

Dear Tina:

Thank you very much for handling this paper. I have uploaded a revised version as well as the original one with all the annotations.

As I wrote on the public pages, I basically incorporated all feedback but for two aspects of referee # 1: A: bioturbation/bio-irrigation terminology: all through I state specifically what I mean (e.g., sediment reworking/mixing instead of bioturbation). B: suggestion to delete paleoceanography from introduction/Figure 1: I have not done so because that community also looks at carbon processing, although I do not discuss it in detail.

Has the paper improved: Yes, it has (thank you referees). I have included the role of bio-irrigation in stimulation organic carbon processing more explicitly (feedback from #1 and Don Canfield), have included about 15 additional references (all the suggested ones, references added because there was a need identified by the referees and a few more), checked for consistent use of terminology (C:N vs C/N; biogeochemistry vs. geochemistry, etc) and clarified where needed.

I hope that the present version is suitable for publication.

With best regards,

Jack Middelburg

1
2 **Reviews and Synthesis: To the bottom of carbon processing at**
3 **the seafloor**

4
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6
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8 Netherlands

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10 ** Invited contribution by Jack J. Middelburg, recipient of the EGU Vladimir*
11 *Vernadsky Medal 2017.*

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12
13 **Abstract**

14
15 Organic carbon processing at the seafloor is studied by biogeochemists to
16 quantify burial and respiration, by organic geochemists to elucidate
17 compositional changes and by ecologists to follow carbon transfers within food
18 webs. Here I review these disciplinary approaches and discuss where they agree
19 and disagree. It **will be** shown that the biogeochemical approach (ignoring the
20 identity of organisms) and the ecological approach (focussing on growth and
21 biomass of organisms) are consistent on longer time scales. **Secondary**
22 production by microbes and animals **is identified to potentially** impact the
23 composition of sedimentary organic matter. Animals impact sediment organic
24 carbon processing by microbes in multiple ways: by governing organic carbon
25 supply to sediments, **by aeration via bio-irrigation** and by mixing labile organic
26 matter to deeper layers. **I will present an** inverted microbial loop in which
27 microbes profit from bioturbation rather than animals profiting from microbial
28 processing of otherwise lost dissolved organic resources. Sediments devoid of
29 fauna therefore function differently and are less efficient in processing organic
30 matter with the consequence that more organic matter is buried and transferred
31 from Vernadsky's biosphere to the geosphere.

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34 **1 Introduction**

35
36 The seawater-sediment interface represents one of the largest interfaces
37 on earth and our knowledge of processes at and fluxes through this dynamic and
38 understudied interface is rather limited. This interface extends a few cm-dm
39 upwards into the water column, i.e. benthic boundary layer (Boudreau and
40 Jørgensen, 1992), as well as few cm-dm into the sediments, i.e. the bioturbated,
41 active surface layer (Bernier, 1980; Meysman et al., 2006; Aller, 2013). It serves
42 as a habitat for organisms, governs the partitioning of material being buried or
43 recycled and acts as a filter for the paleorecord (Rhoads, 1974). Processes in the
44 surface sediment layer determine whether **remains from organisms (organic**
45 **matter, biogenic silica) are** recycled within the biosphere (short-term cycle) or
46 transferred to the geosphere (long-term cycle) and as such it functions as a key
47 interface in the System Earth.

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48 This pivotal role of the seafloor in processing material deposited has been
49 studied by scientists from various disciplines with their own interests,

60 techniques and paradigms (Figure 1). Marine geologists and paleoceanographers
61 study sediments with the primary aim to extract information on past
62 environmental conditions using down-core measurements of substances that
63 have survived the processing at the seafloor (Burdige, 2006; Bender, 2013).
64 Biogeochemists quantify the fate of material delivered, in particular how much of
65 that is eventually buried or processed, and determine when and in what form the
66 remaining part is recycled as key nutrients to sustain primary production in the
67 water column (Bernier, 1980; Aller, 1980, 2001, 2013; Soetaert et al., 2000).
68 Organic geochemists investigate how organic matter delivered to the seafloor is
69 degraded, transformed or preserved using changes in the composition at the
70 molecular level (Hedges and Keil, 1995; Dauwe et al, 1999; Burdige, 2006;
71 Bianchi and Canuel, 2011). Ecologists focus on the organisms, i.e. the actors
72 consuming, producing and transporting the material deposited (Gage and Tyler,
73 1992; Gray and Elliot, 2009; Herman et al., 1999; Krumins et al., 2013).

74 Although these disciplines often study the same topic, e.g. organic matter
75 delivered to the seafloor, they focus on different aspects and usually
76 underappreciate or do not incorporate key concepts, findings and approaches
77 from other disciplines. For example, ecologists and biogeochemist studying
78 carbon flows at the seafloor normally ignore detailed molecular information
79 available from organic geochemistry (Bernier, 1980; Glud, 2008). Bioturbation,
80 biological reworking of sediments (Meysman et al., 2006), is often ignored by
81 paleoceanographers, and biogeochemists (Bernier, 1980; Boudreau, 1997) have
82 developed advanced transport-reaction models in which the actors, the animals,
83 mix the sediment, but do so without consuming organic matter.

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

93 2 Biogeochemists focus on quantification of burial and mineralization.

94
95 Organic matter delivered to marine sediments is either mineralized and
96 the metabolites (carbon dioxide and nutrients) accumulate in pore-waters and
97 exchange with the overlying water, or buried through the steady accumulation of
98 particles (Fig. 2). This biogeochemical view (Bernier, 1980; Boudreau, 1997;
99 Aller, 2013) is highly simplified, but for that reason also quantitative and I
100 believe instructive. The percentage of organic matter buried varies from less
101 than one % to a few tens % and is closely and positively related with total
102 sediment accumulation rate (Canfield, 1989, 1994; Middelburg et al., 1993).
103 Since sediment accumulation rates are high in vegetated, coastal, deltaic, shelf
104 and ocean-margin settings, the majority of organic matter burial occurs there,
105 with organic carbon burial in deep-sea sediments accounting for <5 % of the
106 total buried (Bernier, 1982; Duarte et al., 2005; Burdige, 2007). In the deep sea
107 and other settings with low burial efficiency, almost all organic matter is
108 degraded to inorganic carbon at rates that provide an excellent approximation

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133 for organic matter deposition (Jørgensen, 1982; Cai and Reimers, 1995; Glud,
134 2008). Organic matter degradation can be quantified via the consumption of
135 oxygen, the production of dissolved inorganic carbon and through the use of
136 pore-water data and diagenetic models (i.e. reaction-transport models for
137 sediments). At steady state, sediment oxygen consumption provides an accurate
138 measure for total sediment organic matter degradation, independent whether
139 organic matter is degraded aerobically (i.e. with oxygen) or anaerobically (with
140 alternative electron acceptors such as nitrate, metal oxides, sulphate), because
141 almost all reduced metabolites released (ammonium, manganese (II), iron(II),
142 hydrogen sulfide and methane) are re-oxidized (Jørgensen, 1977, 2006; Berner
143 and Westrich, 1985; Aller and Rude, 1988; Soetaert et al., 1996; Boetius et al.,
144 2000; Strous and Jetten, 2004; Raghoebarsing et al., 2006; Middelburg and Levin,
145 2009).

146 Biogeochemists have adopted a transport-reaction modeling approach to
147 accurately quantify organic matter processing (Berner, 1980; Boudreau, 1997;
148 Burdige, 2006). The basic premise of these diagenetic models is that both
149 particles and solutes are subject to transport and reaction, making them distinct
150 from for instance groundwater transport-reaction models in which normally
151 only solutes and gas phases are mobile (Lichtner, 1996; Appelo, 1996).

152 Transport of solutes is due to molecular diffusion, pore-water advection and
153 biologically mediated processes such as, enhanced diffusion due to interstitial
154 fauna (Aller and Aller, 1992) and bio-irrigation due to tube and burrow
155 construction and flushing by macrofauna (Aller, 1980, 1984; 2001; Volkenborn
156 et al., 2010; 2016; Kristensen et al., 2012). Particle transport is not only due to

157 steady particle deposition but also due to sediment reworking by animals
158 (bioturbation, Boudreau, 1997; Aller, 1994, 2013; Rice, 1986; Meysman et al.,
159 2003, 2006, 2010). The reaction terms in these diagenetic models are normally

160 limited to microbial and chemical reactions and are described using zero, first,
161 second order kinetic relationships or Monod/Michaelis-Menten type kinetics
162 (Bouldin, 1968; Berner, 1980; Soetaert et al., 1996; Boudreau, 1997). There is a
163 major inconsistency in the basic conceptual model underlying the (numerical)

164 diagenetic models: animals dominate transport processes via pore-water
165 irrigation and particle mixing, but without consuming any organic matter. This
166 inconsistency has not received much attention because the ruling paradigm
167 within the biogeochemical research community is that animals contribute very

168 little to total carbon processing. Multiple recent studies involving use of ¹³C as
169 deliberate tracers show that this premise does not hold on the short term (days
170 to weeks; Blair et al., 1996; Moodley et al., 2002, 2005a; Woulds et al., 2009,
171 2016). Moreover, detailed studies of oxygen consumption have revealed that
172 animals contribute substantially to total sediment oxygen uptake; directly via
173 their respiration as well as indirectly via particle and solute mixing (Glud, 2008).

174 Nevertheless, diagenetic models can very accurately reproduce most
175 observations (Soetaert et al., 1996; Berg et al., 2003).

176 Diagenetic models combined with solid-phase and pore-water depth
177 profiles, sediment-water exchange fluxes and rate measurement have resulted in
178 a consistent picture of organic matter degradation pathways in marine
179 sediments (Berner, 1980; Boudreau, 1997; Aller, 2013). These models can
180 predict where, when and why organic matter oxidation occurs aerobically or
181 involves nitrate, metal oxides or sulphate as oxidants (Rabouille and Gaillard,

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201 2001; Boudreau, 1996; Soetaert et al., 1996; Middelburg et al. 1996; van
202 Cappellen and Wang, 1996; Archer et al., 2002; Meysman et al., 2003; Berg et al.,
203 2003). They also resolve the re-oxidation of reduced products such as
204 ammonium, manganese(II), iron (II), sulfide and methane (Fig. 2) and as such
205 define the scope for aerobic and anaerobic organisms, **including** the distribution
206 and activity of chemoautotrophs (Middelburg, 2011). **Despite these advances,**
207 **diagenetic models cannot predict organic carbon burial rates, nor do they**
208 **provide much insight into why organic matter is buried, or why it is either labile**
209 **(reactive) or refractory. For this we need to have a detailed look at the organic**
210 **geochemistry of sediment organic carbon.**

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211 **3 Organic geochemists focus on the composition of organic matter** 212 **preserved**

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215 Organic matter delivered to the seafloor is predominantly produced in the
216 surface sunlit layer of the ocean (Fig. 3). This organic matter is rich in proteins,
217 carbohydrates and lipids and **generally** follows Redfield stoichiometry (Sterner
218 **and Elser, 2002**; Bianchi and Canuel, 2011). Organic matter processing leads to
219 preferential degradation of the more labile components with the result that
220 organic matter becomes less reactive (Jørgensen, 1979; Westrich and Berner,
221 1984; Middelburg, 1989; Arndt et al., 2013) and organic matter composition
222 changes (Fig. 1; Wakeham et al. 1997; Dauwe et al., 1999; Lee et al., 2000). The
223 proportion of organic matter that can be characterized molecularly decreases
224 with progressive degradation, i.e. with water depth or depth downcore
225 (Wakeham et al., 1997; Hedges et al., 2000; Middelburg et al., 1999; Nierop et al.,
226 2017). This molecularly uncharacterizable material increases to more than 70%
227 **of the total** in deep-sea **sediment** organic matter. The organic geochemical
228 approach to study organic matter processing is limited not only by our inability
229 to characterize the majority of the sedimentary organic matter, but also by the
230 simple fact that the degraded fraction cannot be **easily** studied and we have to
231 base our knowledge on the small fraction of extensively processed organic
232 material remaining.

233 The changes in organic matter composition due to organic matter
234 processing have been utilized to estimate the lability-digestibility or the
235 refractory nature of organic matter with various proxies such as chlorophyll to
236 bulk organic matter, fraction of nitrogen present as amino acids, and the
237 contribution of proteins and carbohydrates to total organic matter (Cowie et al.,
238 1992; Dell'Anno et al., 2000; Danovaro et al., 2001; Koho et al., 2013). The amino
239 acid based degradation index (Dauwe and Middelburg, 1998) is one of the most
240 commonly used proxies to quantify the extent of degradation or the quality of
241 the remaining particulate organic matter **and is based on subtle changes in the**
242 **amino acid composition due to organic matter processing** (Dauwe et al., 1999;
243 **Keil et al., 2000**).

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244 The compositional changes have also been used to infer transformation of
245 organic matter by bacteria (Cowie and Hedges, 1994; Dauwe et al., 1999;
246 Grutters et al., 2001; Vandewiele et al., 2009; Lomstein et al., 2006, 2012), extent
247 of degradation under oxic and anoxic conditions (Sinninghe Damsté et al., 2002;
248 Huguet et al, 2008; Nierop et al., 2017) and the relative importance of bacteria
249 and **fauna for** organic matter degradation (Sun et al., 1999; Woulds et al., 2012,

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268 2014). Although some organic geochemical studies hint at the importance of
269 secondary production (Hayes et al., 1989; Cowie and Hedges, 1994; Grutters et
270 al., 2001; Lomstein et al., 2006, 2012), this aspect has received little attention in
271 organic geochemistry, yet it is one of the main objectives within the ecological
272 approach.

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274 4 Ecologists focus on the dynamics of organisms using organic matter

275
276 Benthic communities are usually partitioned into different size classes
277 (e.g. macrofauna, meiofauna, and microbes; Gage and Tyler, 1992; Gray and Elliot,
278 2009; Herman et al., 1999), which are often studied by different research
279 communities having distinct objectives, approaches and tools. Organic matter
280 delivered to the seafloor fuels benthic food webs: i.e. it represents food for the
281 animals and the energy substrate for heterotrophic microbes. Microbial
282 ecologists study the growth of microbes on delivered organic matter (e.g.
283 bacterial production) and subsequent microbial loss processes, including
284 predation and viral lysis (Kemp, 1988; 1990; Danovaro et al., 2008, 2011, 2016).
285 Microbial ecologists also study in detail the identities and activities or organisms
286 involved in (an)aerobic respiration pathways and the re-oxidation of reduced
287 metabolites produced during anaerobic organic matter degradation (Canfield et
288 al., 2005). Animal ecologists focus on the response of fauna to food delivery, the
289 diet and growth of animals and transfer of carbon up the food chain to top
290 consumers (Krumins et al., 2013; Fig. 3). Interactions among food-web members
291 are considered the key to understand carbon flows (Pimm et al., 1991; van
292 Oevelen et al., 2010).

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293 During the last two decades, ¹³C-labeled phytodetritus addition
294 experiments have been performed to identify the organisms involved in the
295 immediate processing of organic matter delivered to the seafloor (Middelburg,
296 2014). These studies often covered all size classes (animals and microbes) and
297 could show that respiration was the major fate of added phytodetritus and that
298 all size classes directly profited from recently deposited organic matter (Blair et
299 al., 1996; Moodley et al., 2002, 2005a; Woulds et al., 2007, 2009, 2016; Witte et
300 al., 2003; Nomaki et al., 2005; Sweetman and Witte, 2008). In other words,
301 heterotrophic microbes and small and big animals compete for the same food.
302 Van Nugteren et al. (2009b) have shown that the spatial distribution of resources
303 is a key factor governing the relative use of phytodetritus by bacteria vs. animals.
304 Moreover, the relative share of organisms in the processing of organic matter
305 was in some systems and for some consumers proportional to the biomass of the
306 benthic size class, but not always (Moodley et al., 2005a; Woulds et al., 2009,
307 2016). For instance, foraminifera and amoebid protozoa, sometimes contribute
308 disproportionately to short-term carbon processing reflecting high turn-over of an
309 active community (Moodley et al., 2002; Woulds et al., 2007).

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312 5 Towards a synthesis

313
314 The above discussion on conceptual views within different research disciplines
315 highlights a few discrepancies and gaps in our knowledge. Secondary production
316 by animals and microbes is often not included in the biogeochemical view that

329 focuses on preservation versus mineralization. It is also largely absent from the
330 organic geochemical literature. Consumption of organic matter is restricted to
331 microbes in the **biogeochemical** view, while the non-fed animals move organic
332 matter, microbes and particles around, and enhance solute transfer by bio-
333 irrigation activities. The consumption of organic matter eventually results in
334 compositional changes of the organic matter remaining but there is little
335 information that the identity of the organism matters much. Whole ecosystem
336 labeling experiments revealed direct flow from detritus to most benthic
337 consumers and to the dissolved inorganic carbon pool, but these short-term
338 experimental results cannot directly be compared to the long-term natural
339 processing of deposited organic matter because long-term transfers **within** the
340 food web and eventual carbon preservation cannot be resolved experimentally.

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342 **5.1 On the consistency of food-web carbon processing and the** 343 **biogeochemical burial-respiration partitioning**

344 Food-web **models** describe the exchange of matter (e.g. carbon or energy) among
345 different compartments (organisms) within an ecosystem (Pimm et al., 1991; de
346 Ruyter et al., 1995) and **usually lump respiration losses** (Cole et al., 2006; van
347 Oevelen et al., 2010; **Fig. 3 left**). Experimental studies using ¹³C labelled
348 phytodetritus as a tracer of sediment carbon processing showed that animals
349 and microbes both can assimilate labile carbon directly and confirmed that
350 respiration is the largest sink (Moodley et al., 2005a; Buhning et al., 2006;
351 Andersson et al. 2008; Woulds et al. 2009, 2016). The **biogeochemical** budgeting
352 approach basically distinguishes only between (refractory) carbon preserved
353 and buried versus labile organic carbon that is respired to carbon dioxide (Aller,
354 2013; Fig. 3 right). These ecological and **biogeochemical** concepts **can be**
355 consistent **depending on the timescale**, considered. On the time scale of days to
356 month deposited carbon is processed by the benthic organisms, a small part is
357 assimilated and the majority is respired. On longer time scales and when
358 considering steady-state conditions, i.e. constant faunal and microbial biomass,
359 there is transfer from the detritus pool to the living biomass pool, **but these**
360 **secondary producers die and their remains are returned to the detritus pool for**
361 **another cycle with the result that eventually all labile organic matter is respired**.

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Deleted: because organisms only represent a (temporary) carbon sink when their biomass is building up or when remains of secondary producers are buried.

364 **5.2 Secondary production and the formation of molecularly** 365 **uncharacterizable organic matter.**

366 The mere presence of living organisms in sediments clearly indicates that
367 secondary production is omnipresent. Microbes usually dominate living biomass,
368 but not always, and living biomass typically contributes a few % to the standing
369 stock of total organic carbon in **coastal** sediments (Herman et al., 1999). **The**
370 **importance of microbial biomass relative to total biomass increases with**
371 **increasing water depth** (Rex et al., 2006; Danovaro et al., 2014, 2015). **Moreover,**
372 **living biomass may contribute substantially to total carbon stocks in coarse-**
373 **grained sandy sediments with low background organic carbon contents** (Herman
374 **et al., 1999; Evrard et al., 2012**). Various types of experimental evidence have
375 shown that carbon flow through **the living** compartment is much higher than
376 through the non-living sediment organic matter pool. Short-term, in situ

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398 experiments using ^{13}C and/or ^{15}N labelled organic matter (e.g. phytodetritus)
399 revealed rapid incorporation of $^{13}\text{C}/^{15}\text{N}$ in physically separated organisms
400 (macro- and meiofauna and foraminifera) and microbes, the latter via
401 incorporation of tracers in biomarkers specific for certain microbial groups
402 (Middelburg et al., 2000; Boschker and Middelburg, 2002; Veuger et al., 2007;
403 Oakes et al., 2012; Woulds et al., 2007, 2016) Similarly, ammonium isotope
404 dilution studies have shown that net ammonification (ammonium release) is
405 only a fraction of the total ammonium regeneration because a substantial part of
406 the ammonium liberated is re-assimilated by the microbial community
407 (Blackburn and Henriksen, 1983). Clearly the microbes and animals living in
408 sediment assimilate carbon and synthesize new biomass (Veuger et al., 2012).
409 How can this be reconciled with the biogeochemical and organic geochemical
410 views in which organic matter is either preferentially degraded to carbon dioxide
411 or selectively preserved (Fig. 1, 3). These two apparently inconsistent views are
412 consistent if most of the newly produced organic matter is eventually degraded.

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413 Detailed investigations of organic matter composition might in principle
414 resolve this issue as microbial and animal processing of organic matter results in
415 the formation of distinct compounds (Bradshaw et al., 1990; Sun et al., 1999;
416 Thomas and Blair, 2002; Woulds et al., 2012, 2014). There are few issues with
417 this approach: (1) most sedimentary organic matter is molecularly
418 uncharacterizable and the origin (imported from the water column vs. newly
419 produced within the sediment) can thus not directly be investigated, (2)
420 microbes living within (the guts) of animals may mask the animal signatures
421 (Woulds et al., 2012, 2014) and (3) different analytical windows (amino acids vs.
422 lipids) may result in different inferences. On one hand, the accumulation of
423 bacterial derived non-protein amino acids and peptidoglycan derived D amino
424 acids are clear signs that extensively modified organic matter contains a major
425 fraction that is derived from (heterotrophic) bacteria (Cowie and Hedges, 1994;
426 Dauwe et al., 1999; Grutters et al., 2001; Lomstein et al., 2006; Keil and Fogel,
427 2001; Keil et al., 2000). Using fatty acids, Gong and Hollander (1997) also
428 identified a substantial microbial contribution to sedimentary organic matter. On
429 the other hand, using a combined lipid-isotope approach Hartgers et al. (1994)
430 reported only a minor contribution of bacteria to sedimentary organic carbon
431 pools.

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432 Secondary production has potentially major consequences for the
433 interpretation of sedimentary records. If microbial reworking of deposited
434 organic matter represents a major carbon flow and part of the material is
435 preserved, then one would expect that bulk organic matter properties such as C,
436 N, P elemental ratios and nitrogen and carbon isotopes would reflect this.
437 Degradation of organic matter initially results in the preferential release of
438 nitrogen and phosphorus relative to carbon. Microbes normally have lower C:N
439 ratios than their substrate, (Sterner and Elser, 2002) implying that secondary
440 production and accumulation of microbial derived organic matter should
441 eventually result in a net decrease of sediment C:N ratios (Müller, 1977). In
442 contrast, the C:P ratio of heterotrophic microbes is rather variable because P
443 demands depends on the growth rate (Sterner and Elser, 2002) and slowly
444 growing benthic microbes may have high C:P ratios (Steenbergh et al., 2013).
445 Moreover, microbial P storage also depends on redox conditions with the
446 consequences that sedimentary C:P ratios are highly variable (Algeo and Ingall,

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463 2007). Sediment $\delta^{15}\text{N}$ values often show a post-depositional shift towards
464 heavier values in alternating oxic/anoxic settings (Moodley et al., 2005b). Such a
465 shift is to be expected because regenerated ammonium is either transformed
466 into nitrite/nitrate (nitrification) or re-assimilated by the microbial community.
467 During oxic conditions nitrification occurs with preference for ^{14}N and the
468 remaining ammonium available for re-assimilation by microbes will be relatively
469 rich in ^{15}N , while during anoxic conditions oxidation of ammonium is less
470 important or absent, and the ammonium re-assimilated will have similar $\delta^{15}\text{N}$
471 values as that regenerated. Secondary production within sediment may also
472 impact the interpretation of bulk stable carbon isotope records (Hayes et al.,
473 1998) and paleorecords of microbial biomarkers (Schouten et al., 2010).

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474 To reconcile the strong experimental evidence for preferential
475 degradation (Middelburg, 1989), selective preservation (Tegelaar et al., 1989)
476 and formation of new compounds by secondary producers (Lomstein et al, 2012;
477 Braun et al, 2017) present a new integral concept (Fig. 4). Phytodetritus
478 delivered to sediments is preferentially degraded with the result that new
479 biomass is formed and that some compounds are selectively preserved. The
480 newly formed biomass is after death of the organism added to the pool of
481 degraded detritus and subject to further microbial processing. After multiple
482 cycles of processing by benthic heterotrophs most of the remaining organic
483 matter becomes molecularly uncharacterizable. This conceptual model is
484 consistent with the ruling paradigms of preferential degradation and selective
485 preservation as well as with the occurrence of secondary production and
486 formation of molecular uncharacterizable organic matter, but the next step is to
487 quantify this conceptual view. One approach would be to use proxies for organic
488 matter degradation state such as fraction of total nitrogen present as amino acid,
489 non-protein amino acids accumulation and the degradation index (Cowie and
490 Hedges, 1994; Dauwe and Middelburg, 1998; Dauwe et al., 1999). Lomstein et al.
491 (2012) and Braun et al. (2017) used amino acid racemization to quantify
492 turnover of living microbial biomass as well as of bacterially derived organic
493 matter (necromass) in the deep biosphere. Veuger et al. (2012) executed a
494 $^{13}\text{C}/^{15}\text{N}$ tracer experiment and followed the isotope labels into carbohydrates,
495 amino acids and lipids and basically showed that most of the deliberately added
496 heavy isotopes were recovered from the molecularly uncharacterizable pool
497 within a few weeks and remained in that pool till the end of the experiment (> 1
498 year). Their study provided direct evidence for rapid formation of new microbial
499 biomass and subsequent transfer of microbial biomass to the pool of molecular
500 uncharacterizable organic matter. Moreover, the efficient retention of label was
501 indicative of recycling of molecules (or parts thereof) by microbes rather than de
502 novo synthesis, consistent with findings for archaeal lipids in marine sediments
503 (Takano et al., 2010, Lipsewiers et al., 2017) and bacteria in soils, (Dippold and
504 Kuzyakov, 2016).

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507 5.3 Animals and carbon supply to sediments

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

517 control on its carbon delivery (Fig. 5). It is only on the time-scale of ocean
518 bottom-water renewal (100-1000 years) that nutrient regenerated by benthic
519 organisms may impact primary producers in the sunlit upper part of the ocean
520 (Soetaert et al., 2000). This is obviously different for sediments in the photic
521 zone that make up about 1/3 of the coastal ocean (Gattuso et al, 1996) because
522 animals can directly graze and consume the benthic primary producers at the
523 sediment surface (Middelburg et al., 2000; Evrard et al., 2010, 2012; Oakes et al.,
524 2012; Fig. 5). Donor and consumer controlled food webs have intrinsically
525 different dynamics.

526 Animals living in sediments below the photic zone can in multiple ways
527 impact carbon processing within marine sediments (Fig. 5). Deposit-feeding
528 animals mix particles (and thus particulate organic carbon) as a consequence of
529 their activities. In the case of constant organic carbon delivery (donor-control)
530 bioturbation stimulates organic carbon processing at depth (Herman et al.,
531 1999). In coastal systems, organic matter delivery is more complex because of
532 multiple deposition-resuspension events and lateral transport pathways. Rice
533 and Rhoads (1989) showed that in this case (with constant organic carbon
534 concentration in the top layer) more sediment reworking will increase the
535 organic matter flux into the sediment. Moreover, organic carbon gradients with
536 depth are steeper for high-quality than low-quality material and particle mixing
537 thus results in transfer of high-quality organic matter to (micro-)organisms
538 living at depth. Animals living in permeable sediment can via surface sediment
539 topography (bioroughness) induce pore-water flows resulting in the trapping of
540 phytoplankton (Huettel et al., 2014).

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

553 Some invertebrates have the capability to take up dissolved organic
554 carbon and in particular sponges can assimilate substantial quantities and
555 transform it into biomass (de Goeij et al., 2013; Fiore et al., 2017; Hoer et al.,
556 2017). This sponge tissue and in particular its detritus can be consumed by
557 benthic organisms. This sponge loop (de Goeij et al., 2013; Rix et al., 2016) is
558 another example how animals can manipulate the transfer of organic carbon
559 from the water-column to the sediments (Fig. 5).

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562 5.4 Animal stimulation of microbes: An inverted microbial loop?

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The microbial loop is a key concept in ocean biogeochemistry (Pomeroy,
1974; Azam et al., 1983). Dissolved organic matter released by phytoplankton,

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573 zooplankton or viral lysis of bacteria, archaea and algae is consumed by
574 heterotrophic microbes. These heterotrophs are in turn consumed by flagellates,
575 ciliates and other small consumers that are predated upon by zooplankton
576 (Azam et al., 1983; Jumars et al. 1989). Energy shunted into the large,
577 heterogeneous dissolved organic matter pool is in this way made available again
578 for animals (Fig. 6).

579 After discovery of this loop in the surface ocean water, research has been
580 executed to identify and quantify it in sediments (Kemp, 1988, 1990). This
581 required substantial investment in developing new methods: these studies
582 basically revealed that predation on sedimentary bacteria was not that
583 important (Kemp, 1990; Hondeveld et al., 1992; Hamels et al., 2001; Guilini et al.,
584 2009). Van Oevelen et al., (2006) made a detailed study on the fate of bacterial
585 production using in situ ¹³C labelling of bacteria. They observed that 8% was lost
586 by physical processes, 27% was consumed by animal predation, while bacterial
587 mortality accounted for 65%. Viruses are the most important loss term for
588 sedimentary microbes (Danovaro et al, 2009, 2011, 2016) and the viral lysis
589 products (dissolved organic matter) are consumed by microbes. This results in a
590 dissolved organic carbon-microbes cycle (Fig. 6). This benthic microbial cycle
591 represents a dead end in terms of food web topology, because there is little
592 transfer to higher trophic levels and most carbon is eventually respired as
593 needed for mass-balance closure on the long term (Fig. 3).

594 In fact, the benthic microbial cycle represents more an *inverted microbial*
595 *loop*: rather than animals profit from the microbial loop sensu Azam et al. (1983),
596 it appears that benthic microbes profit from animals mixing labile organic matter
597 downwards into the sediments (Fig. 6). Labile organic matter delivered to the
598 sediment surface is mixed by animals inhabiting the sediments (Fig. 5). The
599 transfer of high quality organic matter to deeper sediment layer may prime
600 sediment microbial communities and in this way stimulate degradation of
601 indigenous organic matter (Canfield, 1994; van Nugteren et al, 2009a, Bianchi,
602 2011; Hannadis & Aller, 2017). Moreover, tube construction and ventilation by
603 animals brings dissolved oxygen to deeper sediment layers and will in this way
604 stimulate organic matter mineralization (Canfield, 1994; Kristensen et al., 1995;
605 Dauwe et al., 2001). Bio-irrigation activities may be intermittent (Volkenborn et
606 al., 2016) and cause oscillations in oxygen availability that stimulate organic
607 matter degradation (Aller and Aller, 1998). This inverted microbial loop is a
608 prime example how animals as ecosystem engineers impact sediment carbon
609 processing (Meysman et al., 2006).

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611

612 5.5 Imagine a world without animals.

613

614 An ocean floor inhabited solely by microbes and without animals was likely the
615 reference state during the first four billion of years of Earth's history (Canfield,
616 2014; Lenton and Watson, 2011). Moreover, in modern systems with anoxic
617 bottom waters benthic animals are absent (Rhoads and Morse, 1971; Diaz and
618 Rosenberg, 1995, 2008; Levin, 2003; Levin et al, 2009). In these systems, organic
619 matter degradation pathways are different not only because of a lack of oxygen
620 and use of alternative electron acceptors, but also because bio-irrigation and
621 sediment reworking are absent (Aller and Aller, 1998; Levin et al., 2009;

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623 Middelburg and Levin, 2009). Consequently, microbe-fauna interactions
624 (enhanced carbon delivery, Fig. 5; animal stimulation of microbes, Fig. 6) are
625 impeded.
626 While organic matter mineralization in the presence of oxygen may be more
627 efficient than in anoxic environments (Canfield, 1994; Kristensen et al., 1995;
628 Dauwe et al. 2001) , the lack of animal stimulation of microbes may also
629 contribute to burying organic carbon more efficiently in sediments underlying
630 anoxic bottom waters (Hartnett et al., 1998; Hartnett and Devol, 2003;
631 Middelburg and Levin, 2009; Jessen et al., 2017). Moreover, the organic matter
632 buried in hypoxic and anoxic settings is usually less degraded (Cowie, 2005,
633 Cowie et al., 2009; Vandewiele et al., 2009; Koho et al., 2013; Jessen et al., 2017).
634 This presence of animals and all their interactions with organic matter and
635 microbes has consequences for organic carbon processing in marine sediments
636 and thus the global carbon cycle. It is obvious for any terrestrial microbiologist
637 that a world with trees and other macrophytes would be different than one
638 without. Moreover, biological oceanographers and limnologists agree that
639 zooplankton and other metazoan consumers contribute to biogeochemical cycles
640 (Vanni, 2002; Vanni and McIntyre, 2016), and I hope that colleagues studying
641 marine sediments are aware that BIO in sediment biogeochemistry is more than
642 just microbiology.

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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. The red-orange-yellow fractions of organic matter have a different lability.

Figure 2. Conceptual model of organic matter (OM) degradation and re-oxidation pathways (based on Middelburg and Levin, 2009). The red arrows reflect the fate of (energy-rich) substrates released during anaerobic mineralization.

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. The red-orange-yellow fractions of organic matter have a different lability.

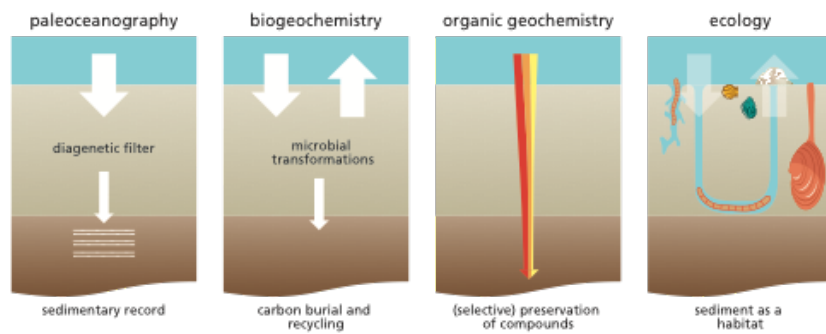
Figure 5. Organic matter supply to sediments. 1. The traditional view of organic matter settling passively from the water column (donor control). 2. Sediments in the photic zone are inhabited by benthic microalgae that produce new organic matter in situ and grazing animals can impact the growth of these primary producers. 3. Bioturbating animals transfer labile carbon from the sediment surface layer to deeper layers in the sediments. (Vertical axis is depth, horizontal is concentration) 4. Suspension feeding organisms enhance the transfer of suspended particulate matter from the water column to the sediments (biodeposition). 5. Sponges 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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Figure 1. Different views, approaches and interests on carbon processing in marine sediments. Paleceanographers 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. The red-orange-yellow fractions of organic matter have a different lability.

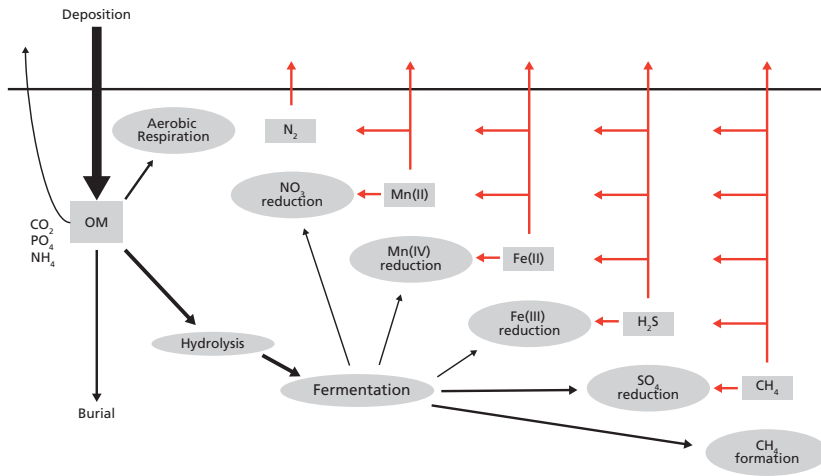


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Figure 2. Conceptual model of organic matter (OM) degradation and re-oxidation pathways (based on Middelburg and Levin, 2009). The red arrows reflect the fate of (energy-rich) substrates released during anaerobic mineralization.

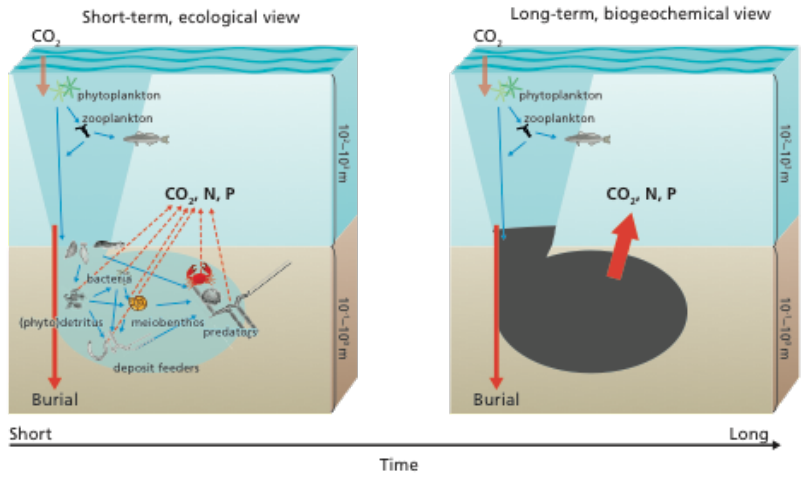


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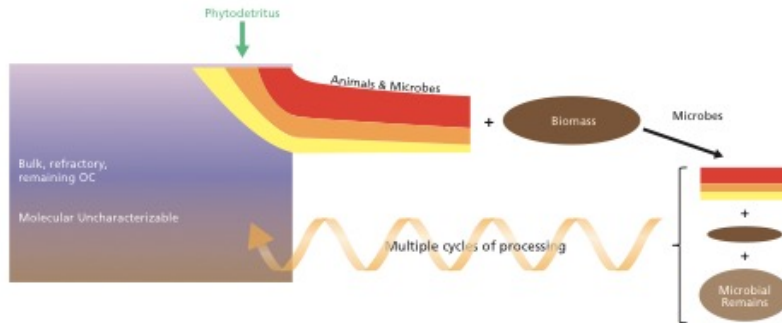
Figure 3. Carbon processing in marine sediments on the short-term (left) and the long-term (right). Organic matter produced in the sunlit layer of the ocean and delivered to the sediments is either consumed by organisms or buried. The organic matter consumed by organisms is used to synthesize biomass 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).



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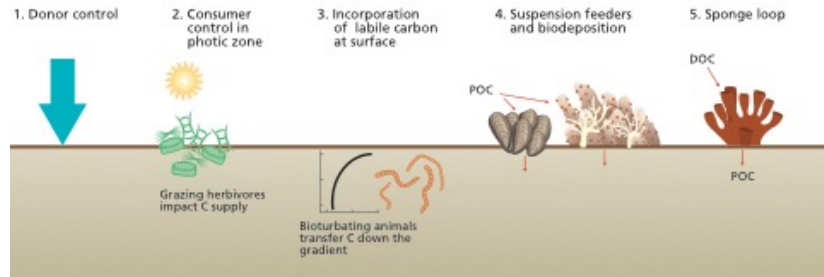


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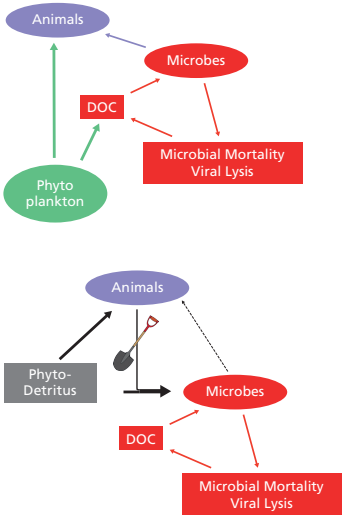


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