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1
2 Reviews and Synthesis: To the bottom of carbon processing at
3 the seafloor
4
5 **Jack J. Middelburg***
6
7 Earth Sciences, Utrecht University, PO Box 80 021, 3508 TA Utrecht, The
8 Netherlands
9
10 ** Invited contribution by Jack J. Middelburg, recipient of the EGU Vladimir*
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12
13 **Abstract**
14
15   Organic carbon processing at the seafloor is studied by geologists to
16 better understand the sedimentary record, by biogeochemists to quantify burial
17 and respiration, by organic geochemists to elucidate compositional changes and
18 by ecologists to follow carbon transfers within food webs. Here I review these
19 disciplinary approaches and discuss where they agree and disagree. It shown
20 that the biogeochemical approach (ignoring the identity of organisms) and the
21 ecological approach (focussing on growth and biomass of organisms) are
22 consistent on longer time scales. It is hypothesized that secondary production by
23 microbes and animals might impact the composition of sedimentary organic
24 matter eventually buried. Animals impact sediment organic carbon processing
25 by microbes in multiple ways: by governing organic carbon supply to sediments
26 and by mixing labile organic matter to deeper layers. An inverted microbial loop
27 is presented in which microbes profit from bioturbation rather than animals
28 profiting from microbial processing of otherwise lost dissolved organic
29 resources. Sediments devoid of fauna therefore function differently and are less
30 efficient in processing organic matter with the consequence that more organic
31 matter is buried and transferred from Vernadsky's biosphere to the geosphere.
32
33
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 (Berner, 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 carbon is recycled within the
45 biosphere (short-term cycle) or transferred to the geosphere (long-term cycle)
46 and as such it functions as a key interface in the System Earth.
47   This pivotal role of the seafloor in processing material deposited has been
48 studied by scientists from various disciplines with their own interests,
49 techniques and paradigms (Figure 1). Marine geologists and paleoceanographers

50   study sediments with the primary aim to extract information on past
51   environmental conditions using down-core measurements of substances
52   delivered to the seafloor and that have survived the processing at the seafloor
53   (Burdige, 2006; Bender, 2013). Biogeochemists quantify the fate of material
54   delivered, in particular how much of the material is eventually buried or
55   processed, and determine when and in what form the remaining part is recycled
56   to the water column, because recycling of key nutrients (e.g. N, P, Si, Fe) sustains
57   primary production (Berner, 1980; Aller, 1980, 2001, 2013; Soetaert et al.,
58   2000). Organic geochemists investigate how organic matter delivered to the
59   seafloor is degraded, transformed or preserved using changes in the composition
60   at the molecular level (Hedges and Keil, 1995; Dauwe et al, 1999; Burdige, 2006;
61   Bianchi and Canuel, 2011). Ecologists focus on the organisms, i.e. the actors
62   consuming, producing and transporting the material deposited (Gage and Tyler,
63   1992; Gray and Elliot, 2009; Herman et al., 1999; Krumins et al., 2013).
64   Although these disciplines often study the same topic, e.g. organic matter
65   delivered to the seafloor, they focus on different aspects and usually ignore key
66   concepts, findings and approaches from other disciplines. For example,
67   ecologists and biogeochemist studying carbon flows at the seafloor normally
68   ignore detailed molecular information available from organic geochemistry.
69   Bioturbation, particle transport and mixing by animals at the seafloor , is often
70   ignored by paleoceanographers, and biogeochemists have developed advanced
71   transport-reaction models in which the actors, the animals, mix the particles but
72   do so without consuming organic matter, their food.
73   Here I present the existing views on organic carbon processing at the
74   seafloor, discuss where they agree and disagree and aim to arrive at an
75   integrated view of carbon processing at the seafloor that is consistent with
76   recent views within the organic geochemical, sediment geochemical, ecological
77   and microbiological research communities. This overview is necessarily and
78   admittedly incomplete but rather covers personal interests and presents new
79   concepts on this topic. It is a concise version of the Vernadsky Medal Lecture
80   presented at the 2017 EGU meeting.
81
82   **2 Geochemists focus on quantification of burial and mineralization**.
83
84   Organic matter delivered to marine sediments eventually is either
85   mineralized and the metabolites (carbon dioxide and nutrients) accumulate in
86   pore-waters and exchange with the overlying water, or it is not consumed and
87   then buried through the steady accumulation of particles (Fig. 2). This
88   geochemical view is highly simplified, but for that reason also quantitative and
89   instructive (Berner, 1980; Boudreau, 1997; Aller, 2013). The percentage of
90   organic matter buried varies from less than one % to a few tens % and is closely
91   related with total sediment accumulation rate (Canfield, 1989, 1994; Middelburg
92   et al., 1993). Since sediment accumulation rates are much higher in vegetated,
93   coastal, deltaic, shelf and ocean-margin settings, the majority of organic matter
94   burial occurs there, with organic carbon burial in deep-sea sediments accounting
95   for <5 % (Berner, 1982; Duarte et al., 2005; Burdige, 2007). In the deep sea and
96   other low burial efficiency settings, almost all organic matter is degraded to
97   inorganic carbon and organic matter degradation rates provide an excellent
98   proxy for organic matter deposition (Jørgensen, 1982; Cai and Reimers, 1995;

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

148 ammonium, manganese(II), iron (II), sulfide and methane (Fig. 2) and as such
149 define the scope for aerobic and anaerobic organisms and the distribution and
150 activity of chemoautotrophs. Chemoautotrophs in sediments produce about 0.4
151 Tg C y^{-1}, similar to the riverine delivery of organic carbon to the ocean
152 (Middelburg, 2011). However, these diagenetic models cannot predict organic
153 carbon burial rates, nor do they provide much insight why organic matter is
154 buried or why it is labile (reactive) or rather refractory. For this we need to have
155 a detailed look at the organic geochemistry of sediment organic carbon.
156
157 **3 Organic geochemists focus on the composition of organic matter**
158 **preserved**
159
160   Organic matter delivered to the seafloor is predominantly produced in the
161 surface sunlit layer of the ocean (Fig. 3). This organic matter is rich in proteins,
162 carbohydrates and lipids and follows Redfield stoichiometry (Bianchi and
163 Canuel, 2011). Organic matter processing leads to preferential degradation of the
164 more labile components with the result that organic matter becomes less
165 reactive (Middelburg, 1989; Arndt et al., 2013) and organic matter composition
166 changes (Fig. 1; Wakeham et al. 1997; Dauwe et al., 1999; Lee et al., 2000). The
167 proportion of organic matter that can be characterized molecularly decreases
168 with progressive degradation, i.e. with water depth or depth downcore
169 (Wakeham et al., 1997; Hedges et al., 2000; Middelburg et al., 1999; Nierop et al.,
170 2017). This molecularly uncharacterizable material increases to more than 70%
171 in deep-sea organic matter. The organic geochemical approach to study organic
172 matter processing is limited not only by our inabilities to characterize the
173 majority of the sedimentary organic matter, but also by the simple fact that the
174 degraded fraction cannot be studied and we have to base our knowledge on the
175 small fraction of extensively processed organic material remaining.
176   The changes in organic matter composition due to organic matter
177 processing have been utilized to estimate the lability-digestability or its reverse
178 the refractory nature of organic matter with various proxies such as chlorophyll
179 to bulk organic matter, fraction of nitrogen present as amino acid, and the
180 contribution of proteins and carbohydrates to total organic matter (Cowie et al.,
181 1992; Dell'Anno et al., 2000; Danovaro et al., 2001; Koho et al., 2013). The amino-
182 acid based degradation index (Dauwe and Middelburg, 1998) is one of the most
183 commonly used proxies to quantify the extent of degradation or the quality of
184 the remaining particulate organic matter (Dauwe et al., 1999; Keil et al., 2000).
185   The compositional changes have also been used to infer transformation of
186 organic matter by bacteria (production of bacterial transformation products;
187 accumulation of D-amino acids; Cowie and Hedges, 1994; Dauwe et al., 1999;
188 Grutters et al., 2001; Vandewiele et al., 2009; Lomstein et al., 2006, 2012), extent
189 of degradation under oxic and anoxic conditions (Sinninghe Damsté et al., 2002;
190 Huguet et al, 2008; Nierop et al., 2017) and the relative importance of bacterial
191 and faunal pathways of organic matter degradation pathways (Sun et al., 1999;
192 Woulds et al., 2012, 2014). Although some organic geochemical studies hint at
193 the importance of secondary production (new organic matter produced by
194 microbes and animals and other heterotrophs; Cowie and Hedges, 1994; Grutters
195 et al., 2001; Lomstein et al., 2006, 2012), this aspect has received little attention

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

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245   bio-irrigation activities. The consumption of organic matter eventually results in
246   compositional changes of the organic matter remaining but there is little
247   information that the identity of the organism processing the organic carbon
248   matters much. Whole ecosystem labeling experiments revealed direct flow from
249   detritus to most benthic consumers and to the dissolved inorganic carbon pool,
250   but these short-term experimental results cannot directly be compared to the
251   long-term natural processing of deposited organic matter because long-term
252   transfers in the food web and eventual carbon preservation cannot be resolved
253   experimentally.

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

258   Food webs describe the exchange of matter (e.g. carbon or energy) among
259   different compartments (organisms) within an ecosystem (Pimm et al., 1991; de
260   Ruiter et al., 1995) and thus formalize the ecological view on carbon processing
261   (Cole et al., 2006; van Oevelen et al, 2010). The emphasis is on interaction among
262   organisms and respiration losses are normally lumped into a single carbon
263   dioxide loss term (Fig. 3 left). Experimental studies using ^{13}C labelled
264   phytodetritus as a tracer of sediment carbon processing showed that animals
265   and microbes both can assimilate labile carbon directly and confirmed that
266   respiration is the largest sink (Moodley et al, 2005a; Buhring et al., 2006;
267   Andersson et al. 2008; Woulds et al. 2009, 2016). The geochemical budgeting
268   approach basically distinguishes only between (refractory) carbon preserved
269   and buried versus labile organic carbon that is respired to carbon dioxide (Glud,
270   2008; Aller, 2013; Fig. 3 right). These ecological and geochemical concepts are
271   consistent when the typical timescale of interest is considered. On the time scale
272   of days to month deposited carbon is processed by the benthic organisms, a
273   small part is assimilated and the majority is respired. On longer time scales and
274   when considering steady-state conditions, i.e. constant faunal and microbial
275   biomass, there is no net transfer from the detritus pool to the living biomass pool
276   and all labile carbon is eventually respired because organisms only represent a
277   (temporary) carbon sink when their biomass is building up or when remains of
278   secondary producers are buried.

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

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

294   Veuger et al., 2007; Oakes et al., 2012;, Woulds et al., 2007, 2016) Similarly,
295   ammonium isotope dilution studies have shown that net ammonification is only
296   a small fraction of the total ammonium regeneration because most of the
297   ammonium liberated is re-assimilated by the microbial community (Blackburn
298   and Henriksen, 1983). Clearly the microbes and animals living in sediment
299   assimilate carbon and synthesize new tissues. How can this be reconciled with
300   the geochemical and organic geochemical views in which organic matter is either
301   preferentially degraded to carbon dioxide or selective preserved (Fig. 1, 3).
302   These two apparently inconsistent views are consistent if all of the newly
303   produced organic matter is eventually degraded.
304   Detailed investigations of organic matter composition might in principle
305   resolve this issue as microbial and animal processing of organic matter results in
306   the formation of distinct compounds (Bradshaw et al., 1990; Sun et al., 1999;
307   Thomas and Blair, 2002; Woulds et al., 2012, 2014). There are few issues with
308   this approach: (1) most sedimentary organic matter is molecularly
309   uncharacterizable and the origin (imported from the water column vs. newly
310   produced within the sediment) can thus not be investigated, (2) microbes living
311   within (the guts) of animals may mask the animal signatures (Woulds et al.,
312   2012, 2014) and (3) different analytical windows (amino acids vs. lipids) may
313   result in different inferences. On the one hand, the accumulation of bacterial
314   derived non-protein amino acids and peptidoglycan derived D amino acids are
315   clear signs that extensively modified organic matter contains a major fraction
316   that is derived from (heterotophic) bacteria (Cowie and Hedges, 1994; Dauwe et
317   al., 1999; Grutters et al., 2001; Lomstein et al., 2006; Keil and Fogel, 2001; Keil et
318   al., 2000). On the other hand, using a combined lipid-isotope approach Hartgers
319   et al. (1994) reported only a minor contribution of bacteria to sedimentary
320   organic carbon pools. However, Gong and Hollander (1997) used fatty acids and
321   identified a substantial microbial contribution to sedimentary organic matter.
322   Secondary production has potentially major consequences for the
323   interpretation of sedimentary records. If microbial reworking of deposited
324   organic matter represents a major carbon processing flow and part of the
325   material is preserved then one would expect that bulk organic matter properties
326   such as C, N, P elemental ratios and nitrogen isotopes would reflect this.
327   Degradation of organic matter usually results in the preferential release of
328   nitrogen and phosphor relative to carbon. Microbes normally have lower C/N
329   ratios than their substrate, implying that secondary production and
330   accumulation of microbial derived organic matter results in a net decrease of
331   sediment C/N ratios (Müller, 1977). In contrast, the C/P ratio of heterotrophic
332   microbes is rather variable because P demands depends on the growth rate
333   (Sterner and Elser, 2002) and slowly growing benthic microbes may have high
334   C:P ratios (Steenbergh et al., 2013). Moreover, microbial P storage also depends
335   on redox conditions with the consequences that sedimentary C:P ratios are
336   highly variable (Algeo and Ingall, 2007). Sediment $\delta^{15}N$ values often show a post-
337   depositional shift towards heavier values in alternating oxic/anoxic settings
338   (Moodley et al., 2005b). Such a shift is to be expected because regenerated
339   ammonium is either transformed into nitrite/nitrate (nitrification) or re-
340   assimilated by the microbial community. During oxic conditions nitrification
341   occurs with preference for ^{14}N and the remaining ammonium available for re-
342   assimilation by microbes will be relatively rich in ^{15}N, while during anoxic

343   conditions oxidation of ammonium is less important or absent, and the
344   ammonium re-assimilated will have similar $\delta^{15}N$ values as that regenerated.
345   Secondary production of microbial biomarkers within sediment may also impact
346   the interpretation of paleorecords (Schouten et al., 2010).
347   To reconcile the strong experimental evidence for preferential
348   degradation (Middelburg, 1989), selective preservation (Tegelaar et al., 1989)
349   and formation of new compounds by secondary producers (Lomstein et al, 2012;
350   Braun et al, 2017) we present a new integral concept (Fig. 4). Phytodetritus
351   delivered to sediments is preferentially degraded with the result that new
352   biomass is formed and that some compounds are selectively preserved. The
353   newly formed biomass is after death of the organism added to the pool of
354   degraded detritus and subject to further microbial processing. After multiple
355   cycles of processing by benthic heterotrophs most of the remaining organic
356   matter becomes molecularly uncharacterizable. This conceptual model is
357   consistent with the ruling paradigms of preferential degradation and selective
358   preservation as well as with the occurrence of secondary production and
359   formation of molecular uncharacterizable organic matter, but the next step is to
360   quantify this conceptual view. One approach would be to use proxies for organic
361   matter degradation state such as fraction of total nitrogen present as amino acid,
362   non-protein amino acids accumulation and the degradation index (Cowie and
363   Hedges, 1994; Dauwe and Middelburg, 1998; Dauwe et al., 1999). Lomstein et al.
364   (2012) and Braun et al. (2017) used amino acid racemization to quantify
365   turnover of living microbial biomass as well as of bacterially derived organic
366   matter (necromass) in the deep biosphere. Veuger et al. (2012) executed a
367   $^{13}C/^{15}N$ tracer experiment and followed the isotope labels into carbohydrates,
368   amino acids and lipids and basically showed that most of the deliberately added
369   heavy isotopes were recovered from the molecularly uncharacterizable pool
370   within a few weeks and remained in that pool till the end of the experiment (>
371   1year). Their study provided direct evidence for rapid formation of new
372   microbial biomass and subsequent transfer of microbial biomass to the pool of
373   molecular uncharacterizable organic matter. Moreover, the efficient retention of
374   label was indicative of recycling of molecules (or parts thereof) by microbes
375   rather than de novo synthesis, consistent with findings in soil science (Dippold
376   and Kuzyakov, 2016).
377
378
379   **5.3 Animals and carbon supply to sediments**
380
381   Marine sediments are often considered donor-controlled systems, i.e. organic
382   matter is delivered via settling of organic matter produced in the sunlit upper
383   part of the ocean (Fig. 3) and the consuming sediment communities have no
384   control on its carbon delivery (Fig. 5). It is only on the time-scale of ocean
385   bottom-water renewal (10-100 years) that nutrient regenerated by benthic
386   organisms may impact primary producer in the sunlit upper part of the ocean
387   (Soetaert et al., 2000). This is obviously different for sediments in the photic
388   zone that make up about 1/3 of the coastal ocean (Gattuso et al, 1996) because
389   animals can directly graze and consume the benthic primary producers at the
390   sediment surface (Middelburg et al., 2000; Evrard et al., 2010, 2012; Oakes et al.,

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391   2012; Fig. 5). Donor and consumer controlled food webs have intrinsic different
392   dynamics.
393   Animals living in sediments below the photic zone can in multiple ways
394   impact carbon processing within marine sediments (Fig. 5). Deposit-feeding
395   animals mix particles (and thus particulate organic carbon) as a consequence of
396   their activities. In the case of constant organic carbon delivery (donor-control)
397   bioturbation stimulates organic carbon processing at depth (Herman et al.,
398   1999). In coastal systems, organic matter delivery is more complex because of
399   multiple deposition-resuspension events and lateral transport pathways. Rice
400   and Rhoads (1989) showed that in this case (with constant organic carbon
401   concentration in the top layer) more bioturbation will increase the organic
402   matter flux into the sediment. Moreover, organic carbon gradients with depth
403   are steeper for high-quality than low-quality material and bioturbation thus
404   results in transfer of high-quality organic matter to (micro-)organisms living at
405   depth. Animals living in permeable sediment can via surface sediment
406   topography (bioroughness) induce pore-water flows resulting in the trapping of
407   phytoplankton (Huettel et al., 2014).
408   Tropical and cold-water corals, coastal and deep-sea sponges, suspension
409   feeding bivalves and other marine forests communities utilize particulate
410   organic matter suspended in the water (Herman et al., 1999; Roberts et al., 2006;
411   Rossi et al., 2017). This organic carbon is used for maintenance respiration and
412   growth, but part is excreted as faeces or pseudofaeces and becomes then
413   available for consumers in the sediments. This can result in local hotspots of
414   biodiversity and microbial activity in the sediments (Herman et al., 1999;
415   Gutierrez et al., 2003; Cathalot et al., 2015). Moreover, the physical structures
416   build by these ecosystem engineers impact hydrodynamics with consequences
417   for local and distant carbon deposition rates. Soetaert et al. (2016) reported
418   elevated carbon deposition to ocean margin sediments due to cold-water corals
419   reefs at very large distances.
420   Some sponges have the capability to take up dissolved organic carbon and
421   transform it into sponge tissue (de Goeij et al., 2013; Fiore et al., 2017; Hoer et
422   al., 2017). This sponge tissue and in particular its detritus can be consumed by
423   benthic organisms. This sponge loop (de Goeij et al., 2013; Rix et al., 2016) is
424   another example how animals can manipulate the transfer of organic carbon
425   from the water-column to the sediments (Fig. 5).
426
427
428   **5.4 Animal stimulation of microbes: An inverted microbial loop?**
429
430   The microbial loop is a key concept in ocean biogeochemistry (Pomeroy,
431   1974; Azam et al., 1983). Dissolved organic matter released by phytoplankton,
432   zooplankton or viral lysis of bacteria, archaea and algae is consumed by
433   heterotrophic microbes. These heterotrophs are in turn consumed by flagellates,
434   ciliates and other small consumers that are predated upon by zooplankton
435   (Azam et al., 1983; Jumars et al. 1989). Energy shunted into the large,
436   heterogeneous dissolved organic matter pool is in this way made available again
437   for animals (Fig. 6).
438   After discovery of this loop in the surface ocean water, research has been
439   executed to identify and quantify it in sediments (Kemp, 1988, 1990). This

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440   required substantial investment in developing new methods: these studies
441   basically revealed that predation on sedimentary bacteria was not that
442   important (Kemp, 1990; Hondeveld et al., 1992; Hamels et al., 2001; Guilini et al.,
443   2009). Van Oevelen et al., (2006) made a detailed study on the fate of bacterial
444   production using in situ ^{13}C labelling of bacteria. They observed that 8% was lost
445   by physical processes, 27% was consumed by animal predation, while bacterial
446   mortality accounted for 65%.   Viruses are the most important loss term for
447   sedimentary microbes (Danovaro et al, 2009, 2011, 2016) and the viral lysis
448   products (dissolved organic matter) are consumed by microbes. This results in a
449   dissolved organic carbon-microbes cycle (Fig. 6). This benthic microbial cycle
450   represents a dead end in terms of food web topology, because there is little
451   transfer to higher trophic levels and most carbon is eventually respired as
452   needed for mass-balance closure on the long term (Fig. 3).
453   In fact, the benthic microbial cycle represents more an *inverted microbial*
454   *loop*: rather that animals profit from the microbial loop sensu Azam et al. (1983),
455   it appears that benthic microbes profit from animals mixing labile organic matter
456   downwards into the sediments (Fig. 6). Labile organic matter delivered to the
457   sediment surface is mixed by animals inhabiting the sediments (Fig. 5). The
458   transfer of high quality organic matter to deeper sediment layer may prime
459   sediment microbial communities and in this way stimulate degradation of
460   indigenous organic matter (van Nugteren et al, 2009a, Bianchi, 2011; Hannadis &
461   Aller, 2017). This inverted microbial loop is a prime example how animals as
462   ecosystem engineers impact sediment carbon processing (Meysman et al., 2006).
463
464
465   **5.5 Imagine a world without animals.**
466
467   An ocean floor inhabited solely by microbes and without animals was likely the
468   reference state during the first four billion of years of Earth's history (Canfield,
469   2014; Lenton and Watson, 2011). Moreover, in modern systems with anoxic
470   bottom waters benthic animals are absent (Rhoads and Morse, 1971; Diaz and
471   Rosenberg, 1995, 2008; Levin, 2003; Levin et al, 2009). In these systems, organic
472   matter degradation pathways are different not only because of a lack of oxygen
473   and use of alternative electron acceptors, but also because bio-irrigation and
474   bioturbation are absent (Aller and Aller, 1998; Levin et al., 2009; Middelburg and
475   Levin, 2009). Consequently, microbe-fauna interactions (enhanced carbon
476   delivery, Fig. 5; animal stimulation of microbes, Fig. 6) are impeded.
477   This likely is the reason why more organic carbon is buried in sediments
478   underlying anoxic bottom waters (Hartnett et al., 1998; Hartnett and Devol,
479   2003; Middelburg and Levin, 2009; Jessen et al., 2017). Moreover, the organic
480   matter buried in hypoxic and anoxic settings is usually less degraded (Cowie,
481   2005, Cowie et al., 2009; Vandewiele et al., 2009; Koho et al., 2013; Jessen et al.,
482   2017). This presence of animals and all their interactions with organic matter
483   and microbes has consequences for organic carbon processing in marine
484   sediments and thus the global carbon cycle. It is obvious for any terrestrial
485   microbiologist that a world with trees and other macrophytes would be different
486   than one without. Moreover, biological oceanographers and limnologists agree
487   that zooplankton and other metazoan consumers contribute to biogeochemical
488   cycles (Vanni, 2002; Vanni and McIntyre, 2016), and I hope that colleagues

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489   studying marine sediments are aware that BIO in sediment biogeochemistry is
490   more than just microbiology.
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492   *Acknowledgement*
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509 **References**
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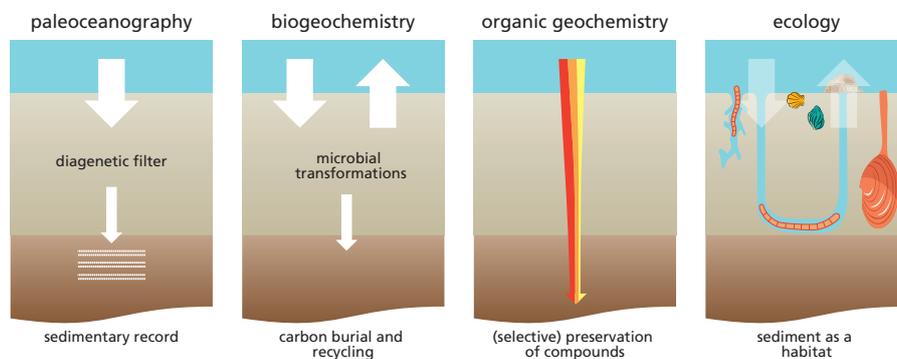935   10.4319/lo.2007.52.4.1698, 2007.

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950   biogeochemists quantify carbon burial and recycling, organic geochemists study
951   alteration of organic matter and ecologists focus on carbon as food for organisms
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954 Figure 2. Conceptual model of organic matter (OM) degradation and re-oxidation
955   pathways (based on Middelburg and Levin, 2009).

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

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

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

983
984 Figure 6. The microbial and inverted microbial loop. In the water column dissolved
985   organic carbon derived from phytoplankton, zooplankton or microbes (via viral
986   loop) is consumed by heterotrophic microbes, which in turn are consumed by
987   protists and small animals with the consequence that carbon flowing through
988   dissolved organic carbon pools eventually can be used by larger animals
989   (microbial loop). In sediments, the dissolved organic carbon (from viral lysis
990   and other sources) is also consumed by heterotrophic microbes but this carbon
991   is inefficiently transferred to animals. The engineering activities of animals are
992   key in delivering labile organic matter (phytodetritus) to microbes living in the
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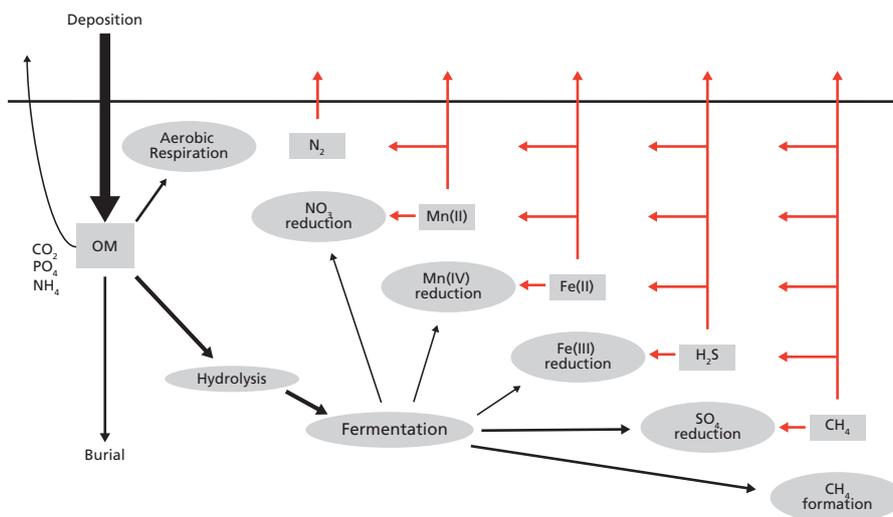
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paleoceanography	biogeochemistry	organic geochemistry	ecology
diagenetic filter	microbial transformations		
sedimentary record	carbon burial and recycling	(selective) preservation of compounds	sediment as a habitat

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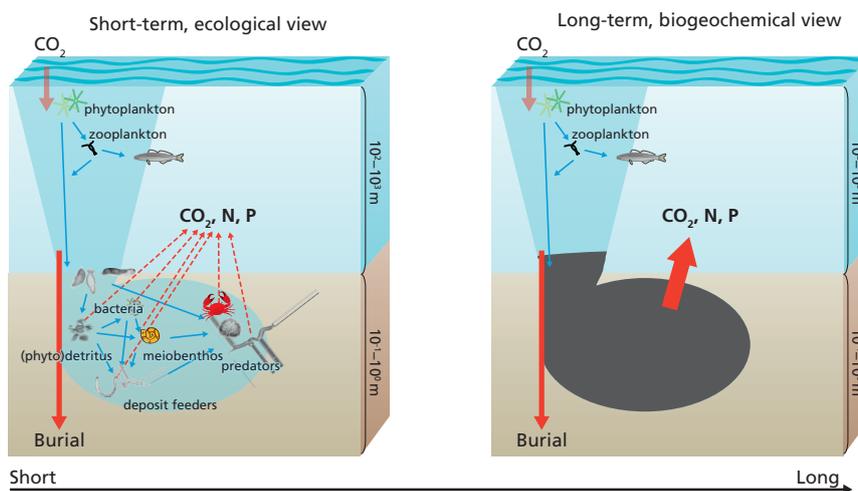1007   pathways (based on Middelburg and Levin, 2009).
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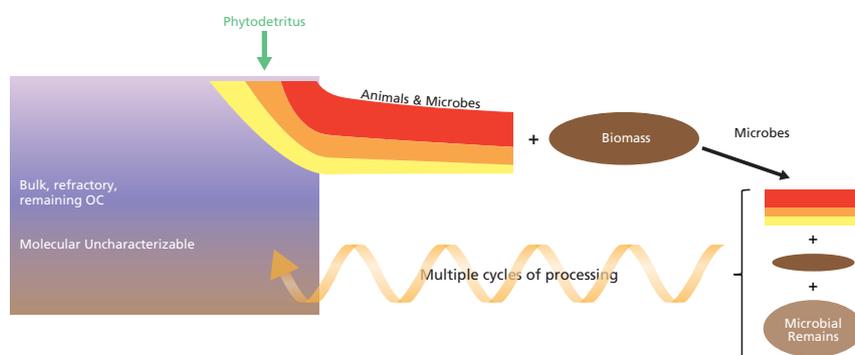1020   metabolites or into the geosphere (burial).
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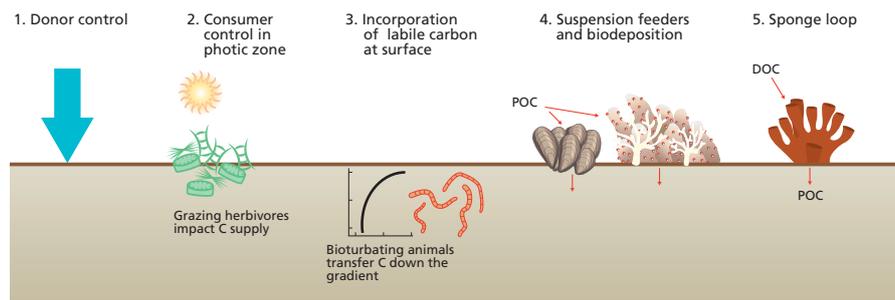1031   formation of molecular uncharacterizable organic matter.
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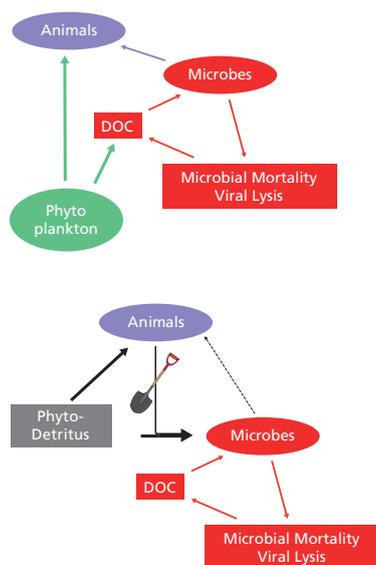1045   sponge loop).
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