 of the coastal ocean (Gattuso et al, 1996) because
398 animals can directly graze and consume the benthic primary producers at the
399 sediment surface (Middelburg et al., 2000; Evrard et al., 2010, 2012; Oakes et al.,
400 2012; Fig. 5). Donor and consumer controlled food webs have intrinsicly
401 different dynamics.
402   Animals living in sediments below the photic zone can in multiple ways
403 impact carbon processing within marine sediments (Fig. 5). Deposit-feeding
404 animals mix particles (and thus particulate organic carbon) as a consequence of
405 their activities. In the case of constant organic carbon delivery (donor-control)
406 bioturbation stimulates organic carbon processing at depth (Herman et al.,
407 1999). In coastal systems, organic matter delivery is more complex because of
408 multiple deposition-resuspension events and lateral transport pathways. Rice
409 and Rhoads (1989) showed that in this case (with constant organic carbon
410 concentration in the top layer) more sediment reworking will increase the
411 organic matter flux into the sediment. Moreover, organic carbon gradients with
412 depth are steeper for high-quality than low-quality material and particle mixing
413 thus results in transfer of high-quality organic matter to (micro-)organisms
414 living at depth. Animals living in permeable sediment can via surface sediment
415 topography (bioroughness) induce pore-water flows resulting in the trapping of
416 phytoplankton (Huettel et al., 2014).
417   Tropical and cold-water corals, coastal and deep-sea sponges, suspension
418 feeding bivalves and other marine forests communities utilize particulate
419 organic matter suspended in the water (Herman et al., 1999; Roberts et al., 2006;
420 Rossi et al., 2017). This organic carbon is used for maintenance respiration and
421 growth, but part is excreted as faeces or pseudofaeces and becomes then
422 available for consumers in the sediments. This can result in local hotspots of
423 biodiversity and microbial activity in the sediments (Herman et al., 1999;
424 Gutierrez et al., 2003; Cathalot et al., 2015). Moreover, the physical structures
425 built by these ecosystem engineers impact hydrodynamics with consequences
426 for local and distant carbon deposition rates. Soetaert et al. (2016) reported
427 elevated carbon deposition to ocean margin sediments due to cold-water corals
428 reefs at very large distances.
429   Some invertebrates have the capability to take up dissolved organic
430 carbon and in particular sponges can assimilate substantial quantities and
431 transform it into biomass (de Goeij et al., 2013; Fiore et al., 2017; Hoer et al.,
432 2017). This sponge tissue and in particular its detritus can be consumed by
433 benthic organisms. This sponge loop (de Goeij et al., 2013; Rix et al., 2016) is
434 another example how animals can manipulate the transfer of organic carbon
435 from the water-column to the sediments (Fig. 5).
436
437
438 **5.4 Animal stimulation of microbes: An inverted microbial loop?**
439
440   The microbial loop is a key concept in ocean biogeochemistry (Pomeroy,
441 1974; Azam et al., 1983). Dissolved organic matter released by phytoplankton,

442 zooplankton or viral lysis of bacteria, archaea and algae is consumed by
443 heterotrophic microbes. These heterotrophs are in turn consumed by flagellates,
444 ciliates and other small consumers that are predated upon by zooplankton
445 (Azam et al., 1983; Jumars et al. 1989). Energy shunted into the large,
446 heterogeneous dissolved organic matter pool is in this way made available again
447 for animals (Fig. 6).
448   After discovery of this loop in the surface ocean water, research has been
449 executed to identify and quantify it in sediments (Kemp, 1988, 1990). This
450 required substantial investment in developing new methods: these studies
451 basically revealed that predation on sedimentary bacteria was not that
452 important (Kemp, 1990; Hondeveld et al., 1992; Hamels et al., 2001; Guilini et al.,
453 2009). Van Oevelen et al., (2006) made a detailed study on the fate of bacterial
454 production using in situ ^{13}C labelling of bacteria. They observed that 8% was lost
455 by physical processes, 27% was consumed by animal predation, while bacterial
456 mortality accounted for 65%.   Viruses are the most important loss term for
457 sedimentary microbes (Danovaro et al, 2009, 2011, 2016) and the viral lysis
458 products (dissolved organic matter) are consumed by microbes. This results in a
459 dissolved organic carbon-microbes cycle (Fig. 6). This benthic microbial cycle
460 represents a dead end in terms of food web topology, because there is little
461 transfer to higher trophic levels and most carbon is eventually respired as
462 needed for mass-balance closure on the long term (Fig. 3).
463   In fact, the benthic microbial cycle represents more an *inverted microbial*
464 *loop*: rather that animals profit from the microbial loop sensu Azam et al. (1983),
465 it appears that benthic microbes profit from animals mixing labile organic matter
466 downwards into the sediments (Fig. 6). Labile organic matter delivered to the
467 sediment surface is mixed by animals inhabiting the sediments (Fig. 5). The
468 transfer of high quality organic matter to deeper sediment layer may prime
469 sediment microbial communities and in this way stimulate degradation of
470 indigenous organic matter (Canfield, 1994; van Nugteren et al, 2009a, Bianchi,
471 2011; Hannadis & Aller, 2017). Moreover, tube construction and ventilation by
472 animals brings dissolved oxygen to deeper sediment layers and will in this way
473 stimulate organic matter mineralization (Canfield, 1994; Kristensen et al., 1995;
474 Dauwe et al., 2001). Bio-irrigation activities may be intermittent (Volkenborn et
475 al., 2016) and cause oscillations in oxygen availability that stimulate organic
476 matter degradation (Aller and Aller, 1998). This inverted microbial loop is a
477 prime example how animals as ecosystem engineers impact sediment carbon
478 processing (Meysman et al., 2006).
479
480
481 **5.5 Imagine a world without animals.**
482
483 An ocean floor inhabited solely by microbes and without animals was likely the
484 reference state during the first four billion of years of Earth's history (Canfield,
485 2014; Lenton and Watson, 2011). Moreover, in modern systems with anoxic
486 bottom waters benthic animals are absent (Rhoads and Morse, 1971; Diaz and
487 Rosenberg, 1995, 2008; Levin, 2003; Levin et al, 2009). In these systems, organic
488 matter degradation pathways are different not only because of a lack of oxygen
489 and use of alternative electron acceptors, but also because bio-irrigation and
490 sediment reworking are absent (Aller and Aller, 1998; Levin et al., 2009;

491   Middelburg and Levin, 2009). Consequently, microbe-fauna interactions
492   (enhanced carbon delivery, Fig. 5; animal stimulation of microbes, Fig. 6) are
493   impeded.
494   While organic matter mineralization in the presence of oxygen may be more
495   efficient than in anoxic environments (Canfield, 1994; Kristensen et al., 1995;
496   Dauwe et al. 2001) , the lack of animal stimulation of microbes may also
497   contribute to burying organic carbon more efficiently in sediments underlying
498   anoxic bottom waters (Hartnett et al., 1998; Hartnett and Devol, 2003;
499   Middelburg and Levin, 2009; Jessen et al., 2017). Moreover, the organic matter
500   buried in hypoxic and anoxic settings is usually less degraded (Cowie, 2005,
501   Cowie et al., 2009; Vandewiele et al., 2009; Koho et al., 2013; Jessen et al., 2017).
502   This presence of animals and all their interactions with organic matter and
503   microbes has consequences for organic carbon processing in marine sediments
504   and thus the global carbon cycle. It is obvious for any terrestrial microbiologist
505   that a world with trees and other macrophytes would be different than one
506   without. Moreover, biological oceanographers and limnologists agree that
507   zooplankton and other metazoan consumers contribute to biogeochemical cycles
508   (Vanni, 2002; Vanni and McIntyre, 2016), and I hope that colleagues studying
509   marine sediments are aware that BIO in sediment biogeochemistry is more than
510   just microbiology.
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530 **References**
531

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1028   delivered to the sediments is either consumed by organisms or buried. The
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1031   state, i.e. the biomass of benthic organisms does not change, the benthic
1032   community can be considered a black box diverting organic matter either into
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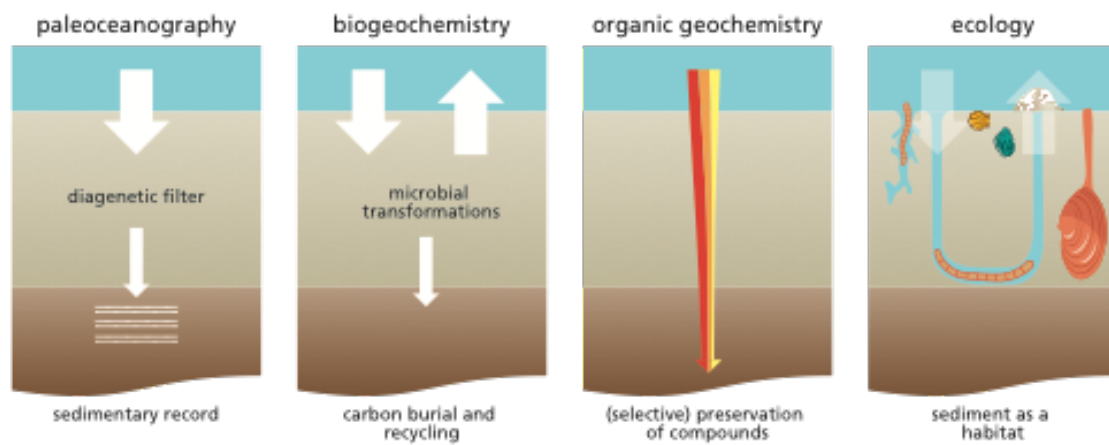
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1035 Figure 4. Conceptual diagram showing the relationships between molecular
1036   uncharacterizable organics, deposited phytodetritus and secondary production.
1037   Phytodetritus is degraded preferentially and new biomass is formed, which after
1038   death of the organisms is added to the pool of detritus and subject to
1039   degradation. Multiple cycles of organic matter processing eventually results in
1040   the formation of molecular uncharacterizable organic matter. The red-orange-
1041   yellow fractions of organic matter have a different lability.

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1044 Figure 5. Organic matter supply to sediments. 1. The traditional view of organic matter
1045   settling passively from the water column (donor control). 2. Sediments in the
1046   photic zone are inhabited by benthic microalgae that produce new organic
1047   matter in situ and grazing animals can impact the growth of these primary
1048   producers. 3. Bioturbating animals transfer labile carbon from the sediment
1049   surface layer to deeper layers in the sediments. (Vertical axis is depth, horizontal
1050   is concentration) 4. Suspension feeding organisms enhance the transfer of
1051   suspended particulate matter from the water column to the sediments
1052   (biodeposition). 5. Sponge consume dissolved organic carbon and produce
1053   cellular debris that can be consumed by benthic organisms (i.e. the sponge loop).

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1055 Figure 6. The microbial (upper panel) and inverted microbial (lower panel) loops. In the
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1057   zooplankton or microbes (via viral loop) is consumed by heterotrophic
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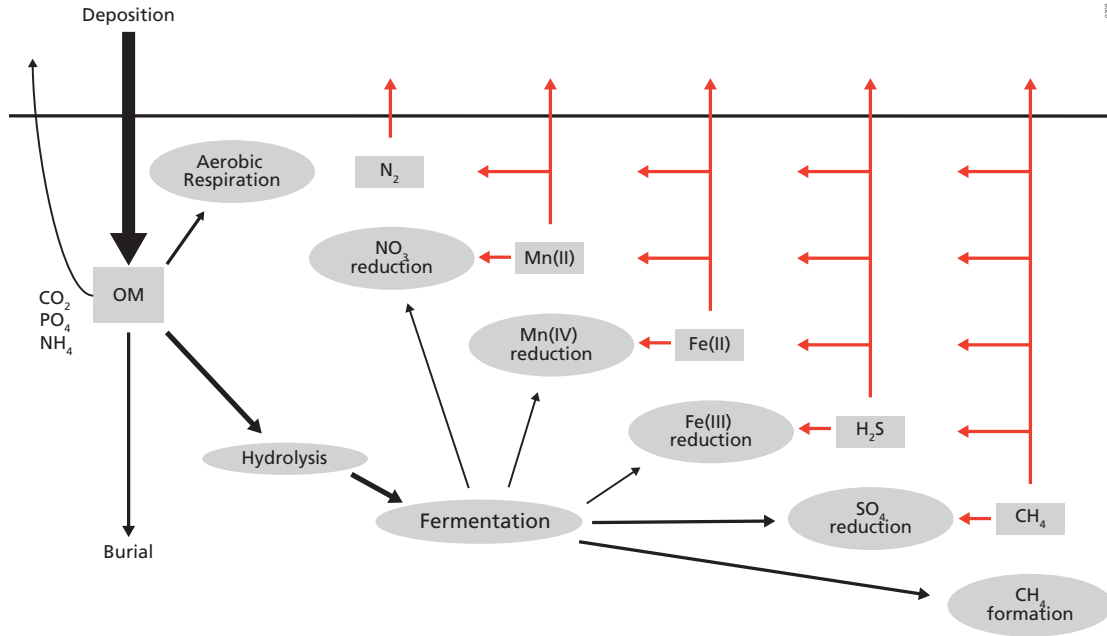
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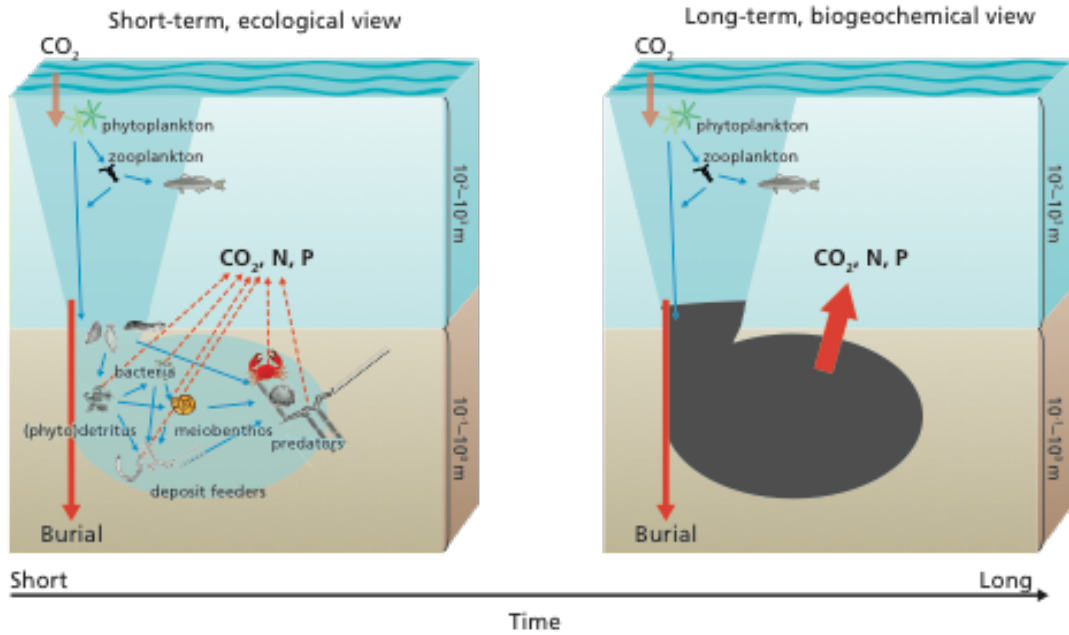1075   different lability.
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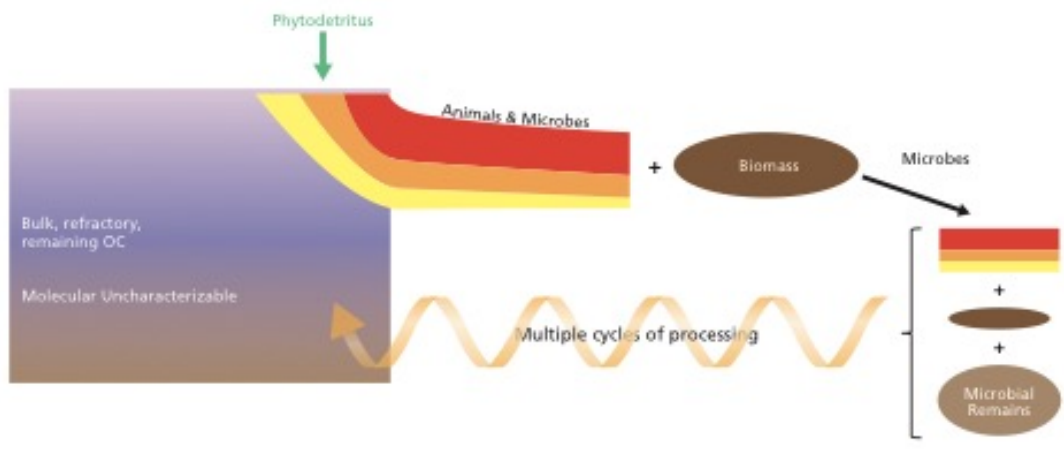
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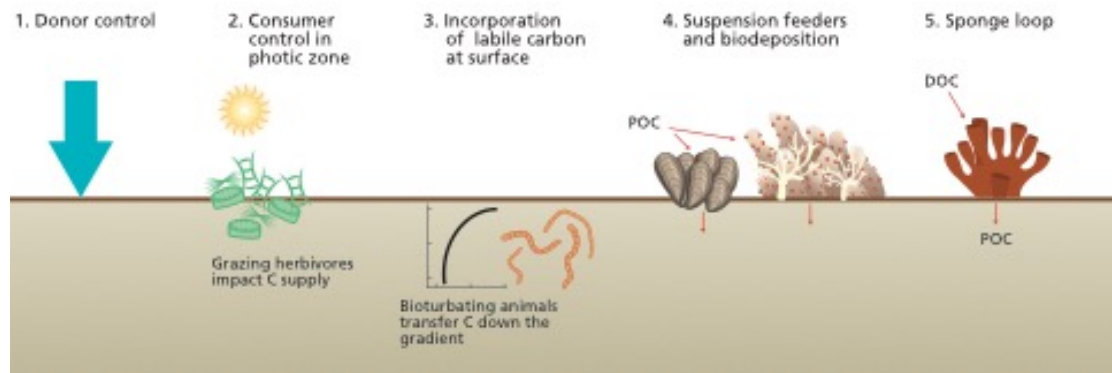1097
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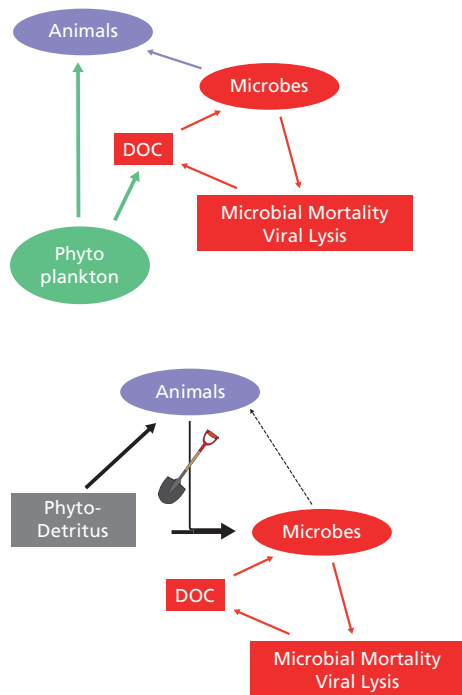1108

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