

The fate of organic carbon in marine sediments - new insights from recent data and analysis

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47 **Abstract**

48 Organic carbon in marine sediments is a critical component of the global carbon cycle, and
49 its degradation influences a wide range of phenomena, including the magnitude of carbon
50 sequestration over geologic timescales, the recycling of inorganic carbon and nutrients, the
51 dissolution and precipitation of carbonates, the production of methane and the nature of the
52 seafloor biosphere. Although much has been learned about the factors that promote and hinder
53 rates of organic carbon degradation in natural systems, the controls on the distribution of organic
54 carbon in modern and ancient sediments are still not fully understood. In this review, we
55 summarize how recent findings are changing entrenched perspectives on organic matter
56 degradation in marine sediments: a shift from a structurally-based chemical reactivity viewpoint
57 towards an emerging acceptance of the role of the ecosystem in organic matter degradation rates.
58 That is, organic carbon has a range of reactivities determined by not only the nature of the organic
59 compounds, but by the biological, geochemical, and physical attributes of its environment. This
60 shift in mindset has gradually come about due to a greater diversity of sample sites, the molecular
61 revolution in biology, discoveries concerning the extent and limits of life, advances in quantitative
62 modeling, investigations of ocean carbon cycling under a variety of extreme paleo-conditions (e.g.
63 greenhouse environments, euxinic/anoxic oceans), the application of novel analytical techniques
64 and interdisciplinary efforts. Adopting this view across scientific disciplines will enable additional
65 progress in understanding how marine sediments influence the global carbon cycle.

66
67 **Keywords:** organic carbon; marine sediments; reactivity; microorganisms; deep biosphere

68
69 **1. Introduction**

70 To contextualize the recent biogeochemical breakthroughs that have been made regarding
71 the fate of organic carbon in marine sediments, the first section of this review consists of a
72 summary of its role in the global carbon cycle and how this has varied over space and time.
73 Secondly, we describe the sources of new data that are shaping the transformation in how we think
74 about organic carbon in the marine system. This is followed by a section on organic carbon in
75 adjacent environments such as hydrothermal systems and the ocean basement, and then a brief
76 overview of modelling advances. The topics covered in this communication are summarized in the
77 schematic shown in Figure 1.

78
79 **1.1 Sedimentary organics and the global carbon cycle**

80 Organic carbon (OC) degradation in marine sediments is a critical component of the global
81 carbon cycle and is intricately linked to Earth's climate (Berner and Canfield, 1989; Berner, 1990;
82 Siegenthaler and Sarmiento, 1993; Archer and Maier-Reimer, 1994; Mackenzie et al., 2004;
83 Ridgwell and Zeebe, 2005; Ridgwell and Hargreaves, 2007; Hülse et al., 2017). The specific
84 consequences of this process on biogeochemical cycles vary considerably depending on location
85 as well as the temporal and spatial scales of concern. In the upper few meters of relatively recently
86 deposited sediment, the oxidation of organic carbon controls the fluxes of oxygen and nutrients
87 across the sediment-water interface (SWI), ultimately impacting primary productivity in the water
88 column (Van Cappellen and Ingall, 1994; Lenton and Watson, 2000). As organic carbon is
89 aerobically oxidized, pore water pH is decreased, potentially leading to dissolution of calcium
90 carbonate and amplifying the direct effect of OC oxidation on the carbon cycle (Emerson and
91 Bender, 1981; Hales and Emerson, 1996). Deeper in sediments, organic carbon that escapes
92 oxidation can still be microbially reduced to CH₄, and under some conditions, fuel the slow build-

93 up of methane hydrates (e.g. Wallmann et al., 2012). Although hydrates represent a relatively small
94 carbon reservoir, perturbations in temperature and/or pressure can render hydrates unstable,
95 potentially leading to sudden transfers of carbon back into the ocean-atmosphere system that would
96 have important consequences for global carbon cycling and climate (Ruppel and Kessler, 2017).
97 The small fraction of photosynthetically produced organic carbon that entirely escapes degradation
98 and thus is buried over longer timescales in sediments helps to modulate the long-term evolution
99 of atmospheric CO₂, has enabled oxygen to accumulate in the atmosphere (e.g. Berner, 2003) and
100 has led to the formation of large reservoirs of hydrocarbons that provide most of the energy that
101 humans use. Whether marine sediment organic carbon contributes to water column anoxia,
102 becomes trapped in a clathrate, is transformed into petroleum or ends up as atmospheric CO₂ is
103 ultimately based on the flux of particulate organic carbon (POC) to sediments and the many factors
104 that dictate its rate of degradation.

105

106 **1.2 POC fluxes and degradation rates**

107 The concentrations of POC shown in Figure 2 illustrate that the flux of organic carbon to
108 and through sediments vary tremendously (Seiter et al., 2004; Wallmann et al., 2012; LaRowe et
109 al., 2020). In this figure, it can be seen that POC concentrations are highest in recently deposited
110 sediment underlying northern high-latitude and south-east Asian coastal regions and the Humboldt
111 and South Equatorial currents to the west of Peru. They are generally lowest in abyssal regions far
112 from land, and in older and deeper sediments. This span of concentrations is due to variable
113 depositional fluxes and degradation rates.

114 Field observations have revealed that rates of POC degradation are not constant (e.g.
115 (Canfield et al., 2005), leading to burial rates that vary significantly in space (e.g. Canfield, 1994;
116 Blair and Aller, 2012) and time (e.g. Arthur et al., 1985). In fact, first-order rate constants for POC
117 degradation rates derived from field and laboratory data span over eight orders of magnitude, with
118 older sediments having the smallest values (Middelburg, 1989). Many different factors have been
119 invoked to explain this variability. They include, but are not limited to, organic matter composition
120 (e.g. Westrich and Berner, 1984; Hedges et al., 1988; Tegelaar et al., 1989; Cowie et al., 1992;
121 Canfield, 1994; Hedges and Keil, 1995), electron acceptor (EA) availability (e.g. Demaison and
122 Moore, 1980; Emerson, 1985; Canfield, 1994; Hedges and Keil, 1995; Dauwe et al., 2001), benthic
123 microbial community composition and functional capacities (e.g. Canfield, 1994; Arnosti, 2011;
124 Steen et al., 2019), microbial inhibition by specific metabolites (e.g. Aller and Aller, 1998),
125 priming (e.g. Stevenson, 1986; Graf, 1992; Aller et al., 1996; Sun et al., 2002a; van Nugteren et
126 al., 2009), physical and physicochemical protection (e.g. Keil and Kirchman, 1994; Mayer, 1994;
127 Kennedy et al., 2002; Estes et al., 2019; Hemingway et al., 2019), sediment deposition rate (e.g.
128 Müller and Suess, 1979; Calvert and Pedersen, 1992b; Tromp et al., 1995) and macrobenthic
129 activity (e.g. Aller, 1982; Aller and Cochran, 2019; Middelburg, 2019).

130 The rates of POC degradation in marine sediments are first and foremost controlled by the
131 source and transport of organic carbon. A higher lateral and/or vertical (i.e. sedimentation)
132 transport rate not only increases the deposition flux but also influences the quality of the organic
133 carbon deposited, since the degree of pelagic degradation during transport through the water
134 column - and thus the nutritive value of POC - is reduced with extended sinking times. A
135 compilation of deep sediment trap data reveals large regional variations in vertical export
136 efficiency (Lutz et al., 2002; Henson et al., 2012a; Wilson et al., 2012). For instance, the fraction
137 of the organic carbon export flux that reaches water depths greater than 1.5 km varies between
138 0.28 and 30% (5.7% average) of the POC that escapes the photic zone (Lutz et al., 2002). Although

139 differences in export efficiencies are most likely not attributable to a single process, factors
140 invoked to explain variations in export efficiency include sinking rates and ballast (e.g. Armstrong
141 et al., 2002; Francois et al., 2002; Klaas and Archer, 2002; Lutz et al., 2002), the seasonality of
142 export production (Antia et al., 2001) and ecosystem structure (Buesseler et al., 2008; Lam et al.,
143 2011; Henson et al., 2012a; Mayor et al., 2012). And while export of large particles from surface
144 waters has been extensively investigated, it has also been shown that very small particles ($< 1 \mu\text{m}$)
145 contribute to the chemical composition of exported POC (Close et al., 2013). In addition to the
146 vertical transport of POC from the euphotic zone, the efficient lateral transport of POC in nepheloid
147 layers, benthic storms, mud waves, strong (bottom) water currents or mass wasting events can
148 support an important fraction of the POC deposition flux to continental slope and abyssal
149 sediments in the vicinity of dynamic continental margins (e.g. Ohkouchi et al., 2002; Levin and
150 Gooday, 2003; Mollenhauer et al., 2003; Inthorn et al., 2006b; Mollenhauer et al., 2007; Kusch et
151 al., 2010; Henson et al., 2012b; Bao et al., 2019). The efficiency of terrestrial organic matter export
152 from land is even more difficult to predict, given variable controls on residence times in soils,
153 followed by widely varying degrees of alteration during transport through the
154 riverine/estuarine/deltaic system and across the continental shelf (Hedges et al., 1997; Schlünz
155 and Schneider, 2000; Bianchi, 2011; Blair and Aller, 2011; Bauer et al., 2013a; Regnier et al.,
156 2013; Canel and Hardison, 2016; Kandasamy and Nagender Nath, 2016). Organic carbon is also
157 produced in sediments, by phototrophs in shallow waters (Middelburg, 2018, 2019) and
158 chemoautotrophically (Veuger et al., 2012; Sweetman et al., 2017). Although the exact
159 mechanisms controlling the high variability in POC degradation are not well understood, the
160 variety of environments that have been sampled and examined in recent years has provided new
161 insights to constrain which variables are most important in particular settings.
162

163 **1.3 Observations: Increased diversity of sample sites and data types**

164 Over the last several decades, scientific drilling of the seafloor by the International Ocean
165 Discovery Program (IODP) and its precursors, the Integrated Ocean Drilling Program (IODP), the
166 Ocean Drilling Program (ODP) and the Deep Sea Drilling Program (DSDP), have enabled critical
167 expansion of sampled environments and new data that have dramatically increased our knowledge
168 of the distribution of organic carbon in marine sediments. The sample sites targeted by most of
169 these expeditions were motivated by scientific questions about the structure of ocean crust, past
170 climate, and tectonics, leading to drilling locations and sampling methods that were optimized for
171 study of these topics. Although total organic carbon was regularly measured on these samples,
172 tools to study the agents of their transformation, i.e. microorganisms, were relatively rudimentary
173 until culture-independent methods (e.g. DNA and RNA sequencing) became widely available in
174 the early 2000's. Much of the new understanding of controls on organic carbon degradation in
175 marine sediments has to do with recent insight into the role of microorganisms. As pointed out in
176 the ODP Leg 201 summary (D'Hondt et al., 2003), this is despite the fact that deep-sea drilling had
177 revealed indirect evidence of microbial activity as early as the 1980s (Oremland et al., 1982;
178 Whelan et al., 1986; Tarafa et al., 1987) and, by the 1990s, microbial abundances (see Parkes et
179 al., 2014)) for a review). Remarkably, ODP Leg 201, the first ODP cruise dedicated to studying
180 microorganisms, did not sail until 2002. Since this time, a number of IODP expeditions have been
181 focused on studying the limits to life: Expeditions 329 (South Pacific Gyre Subseafloor Life), 331
182 (Deep Hot Biosphere), 336 (Mid-Atlantic Ridge Microbiology), 337 (Deep Coalbed Biosphere off
183 Shimokita), 357 (Atlantis Massif Seafloor Processes: Serpentinization and Life), 370
184 (Temperature Limit of the Deep Biosphere off Muroto), and 385 (Guaymas Basin Tectonics and

185 Biosphere). This explicit exploration of microbial communities further informs the perspective
186 that the reactivity of organic carbon in marine sediments is an ecosystem property (Middelburg,
187 2018).

188

189 **2. Ecosystem nature of the problem**

190 Organic carbon in natural systems is often referred to as being either labile or recalcitrant
191 (e.g. Hedges et al., 2000). Some have expended considerable effort expanding this classification
192 to intermediate states such as semi-labile and semi-recalcitrant (Hansell, 2013). This reductionist
193 classification system implies that the degradation rate of organic compounds is determined from
194 specific attributes of the chemical compounds themselves. While the reactivity of organic
195 compounds is certainly related to their chemical composition and structure, numerous factors have
196 been invoked to explain the reactivity of organic carbon that are not intrinsic to the compounds,
197 but rather the properties of the surrounding environment (e.g. see Hedges et al., 2000; Burdige,
198 2007b; Arndt et al., 2013; Middelburg, 2018, 2019 and references therein). Examples include
199 temperature, microbial community structure and benthic ecosystem, mineral types and surface
200 area, redox state, light, nutrient availability, pH, salinity, porosity, permeability, water content and
201 oxygen exposure time. Because these variables are biophysiochemical properties of the
202 environment, the reactivity of organic matter is determined by the interaction between the
203 compound and its ecosystem, not just the chemical nature of the organic compounds. Indeed, a
204 particular organic compound can be extremely resistant to degradation under certain conditions,
205 and be rapidly degraded in a different physiochemical context. For example, aerobic heterotrophic
206 bacteria in incubation experiments have been shown to oxidize and incorporate ^{14}C -free organic
207 carbon preserved in marine black shales for millions of years (Petsch et al., 2001). This idea of
208 ecosystem properties governing organic compound reactivity is not a new one (Middelburg et al.,
209 1993; Canfield, 1994; Harvey et al., 1995; Mayer, 1995), but it is only recently becoming the new
210 paradigm in the soil science community (Marschner et al., 2008a; Kleber and Johnson, 2010;
211 Schmidt et al., 2011; Lehmann and Kleber, 2015), and there are indication that it should prevail
212 among sediment scientists as well (Eglington and Repeta, 2014; Middelburg, 2018, 2019). In fact,
213 we suggest that the terms *labile* and *recalcitrant* be retired and replaced with the single term
214 *reactivity*. Similarly, since the fate of organic carbon in natural systems can include oxidation to
215 CO_2 , hydrolysis and fermentation into smaller organics, reduction to methane, adsorption to
216 surfaces, incorporation into biomass and conversion to petroleum products and complex organic
217 compounds, we recommend that the more inclusive term *transformation* be used to refer to the
218 fate of organic carbon rather than the relatively restrictive term *mineralization*. In the following
219 sections, we highlight some of the recent research that seeks to determine how a variety of
220 ecosystem properties influence the rates of organic carbon degradation.

221

222 **2.1 Source and transit path**

223 A large fraction of the organic carbon that is buried in marine sediments originates from
224 photosynthetic activity in the terrestrial (net primary productivity (NPP) = 56 Pg C yr^{-1}) or marine
225 biosphere (NPP = 49 Pg C yr^{-1}) (Field et al., 1998). In addition, organic carbon can be transported
226 to sediments by other means including the weathering of ancient organic carbon in rocks (Blair et
227 al., 2003), the remobilization of organic matter from thawing permafrost (Mann et al., 2015) and
228 resuspension of already-deposited carbon (see below). Autotrophic and Chemoautotrophic
229 production as well as secondary production by microorganisms and animals can also contribute to
230 the organic carbon deposition flux (Eglington and Repeta, 2010; Middelburg, 2011; Lengger et al.,

231 2019). Approximately two-thirds of terrestrially produced OC is rapidly degraded within soils or
232 glacial environments. The remainder that escapes immediate degradation is either partially
233 degraded or temporarily stored before being transported downstream with old, weathered OC
234 within lakes, streams, rivers, estuaries, deltas, fjords, and ultimately, the oceans (Regnier et al.,
235 2013). An estimated $1.9 \text{ Pg C yr}^{-1} \pm 1.0 \text{ Pg C yr}^{-1}$ of total soil carbon (mostly POC and dissolved
236 organic carbon, DOC, but also dissolved inorganic carbon, DIC) is exported to inland waters. Only
237 $0.45 \text{ Pg C yr}^{-1}$ of the terrestrial-derived OC reaches the coastal ocean and $0.1\text{-}0.35 \text{ Pg C yr}^{-1}$ makes
238 it to the open ocean (Bauer et al., 2013b; Regnier et al., 2013). Thus, the land-ocean transition zone
239 acts as an important modulator of OC fluxes that not only further degrades and transforms
240 terrestrial OC inputs, but also stores OC on short and long timescales (Canuel and Hardison, 2016).
241 However, the exact amounts of OC that are degraded and temporarily or permanently preserved
242 during transit from land to ocean remain unknown (Regnier et al., 2013).

243 Similar to terrestrially-derived organic carbon, a large fraction (80-90%) of the OC
244 produced in the surface ocean is rapidly oxidized (Dunne et al., 2007; Hansell and Carlson, 2015).
245 Just over one-quarter (27%) of OC produced in the marine photic zone is DOC that can be
246 transported to the deep ocean by convection and mixing. While most of the exported DOC is
247 degraded at mid-depths, an estimated 0.1 Pg C yr^{-1} is contributed to the large, apparently
248 unreactive, deep ocean DOC reservoir ($\sim 680 \text{ Pg}$) that persists through multiple ocean mixing
249 cycles (Hansell and Carlson, 2015). As POC sinks to the ocean floor, it can be laterally transported
250 by ocean currents (Eglinton and Repeta, 2004) as it is further degraded. Degradation during burial
251 further reduces this flux such that $< 0.3\%$ of the original exported flux is ultimately sequestered in
252 deep marine sediments (Hedges and Keil, 1995; Eglinton and Repeta, 2004; Burdige, 2007b;
253 Dunne et al., 2007; Middelburg and Meysman, 2007; Honjo et al., 2008).

254 In addition to the vertical transport from the photic zone to sediments, POC can also be
255 transported after deposition on the seafloor via bioturbation and lateral motion following the
256 resuspension of sediments into the water column. Bioturbation, the biological reworking of
257 sediments near the SWI by macrofauna such as polychaetes and bivalves (Rhoads, 1974a; Aller,
258 1982), can exert an important influence of organic carbon transformation (Meysman et al., 2006;
259 Middelburg, 2018) in the upper 20 cm of sediments (Boudreau, 1994, 1998). These animals can
260 have a complex impact on sediment POC – in some cases accelerating POC degradation through
261 grazing, the redistribution of particles and reintroduction of electron acceptors and DOC,
262 (Kristensen, 1985; Rice, 1986; Kemp, 1988; Aller, 1994; Aller and Aller, 1998; Kristensen and
263 Holmer, 2001a; Kristensen et al., 2011) and, in other cases, depositing organics in the form of tube
264 casings that can inhibit organic transformation (Kristensen et al., 1992; Kristensen, 2001).
265 Generally, it seems that bioturbation accelerates POC degradation (Rhoads, 1974b; Findlay and
266 Tenore, 1982; Aller and Aller, 1986; Herman et al., 1999; Aller et al., 2001; Kristensen and
267 Holmer, 2001b; Kristensen and Kostka, 2005; Aller and Cochran, 2019). Furthermore, benthic
268 macrofauna, in addition to being a source of OC, can affect sediment resuspension (Aller and
269 Cochran, 2019) by altering the bulk properties of sediments (Eckman et al., 1981; Rhoads et al.,
270 1984), which in turn influences their lateral transport.

271 Sediments, and the POC within, on continental shelves and slopes can also be mobilized
272 after initial deposition and redeposited under open-ocean waters. Not only does this process move
273 organic carbon laterally to parts of the seafloor that typically have low POC deposition rates
274 (Jahnke et al., 1990; Walsh, 1991; Bauer and Druffel, 1998; Ransom et al., 1998a; Thomsen and
275 van Weering, 1998; Jahnke and Jahnke, 2000; Romankevich et al., 2009; Hwang et al., 2010), but
276 it has the effect of accelerating the oxidation of POC that was buried in margin sediments (see

277 Section 2.5 for a discussion) (de Lange et al., 1987; Prahl et al., 1989; Cowie et al., 1995; Prahl et
278 al., 1997; Cowie et al., 1998; Hoefs et al., 1998; Prahl et al., 2003). However, the scale of this
279 phenomenon, as well as its impact on the global distribution of organic matter reactivity, remains
280 unclear (Eglinton and Repeta, 2014) due to large uncertainties in lateral particle fluxes (Jahnke et
281 al., 1990; Reimers et al., 1992; Inthorn et al., 2006a; Thullner et al., 2009).

282

283 **2.2 Organic carbon structure and composition**

284 Although the majority of organic carbon inputs to marine sediments originate as POC,
285 these sources can be transformed and contribute to the DOC pool through microbial activities as
286 well as sorption/desorption from mineral surfaces. Chemically, both POC and DOC range in size
287 and complexity from simple monomers to mixtures of large, complex polymers as well as humic
288 substances (de Leeuw and Largeau, 1993; Hedges et al., 2000), the last of which is an ill-defined
289 molecular group of varying sizes that are solely defined by the extraction procedure used to isolate
290 them. Most POC and DOC in marine sediments cannot be chemically identified at the structural
291 level, leading to terms such as “molecularly uncharacterizable carbon, MUC” (Cowie et al., 1995;
292 Prahl et al., 1997; Wakeham et al., 1997; Burdige and Gardner, 1998; Hedges et al., 2000; Burdige,
293 2007b; Burdige and Komada, 2015). Depending on the sample, anywhere from 50-90 wt% of OC
294 in marine sediments is referred to as MUC. Approximately 60-90% of pore water DOC has a
295 molecular weight of less than 3 kDa, and the compounds that can be identified tend to be short-
296 chain organic acids such as acetate, amino acids, and carbohydrates (Burdige and Komada, 2015).
297 High-resolution techniques have shown that thousands of organic compounds are found in pore
298 water (e.g. Repeta et al., 2002; Koch et al., 2005; Schmidt et al., 2009; Fox et al., 2018), but many
299 fall into a rather unsatisfactory category known as CRAM, carboxyl-rich alicyclic molecules - a
300 poorly defined pool of organics thought to be less reactive than other DOC compounds (Hertkorn
301 et al., 2006).

302 As with DOC, the bulk of organic compounds in the particulate fraction of marine
303 sediments (i.e. POC) is rarely identified and often said to be ‘uncharacterizable’, at least with
304 respect to partitioning it into compound classes such as amino acids, carbohydrates, lignin or lipids
305 (Cowie et al., 1995; Prahl et al., 1997; Wakeham et al., 1997; Hedges et al., 2000; Benner, 2002;
306 Koch et al., 2005; Burdige, 2007a; Mao et al., 2011; Ball and Aluwihare, 2014; Estes et al., 2019).
307 Although it is not clear why this is the case, one of the explanatory hypotheses, that organics attach
308 to mineral surfaces and condense into large macromolecules that are less accessible by
309 exoenzymes, e.g. (Hedges et al., 1988; Keil and Kirchman, 1994; Hedges et al., 2000), no longer
310 holds in the soil science community. Briefly, it was long thought that complex macromolecular
311 carbon compounds form in soils through abiotic processes and that these large compounds were
312 especially resistant to biological degradation. More recently, however, there is a growing
313 consensus that these larger compounds are an artifact of extraction procedures and there is no
314 evidence for their presence *in situ* (Kelleher and Simpson, 2006; Lehmann and Kleber, 2015).

315 The structure and composition of organic matter serves as the first guidepost to determining
316 its reactivity. For instance, relatively weak bonds between monomers render a biopolymer more
317 reactive over a wide range of environmental conditions, than aliphatic moieties cross-linked by
318 ether bonds (Tegelaar et al., 1989; de Leeuw and Largeau, 1993). At the most fundamental level,
319 this structural heterogeneity is responsible for the higher reactivities of most algal organic carbon
320 over most terrestrial organic matter (Canel and Martens, 1996; Hedges and Oades, 1997; Dauwe
321 and Middelburg, 1998; Camacho-Ibar et al., 2003; Burdige, 2005; Dai and Sun, 2007), the
322 selective preservation of certain compounds in the geological record and the widely observed

323 decrease of organic carbon with depth and or transport/burial time (Goth et al., 1988; Tegelaar et
324 al., 1989). However, the relative importance of organic structure and composition in controlling
325 overall preservation/degradation remains unclear (see de Leeuw et al., 2006; Gupta et al., 2007;
326 Gupta, 2015). In addition, because of the extremely limited availability of compound-specific
327 kinetic data (e.g. Ming-Yi et al., 1993; Harvey and Macko, 1997; Sun et al., 2002b), a
328 comprehensive knowledge of organic structure and composition does not help in quantifying
329 organic matter reactivity. Ultimately, linking the identity of individual organic compounds to their
330 reactivity would require knowledge of how many other biophysiochemical variables impact it as
331 well.

332 **2.3 Sediment matrix**

334 Mineral surfaces are thought to slow or prevent the degradation of organic carbon, largely
335 based on observations that there is a positive correlation between mineral surface area and the
336 amount of organic matter in sediments (e.g. Mayer et al., 1985; Keil et al., 1994; Mayer, 1994).
337 Most hypotheses explaining this phenomenon rest upon the notion that extracellular enzymes
338 cannot access mineral-associated organic compounds. Compounds can associate with minerals via
339 a number of mechanisms, both physical and chemical, including 1) physisorption (physical
340 adsorption) in surface irregularities, 2) strong mineral surface bonding, 3) insertion into clay
341 interlayers, 4) formation of mineral-OC aggregates, 5) co-precipitation with Fe-oxides and other
342 authigenic minerals, 6) seclusion by exopolymeric substances (EPS) and 7) protection within
343 biogenic minerals such as diatom frustules (Keil and Hedges, 1993; Keil et al., 1994; Mayer, 1994;
344 Hedges and Keil, 1995; Ransom et al., 1997; Ransom et al., 1998b; Mayer, 1999; Arnarson and
345 Keil, 2001; Mayer and Xing, 2001; Kennedy et al., 2002; Ingalls et al., 2003; Pacton et al., 2007a;
346 Pacton et al., 2007b; Kennedy and Wagner, 2011; Lalonde et al., 2012; Hemingway et al., 2019).
347 Chemical preservation mechanisms, in particular, are likely important, since OC concentration
348 often correlates more strongly with the abundance of specific mineral classes such as smectite
349 clays (Ransom et al., 1998a), metal oxides (Lalonde et al., 2012; Roy et al., 2013; Barber et al.,
350 2017) or tephra (Longman et al., 2019) rather than total mineral surface area, suggesting that the
351 specific chemical bonds formed by these minerals with organic compounds are essential to
352 decreased reactivity.

353 Given the large variety of organic compounds and minerals found in marine sediments, it
354 is probable that all of the mechanistic hypotheses noted above contribute to the long-term
355 preservation of OC. The array of explanations is likely due to the fact that the samples used to
356 generate them have come from different places and therefore are characterized by a variety of
357 different biogeochemical conditions and timescales of preservation. Although there is a growing
358 appreciation of the complexity of mineral-organic reactions, disentangling which mechanism
359 operates under what set of environmental conditions is complicated by a lack of data that more
360 fully contextualizes mineralogical observations such as oxygen exposure times (OETs). For
361 example a study examining how OETs affect mineral-organic associations in northeast Pacific
362 sediments (Arnarson and Keil, 2007) found that for OETs shorter than a year, OC was mostly in a
363 mineral-free state. For sediments with OETs ranging from years to decades, OC was largely in
364 mineral-organic aggregates. For longer OETs (centuries to millennia), the aggregates broke down
365 and most OC was found sorbed to mineral surfaces or protected inside biogenic diatom frustules
366 (see Section 2.5 for a discussion on electron acceptor availability).

367 The exposure to a variety of geochemical conditions over varying timescales also impacts
368 how solid phases can control organic carbon reactivity. For instance, microorganisms use Fe- and

369 Mn-oxide minerals to oxidize organic carbon in marine sediments (Ehrlich, 1971; Aller, 1980;
370 Berner, 1981; Jones, 1983; Burdige and Nealson, 1986; Lovley, 1991; Thamdrup, 2000; Hyun et
371 al., 2017), especially where manganese- and iron-oxides are abundant or rapidly recycled due to
372 fluctuating redox conditions (Sørensen and Jeørgensen, 1987; Aller et al., 1990; Canfield et al.,
373 1993). In fact, it has been estimated that 3% of the POC degraded in the top 50 cm of global marine
374 sediments is coupled to Fe-oxide reduction (Thullner et al., 2009), though this is spatially quite
375 variable (Burdige, 2012; Dale et al., 2015). Yet, these same mineral phases provide protection and
376 stabilization of organic matter (Lalonde et al., 2012; Johnson et al., 2015; Barber et al., 2017).
377 Substantially more OC is associated with Fe oxides via inner-sphere complexation in coastal
378 environments with short OETs than in low OC, deep-sea sediment (Barber et al., 2017).
379 Experimental evidence additionally demonstrates that the composition of OC matters in
380 determining the balance between degradation and preservation by minerals: the presence of
381 disaccharides inhibits the abiotic degradation of protein by the manganese oxide mineral birnessite
382 (Reardon et al., 2018). Furthermore, carbon compounds can serve as templates for mineral
383 nucleation, and co-precipitate with minerals during mineral growth and aggregation (Mann et al.,
384 1993; Moreau et al., 2007; Kleber et al., 2015 and references therein). Beyond redox chemistry,
385 (Taylor, 1995) showed that under some conditions sorbed proteins are hydrolyzed much faster
386 than dissolved proteins, indicating that surface sorption can in fact enhance organic carbon
387 degradation.

388 Generalizations about organic-mineral interactions are further complicated by the fact that
389 sediment types may vary on the centimeter scale and might be dominated by an array of mineral
390 types that have distinct physiochemical properties. Common sediment lithologies include chert,
391 siliceous ooze, carbonate, clay, silt and sand in the form of turbidites, volcanoclastics and limestone
392 (Plank and Langmuir, 1998). Sediments made of these various constituents respond differently to
393 increasing pressures and temperatures during diagenesis, leading to dissolution, precipitation, and
394 solid-phase reordering reactions (Prothero and Schwab, 2004) that will certainly impact organic-
395 mineral associations. How specific mineral-organic associations change across environmental
396 gradients is not well known, but potentially crucial to understanding the fate of OC in marine
397 sediments. The common clay mineral smectite provides an illustrative example since it has been
398 shown to preferentially sequester organics, relative to chlorite-rich clays (Ransom et al., 1998a).
399 With as little as 1.3 MPa pressure (Hüpers and Kopf, 2012), the interlayer in smectite begins to
400 dewater and collapse, a process that also depends on temperature, the identities of interlayer cations
401 and the concentrations of cations present in solution (Ransom and Helgeson, 1995). If organics are
402 sequestered in this interlayer, they could be expelled during this transition and transported into
403 other parts of the sediment. Likewise, the reductive dissolution of metal oxides may liberate
404 chemically or physically adsorbed organics (Coppola et al., 2007). Other recent work suggests that
405 the salinity gradient experienced by smectite during transport from the terrestrial to marine
406 environments induces cation exchange reactions and the removal of associated pedogenic organic
407 carbon, followed by repopulation of the mineral surface with marine OC (Blattmann et al., 2019).
408 On the other end of the size spectrum, sandy sediments - half of continental shelf seafloor - allow
409 for water column POC to be pumped biologically or tidally into the subsurface. This reactive DOC
410 stimulates organisms (Huettel et al., 2014) to consume it and more of the particulate organic
411 fraction, contributing to low POC in sandy sediments (Boudreau et al., 2001).

412 413 **2.4 Hydrolysis and Fermentation**

414 When free oxygen has been exhausted in sediments, OC is thought to be transformed
415 through a series of steps that include the extracellular enzymatic hydrolysis of large, complex

416 organic compounds into smaller ones that are then fermented into volatile fatty acids, H₂ and other
417 simple chemical species, some of which are then oxidized by microorganisms using electron
418 acceptors such as nitrate, metal-oxides and sulfate, or reduced to methane (Schulz, 2006). Thought
419 to be the rate limiting step in organic matter degradation, extracellular enzymes produced by
420 microorganisms are known to break large and/or complex organic compounds to supply
421 microorganisms with energy and nutrients such as nitrogen and phosphorous (Arnosti, 2011).
422 Extracellular enzymes are diverse and present in low concentrations in marine sediments (Steen et
423 al., 2019). Although temperature and pH are dominant controls on rates of enzyme-catalyzed
424 reactions, patterns of activity across ecosystem types do not necessarily correlate with such physio-
425 chemical variables (Mahmoudi et al., 2020). It seems that the functional diversity of microbial
426 communities, nutrient availability and organic matter reactivity are likely to better explain patterns
427 of extracellular enzyme activities, with a notably strong correlation with particle composition, size
428 and abundance (Arnosti et al., 2014).

429 It is difficult to locate fermenting microorganisms in sediment columns since they do not
430 leave a distinct chemical trace of their activity (Nealson, 1997). A near-limitless number of organic
431 compounds can serve as reactants and products, and a considerable number of inorganic species
432 can be produced and consumed by both fermentative and non-fermentative processes (LaRowe
433 and Amend, 2019). In addition, many organisms can switch between fermentation and other
434 catabolic strategies, and macrofauna can also leave signatures reminiscent of fermentative
435 pathways as they partially digest organic matter during gut passage (McInerney et al., 2008;
436 Jochum et al., 2017). Consequently, the specific forms of fermentation and diversity of
437 fermentative mechanisms in marine sediments remain largely unknown.

438 Recent analyses of biomolecular data (see Section 2.6) from sediments confirm that
439 fermentation generally appears to be a widespread survival strategy for many cosmopolitan groups
440 of microorganisms in anoxic sediments. For example, Bathyarchaeota, Hadesarchaea, and the
441 Atribacteria that are common in marine sediments all utilize fermentative strategies – using
442 peptides, aldehydes, sugars and lignin as substrates (Lloyd et al., 2013; Baker et al., 2016; Nobu
443 et al., 2016; Orsi, 2018; Yu et al., 2018a). As has been often presumed, fermenting bacteria have
444 now been found throughout the anoxic sediment column across multiple geochemical zones (Orsi
445 et al., 2017; Beulig et al., 2018). Many bacteria with the capability to ferment (in particular alpha-
446 and gamma-proteobacteria) have also been found in oxic marine sediment such as deep-sea red
447 clay, though they respire oxygen in these settings (Vuillemin et al., 2019). Eukaryotic
448 microorganisms are also involved in fermentation processes in sediments. For example, the
449 majority of H₂ produced in anoxic permeable sediments results from fermentation by eukaryotic
450 algae (Bourke et al., 2016). In deeper sediments down to at least 2,000 meters below the seafloor
451 (mbsf), fermenting fungal cells can still persist (Ciobanu et al., 2014), suggesting that they have
452 the ability to contribute to H₂ production since this can be a product of their fermentative pathway
453 (Orsi, 2018). Finally, metagenomic and proteomic data taken from terrestrial settings suggest that
454 fermenting organisms constitute a large fraction of the Candidate Phyla Radiation, an uncultured
455 but geographically widespread and genetically diverse group of bacteria (Wrighton et al., 2012;
456 Wrighton et al., 2014; Anantharaman et al., 2016; Danczak et al., 2017).

457

458 **2.5 Electron acceptors**

459 Most sedimentary POC – and its hydrolysis and fermentation products – are consumed by
460 microorganisms using an array of electron acceptors. The identities and concentrations of EAs are
461 in turn determined by the composition of the overlying seawater and the types of mineral phases

462 that are deposited along with organic compounds. The principal EAs encountered in marine
463 sediments, O₂, NO₃⁻, Mn(IV), Fe(III), SO₄²⁻ and CO₂, are traditionally thought to be consumed in
464 the order listed based on the idea that this sequence follows the order of decreasing Gibbs energy
465 yield of the corresponding organic matter oxidation reactions (Claypool and Kaplan, 1974;
466 Froelich et al., 1979; Stumm and Morgan, 1996), though it should be noted that the range of Gibbs
467 energies for reactions involving these EAs can overlap depending on the environmental conditions
468 (LaRowe and Van Cappellen, 2011; LaRowe and Amend, 2014, 2015a). This hierarchy leads to
469 redox zonation in marine sediments – oxic sediments nearest the SWI, followed by so-called sub-
470 oxic zones where NO₃⁻ and Mn(IV) reduction occurs, a ferruginous layer if Fe(III)-bearing
471 minerals are present, then a sulfidic layer where the bulk of SO₄²⁻ reduction takes place and finally
472 a methanogenic zone at the bottom of the sediment column. Not all of these redox zones will
473 necessarily be present in any given sediment column. The thickness of the zones can vary
474 dramatically (Glud, 2008; D'Hondt et al., 2015; Egger et al., 2018) and the order of them can
475 exhibit complex patterns (see Jørgensen et al., 2019). For instance, in many coastal sediments
476 where POC fluxes are high, the oxic zone might be vanishingly thin (Glud, 2008), while the oxic
477 layer in sediments underlying ocean gyres can penetrate tens of meters to the basement since POC
478 fluxes are so low (Røy et al., 2012; D'Hondt et al., 2015). In fact, D'Hondt et al. (2015) estimate
479 that 9-37% of the global sediment-basement interface is oxic (Figure 3a).

480 In an undetermined volume of the ocean crust, deep sediment layers can exhibit higher
481 concentrations of dissolved oxygen than in upper or middle layers due to the penetration and
482 circulation of deep, oxygenated seawater into unsedimented adjacent basaltic outcrops (Orcutt et
483 al., 2013b; Mewes et al., 2016; Kuhn et al., 2017). This subsediment, rapid movement of low-
484 temperature seawater allows oxygen to diffuse upward from basement basalt into sediments, thus
485 creating a C-shaped O₂ curve in these sediments. An example of this is shown in Figure 4 for a
486 sediment pond near the mid-Atlantic Ridge, though it should be noted that these kinds of oxygen
487 profiles have also been observed in the North Pacific near a fracture zone (Mewes et al., 2016;
488 Kuhn et al., 2017). The upward transport of such microbial energy sources could be common
489 globally due to the vast number of seamounts that jut above the sediment-water interface (Wheat
490 et al., 2019 and references therein).

491 Other chemical compounds that can provide energy for microorganisms have been found
492 to be transported upward in sediments. In one such case near the Peru Margin, sulfate diffused
493 upward from a brine in the oceanic basement (D'Hondt et al., 2004; Parkes et al., 2005; Engelen
494 et al., 2008). In another, Cretaceous-aged organic-rich horizons support methane production that
495 seem to, in turn, provide energy for microbial communities in and above it, driving unexpected
496 distributions of EAs that differ from classical expectations (Arndt et al., 2006). In many anoxic
497 sedimentary settings, the reduced products of POC oxidation, compounds such as Fe²⁺, H₂S and
498 NH₄⁺, diffuse upwards to be oxidized by chemolithotrophic microorganisms for energy. If redox
499 conditions oscillate, this process can cycle, creating the impression that POC is being transformed
500 more rapidly than it is (Thullner et al., 2009), though OC oxidation rates can be accelerated due to
501 these oscillations (Sun et al., 1993; Aller, 1994; Sun et al., 2002a; Caradec et al., 2004).

502 The deepest extent of the sulfate-reducing zone and thus the beginning of the methanogenic
503 zone (sulfate-methane transition, SMT) varies widely on a global scale, and has been shown to
504 strongly depend on sedimentation rates and associated organic matter burial fluxes (Berner, 1978;
505 Borowski et al., 1999; Egger et al., 2018). In fact, Egger et al. (2018) recently used a compilation
506 of 1,704 observations to correlate sedimentation rates with SMT depth to map the extent of the
507 SMT globally (Figure 3b). It can be seen in this figure that SMT depth is spatially highly variable:

508 in many shallow continental shelf and slope settings, SMT depth is < 1 mbsf, and up to 10 mbsf.
509 In deeper sediments, particularly water depths >2,000 m, SMT depth is at least 10 mbsf and in
510 many instances, hundreds of meters deep. The majority of sediments in the abyssal plain (>66%)
511 exhibit no SMT.

512 The preservation of POC in sediments is sometimes attributed to anoxia, and therefore
513 ascribed to the identities of the electron acceptors present (e.g. Demaison and Moore, 1980;
514 Emerson, 1985; Calvert and Pedersen, 1992a; Lee, 1992b; Aller, 1994; Canfield, 1994; Wignall,
515 1994), and to some extent the types of organic compounds deposited (Harvey et al., 1995; Harvey
516 and Macko, 1997; Sun et al., 1997; Bianchi et al., 2000; Grossi et al., 2001; Sun et al., 2002a).
517 Though there are many datasets and reports arguing for and against the idea that the presence of
518 free oxygen plays a decisive role in POC reactivity (see Hulthe et al., 1998), there seems to be a
519 growing consensus that the presence O₂ typically enhances organic carbon reactivity in many
520 marine sediments (Hartnett et al., 1998; Hedges et al., 1999; Keil and Cowie, 1999; Keil et al.,
521 2004; Moodley et al., 2005; Cowie et al., 2009; Middelburg and Levin, 2009; Aller, 2014;
522 Eglinton and Repeta, 2014; Keil et al., 2016). Notable exceptions to these observations include
523 studies that show that rates of POC degradation in anoxic sediments have been observed to be
524 nearly equal to (e.g. Henrichs and Reeburgh, 1987; Lee, 1992a; Kristensen and Holmer, 2001b) or
525 far exceeding those in oxic settings (Røy et al., 2012; D'Hondt et al., 2015). On a molecular level,
526 fatty acids can be degraded at similar rates independently of their degree of saturation in the
527 presence of oxygen, whereas unsaturated acids are preferentially degraded under anoxic conditions
528 (Harvey and Macko, 1997; Sun et al., 1997; Grossi et al., 2001). In sediments dominated by sulfate
529 reduction, measured cell specific sulfate-reduction rates vary by 10 orders of magnitude (Jørgensen
530 et al., 2019). Furthermore, recent incubation experiments have built on other studies (e.g. Lee
531 1992) showing that the identity of the electron acceptors used during POC transformation
532 processes has little to no influence on the overall rate of organic carbon degradation (Beulig et al.,
533 2018). Taken together, these studies suggest that the identity of the oxidant/reductant does not
534 necessarily determine the reactivity of organic carbon, but that O₂ has a special role among EAs
535 in evaluating the reactivity of POC.

536

537 **2.6 Microorganisms**

538 Although many factors influence the reactivity of organic carbon in sediments, one of the
539 most unifying is microorganisms. The extent to which organic carbon reactivity is influenced by
540 the taxonomic and functional distribution of microorganisms is only beginning to be explored,
541 after an era in which little attention was paid to microbial life in sediments (see Section 1.3). In
542 the last decade or so, there has been a revolution in understanding the number, identity, functional
543 capabilities and extent of life in marine sediments, and their role in OC degradation.

544

545 **2.6.1 Abundance**

546 Microbial cell numbers correlate with mean sedimentation rate and distance from
547 continental landmasses (Kallmeyer et al., 2012), as well as with the amount of organic matter in
548 sediments (Jørgensen and Marshall, 2016). For surface sediments, those on continental margins
549 contain 10⁸ – 10¹⁰ cells cm⁻³, whereas those underlying oligotrophic gyres contain 10⁵ – 10⁷ cells
550 cm⁻³ (Kallmeyer et al., 2012) (Figure 5). In most sediments, cell concentrations decrease with
551 increasing depth below the seafloor, according to a power law. In OC-poor, oxic sediments, cell
552 concentrations drop below ~10² cells cm⁻³ between 10 and 15 mbsf (Kallmeyer et al., 2012;
553 Vuillemin et al., 2019). Cell abundance in OC-rich, anoxic sediments on continental shelves

554 remain relatively high at great depths in the sediment, and only fall to $\sim 10^2$ cells cm^{-3} between
555 1,000 – 2,500 mbsf (Kallmeyer et al., 2012).

556

557 **2.6.2 Identity**

558 Rapid progress in high-throughput DNA sequencing and analytical tools over the last
559 decade has completely revised our understanding of the tree of life (Hug et al., 2016). Many of the
560 phylogenetic groups found in sediments are candidate phyla that are not yet cultivated, so their
561 role in organic matter transformation is not entirely clear (Lloyd et al., 2018). Though common
562 types of fungi, bacteria, and archaea have been found in sediments (Richards et al., 2012; Orsi et
563 al., 2013), many new groups of microorganisms reside in the subsurface that appear to be endemic
564 to this environment. These endemic groups are repeatedly found to be relatively abundant in
565 subsurface settings (Anantharaman et al., 2016; Orsi, 2018), with widely differing diversity in oxic
566 and anoxic sediments (Orsi, 2018). In addition, sediments of varying redox state reveal evidence
567 of viruses (Engelhardt et al., 2015; Tully and Heidelberg, 2016; Bäckström et al., 2019; Cai et al.,
568 2019), which may contribute to organic processing via lysis of microbial biomass (Danovaro et
569 al., 2008; Orsi, 2018), with archaea potentially being disproportionately lysed in surface sediments
570 under deep waters (Danovaro et al., 2016).

571

572 **2.6.3 Functional capabilities**

573 Before the molecular biology revolution, the functional capabilities of microbial
574 communities in sediments were inferred from pore water profiles, with little to no direct biological
575 information. For example, decreases in sulfate and increases in sulfide suggested microbial sulfate
576 reduction and amendment experiments revealed that the addition of fermentation end products (H_2 ,
577 acetate) stimulated rates of sulfate reduction (Goldhaber et al., 1977; Iverson and Jørgensen, 1985).
578 The ability to sequence and identify genes with known functions, and determine their expression
579 levels, allowed for the discovery of new types of microorganisms as well as new functional
580 capabilities (Biddle et al., 2006; Biddle et al., 2008), which could then be correlated to geochemical
581 profiles.

582 Knowledge of microbial functionality from environmental ‘omics data (the term ‘omics is
583 commonly used to refer to the analysis of DNA, RNA, metabolite and protein sequences extracted
584 from samples) can be inferred from a close similarity of protein encoding genes from
585 environmental samples to those found in genomes of cultured microbes that have been assigned a
586 function based on biochemical experiments (de Bruijn, 2010). Marine sediment communities are
587 dominated by microorganisms that are not closely related to any current pure culture (Parkes et
588 al., 2005; Biddle et al., 2006; Inagaki et al., 2006; Lloyd et al., 2018). Therefore, it is speculative
589 to assume that distant genetic similarities from the *in situ* microorganisms to cultured strains imply
590 that those genes are enabling microorganisms to perform the same function. A large number of
591 genes encoding hypothetical proteins in marine metagenomes, which are digital libraries of all the
592 DNA present from all the microorganisms in a natural sample, remain difficult to annotate with
593 information about their identities or functions. For instance, in the large TARA Oceans
594 metagenomic data set, only about 16% percent of DNA sequences that encoded a hypothetical
595 protein had a statistically significant similarity to proteins with an experimentally determined
596 function. Furthermore, 44% of the hypothetical proteins had no significant similarity to gene
597 families that share general biochemical functions (Sunagawa et al., 2015a). This problem is
598 difficult to solve using traditional bioinformatic approaches, which rely on comparing
599 environmental sequences to genes whose function has been identified.

600 A further complicating factor is that databases of known genes are dominated by well-
601 characterized microorganisms, particularly from a single phylogenetic group (Proteobacteria),
602 whereas marine environments are dominated by uncultured organisms from diverse lineages
603 (Lloyd et al., 2018). Physiologies from some of these uncultured microbes have been inferred from
604 whole genome reconstructions in marine sediments (Lloyd et al., 2013), metatranscriptomics
605 showing which genes were being transcribed at the time of sampling (Orsi et al., 2013),
606 compositions of natural isotopes of biomass (Biddle et al., 2006; Shah et al., 2008; Meador et al.,
607 2015), stable isotope probing (Morono et al., 2011; Trembath-Reichert et al., 2017), direct
608 measurement of metabolites (Bird et al., 2019) and tracking increases in a microbial group's cell
609 abundance during laboratory enrichment of natural marine sediments (Kevorkian et al., 2018; Yu
610 et al., 2018b). The limitations of these approaches are that DNA and RNA sequences from
611 environmental samples can only be given functional annotations based on their similarity to known
612 cultures. Therefore, truly novel functions cannot be determined from sequencing methods alone.
613 Heterologous expression and characterization can be used to identify novel functions (Cottrell et
614 al., 2005; Michalska et al., 2015; Wrighton et al., 2016), but such methods have only been applied
615 to enzymes with enough homology to a known protein to develop a hypothesis. Determining the
616 functions of genes encoding truly novel "hypothetical" proteins will be very important for inferring
617 functions of uncultured microorganisms in marine sediments.

618 It should be noted that genome representation in databases represents one of the largest
619 issues for making correct assignments of protein encoding genes in environmental genomics
620 datasets. For example, the number of genomes from archaea in databases that derive from
621 subsurface environments has grown substantially in recent years (Lloyd et al., 2013; Spang et al.,
622 2015; Anantharaman et al., 2016; Baker et al., 2016; Jungbluth et al., 2017; Dombrowski et al.,
623 2018; Tully et al., 2018; Seitz et al., 2019). Before these genomes were available, protein encoding
624 genes expressed by archaea in marine sediments were estimated to be about 1% to 2% of total
625 genes expressed (Orsi et al., 2013). However, a re-analysis of that same data including these new
626 archaeal genomes in the database showed that archaea actually express 25% of the total genes
627 (Orsi, 2018), clearly demonstrating a database bias. Thus, we imagine that as more genomes from
628 archaea are sequenced, their representation in environmental 'omics datasets will continue to
629 increase. The archaea are thus likely to be critically important for subsurface carbon cycling, as
630 predicted by earlier studies from the marine subsurface (Biddle et al., 2006; Lloyd et al., 2013).

631

632 **2.6.4 OC Degradation potential based on biomolecular data**

633 The advent of inexpensive nucleic acid sequencing technology combined with the
634 availability of user-friendly bioinformatics processing platforms has made it possible for non-
635 specialists in bioinformatics to substantiate biogeochemical work with 'omics data. 'Omics
636 approaches that have proven valuable in sediment biogeochemistry include single-cell genomics,
637 metagenomics and the related practice of "binning" metagenomic sequences into "metagenome-
638 assembled genomes" (Albertsen et al., 2013), metaproteomics, and metabolomics (for a review
639 see Gutleben et al., 2018). These approaches, especially when used in concert, have enabled insight
640 into the mechanisms of organic matter degradation that would be impossible from purely
641 geochemical techniques. For instance, in deep sediments of the Baltic Sea, it appears that
642 Atribacteria have the potential to act as a keystone species, accessing a wide range of organic
643 carbon using a broad spectrum of extracellular enzymes, and then exporting the resulting free
644 amino acids, possibly supporting the rest of the microbial community (Bird et al., 2019).

645 Ideally, the integration of multiple molecular approaches will yield information on the
646 rates and potentials of organic matter oxidation by microbial communities. Progress along this
647 path has been made in studies of the nitrogen cycle, for which the genomic pathways of important
648 transformations (N₂ fixation, nitrification, etc.) are well-characterized and the relevant genes are
649 highly conserved (Pachiadaki et al., 2017). This information has been used to construct a “gene-
650 centric” model of the nitrogen cycle in the Arabian Sea oxygen minimum zone, revealing
651 interactions between the cryptic sulfur cycle and the nitrogen cycle which would have been
652 difficult to observe using purely biogeochemical techniques (Reed et al., 2014).

653 The use of biomolecular data to better understand organic carbon cycling is a nascent area
654 of inquiry that presents researchers with many avenues of research to make sense of the
655 tremendous diversity and complexity of organic structures, and therefore enzymes that catalyze
656 organic matter transformations. One aspect of this complexity is illustrated in Figure 6, which
657 shows that the phylogenetic diversity of putative secreted organic-degrading enzymes in anoxic
658 marine sediments spans the tree of life (Orsi, 2018). Peptidases provide a more specific example:
659 even though all peptidases catalyze essentially the same reaction, breaking a peptide bond, this can
660 be performed by 268 different structural families of proteins via eight separate catalytic
661 mechanisms (Rawlings *et al.*, 2016). Other categories of enzymes related to organic carbon
662 degradation are similarly diverse, obscuring relationships between enzyme structure and function
663 (Michalska et al., 2015). Because many enzymes relevant to OC degradation can catalyze reactions
664 beyond those including their “preferred” substrates, caution must be used when inferring
665 degradation processes from genomic data or enzyme assays (Steen et al., 2015). It is also possible
666 that novel uncultured clades harbor catalytic enzymes not identifiable by current annotation
667 methods. Therefore, even if particular genes are present in an ecosystem, biomolecular data sets
668 alone might not be sufficient for making specific predictions about the rate, quantity and type of
669 organic carbon reacted in a given system. Lastly, recent experimental work using bioreactor
670 incubations with marine sediments and different marine heterotrophs has directly demonstrated
671 species-to-species differences in the rate, quantity, and type of organic matter oxidized, illustrating
672 that the reactivity of organic carbon is also a function of the microorganisms that are present and
673 active in a given environment (Mahmoudi et al., 2019).

674

675 **2.6.5 Energetic and power constraints**

676 Absent photosynthesis, all microbial energy is derived from catalyzing redox reactions,
677 nearly all of which are ultimately driven by the degradation of organic carbon. The amount of
678 Gibbs energy available in a number of sedimentary settings has been determined (e.g. Schrum et
679 al., 2009; Wang et al., 2010; LaRowe and Amend, 2014; Teske et al., 2014), as have the metabolic
680 rates in a number of subsurface habitats (Orcutt et al., 2013a). However, the rate at which this
681 energy is used, microbial power utilization, is less well constrained, despite being critical for
682 understanding activity levels and growth state (Hoehler and Jørgensen, 2013; LaRowe and Amend,
683 2015a). In situ measurements of microbial power utilization are not yet feasible, but calorimetric
684 measurements carried out in the laboratory have begun to assess low rates of heat production from
685 small numbers of cells taken from the subsurface (Robador et al., 2016). However, a growing
686 number of studies have computed power usage by combining geochemical data with modeling
687 tools (e.g. LaRowe and Amend, 2015a, b; Bradley et al., 2018b). In these studies, data gathered by
688 scientific drilling is used to inform POC degradation models (see Section 4) while the energetics
689 of organic carbon degradation can be constrained by either using the total molecular composition

690 of dead microbial cells (Bradley et al., 2018b) or by relating the nominal oxidation state of organic
691 carbon to its energy content (LaRowe and Van Cappellen, 2011).

692 The results of these power studies have shown that in low-energy sediments, such as those
693 underlying the South Pacific Gyre (SPG), microbial activity is limited, more or less, to maintaining
694 cellular integrity through biomolecular repair and replacement (Bradley et al., 2018a), a state akin
695 to dormancy (see Section 4.3). Thus, maintenance activities (the sum of activities that do not
696 produce growth) constitute a much greater fraction of total power utilization by microbial
697 communities in habitats where growth is minimal. Indeed, bioenergetic modelling of the SPG
698 sediments suggested that <0.1% of the power from organic carbon oxidation can be attributed to
699 growth, with maintenance accounting for the rest (Bradley et al., 2019).

700 Power calculations have also been used to constrain the cell-specific power requirement of
701 microorganisms in sediments. Assuming that all counted cells are involved in organic matter
702 degradation, minimal cell-specific power requirement of microbial cells in SPG sediments have
703 been estimated to be around 1.9×10^{-19} W cell⁻¹ (LaRowe and Amend, 2015b). Assuming this value
704 for the non-growing cells in SPG sediments, the degradation of cells that died in the sediments,
705 necromass, was estimated to provide 2 to 13% of the power used by microbial communities in
706 shallow and relatively young sediments (<10,000 years) from SPG (Bradley et al., 2018b). In a
707 similar study, mean cell-specific metabolic rates of functional groups involved in nitrogen cycling
708 in oligotrophic North Pond sediments (on the western flank of the Mid-Atlantic Ridge) showed
709 that an increased power supply in transition zones between oxic and anoxic regimes may be
710 responsible for the revival of organisms from a maintenance state, and even for growth (Zhao et
711 al., 2019).

712 The lack of quantitative data accurately describing the distribution of various functional
713 groups of microorganisms in marine sediments has impeded the calculation of cell-specific power
714 requirements for particular catabolic groups. This has led to sometimes-untested assumptions
715 about the fraction of a community catalyzing a particular reaction (e.g. that ~10% of the total cells
716 in organic-rich sediments are sulfate reducers (Hoehler and Jørgensen, 2013)). Quantification
717 methods like marker-gene-based qPCR and FISH are useful means to measure the abundances of
718 various functional groups in marine sediments (Schippers and Neretin, 2006; Lever, 2013;
719 Buongiorno et al., 2017), though their application is limited by primer and probe biases.

720 One of the goals motivating calculation of cell-specific power requirements for different
721 types of functional groups (e.g. Zhao et al., 2019) under a wide range of natural conditions is to
722 determine the limits that the environment imposes on basal power requirements (Hoehler and
723 Jørgensen, 2013). Knowing what the ultimate limits are would greatly facilitate the prediction of
724 the standing stock of biomass of different functional groups in marine sediments on a global scale
725 using geochemical and physical data (e.g. Bowles et al., 2014; Egger et al., 2018) and without the
726 requirement for the collection, analysis and assembly of biological samples on such a vast scale.

727

728 **2.6.6 Microbial turnover rates**

729 Most early studies focusing on microorganisms in marine sediments were largely
730 conducted in the upper tens of centimeters of sediment, which are both younger and often more
731 carbon-rich than deeper sediments (see Figure 2). While some studies measured microbial
732 activities in subsurface sediments as deep as 1.5 mbsf at the Peru Margin (Parkes et al., 1990),
733 these studies generally depended on laboratory incubations to measure metabolic rates, which tend
734 to overestimate the *in situ* rate.

735 In recent years, new approaches that are incubation-independent and sensitive to low
736 activities have revealed that a large, active, yet slow-growing microbial community inhabits the
737 deep subsurface. These microbes subsist on low power levels and have been ascribed some of the
738 slowest turnover times ever documented. Amino acid racemization modelling has been used to
739 estimate that some marine sediment microorganisms require hundreds to thousands of years to
740 grow or replace all of their biomass (Lomstein et al., 2012), though these estimates have been
741 adjusted to span years to hundreds of years (Braun et al., 2017). It should be noted that this work
742 was carried out in relatively young, organic-rich sediments, (especially when compared to ancient
743 sediments, e.g. from SPG). A different and perhaps more sensitive method, deuterium
744 incorporation into lipids, has been used to estimate microbial community turnover times from tens
745 to hundreds of years in relatively shallow (< 1 mbsf) subsurface sediments from the Baltic Sea
746 (Wegener et al., 2012), as well as in very deep (up to 2,000 mbsf) sediments from offshore Japan
747 (Trembath-Reichert et al., 2017). In all cases, these turnover times are several orders of magnitude
748 slower than the doubling times of laboratory cultures, which are typically on the order of hours to
749 days.

750 With such slow replication rates, it is unlikely that subsurface sedimentary microorganisms
751 have experienced a sufficient number of generations for specific adaptations to have evolved and
752 spread through the community (Starnawski et al., 2017), calling into question whether these
753 organisms can be considered endemic (see Section 2.6.2). Under this scenario, it is more likely
754 that a community that is able to tolerate this increasing energy limitation is selected for as it is
755 buried deeper in the sediment column (Marshall et al., 2019). This idea is substantiated by evidence
756 that the microbial taxa that dominate deep subsurface sediments are common across a wide range
757 of locations (Petro et al., 2017) and are often found in surficial sediments (Walsh et al., 2015;
758 Starnawski et al., 2017), while the converse is not the case – surficial sediments contain microbial
759 taxa that are not found deeper in the sediment column. In fact, it has recently been shown that at
760 sites as diverse as the Indian Ocean and the Bering Sea, the operational taxonomic units that are
761 most abundant at depth are a subset of the local seafloor community (Kirkpatrick et al., 2019).
762 That is, net replication was not required to produce the microbial population observed in deep
763 sediment, which could instead have been produced by differential mortality rates. These lines of
764 evidence suggest that microbial community members with a slow-metabolizing survival strategy
765 are selected for in the energy-limited deep subsurface environment, though it is unclear that these
766 traits are passed on as in Darwinian selection. As noted above, the importance of energetic
767 efficiency as a selective advantage for long-term microbial survival has been supported by
768 modelling (Bradley et al., 2019) and experimental (Vuillemin et al., 2019) work. Metabolomic and
769 transcriptional evidence has identified some specific mechanisms that likely underlie the slow-
770 metabolizing survival strategy – for example, the use of chemical protectants to stabilize nucleic
771 acids and proteins, and metabolic interdependencies among members of the microbial community
772 (Bird et al., 2019). However, many of these mechanisms – and the impact of these slow
773 metabolizers on the long-term carbon cycle – remain underexplored.

774 775 **2.7 Sulfurization**

776 Sulfurization is one of the mechanisms thought to be responsible for the preservation of
777 organic carbon in marine sediments (for reviews see Sinninghe Damsté and De Leeuw, 1990;
778 Werne et al., 2004; Amrani, 2014). Sulfurization is the process whereby sulfur atoms ultimately
779 replace carbon atoms in organic compounds, producing organic sulfur compounds (OSC). OSCs
780 are thought to be less accessible to microbial degradation since S replaces reactive functional

781 groups that tend to be the easiest parts for microorganisms and/or their exoenzymes to access
782 (Kohnen and Sinninghe Damsté, 1989). Sulfur has been found in a wide variety of organic
783 compound types in sediments (Werne et al., 2004), occupying the full range of sulfur oxidation
784 states (-2 to +6) (Amrani, 2014). The preservation potential of OSCs is based on a) observations
785 that the S:C in POC increases with depth in sedimentary systems (Francois, 1987; Eglinton et al.,
786 1994; Hetzel et al., 2009; Amrani, 2014), b) the isotopic composition of organically bound S
787 (Francois, 1987; Mossmann et al., 1991) , c) intense sulfurization of POC-rich Cretaceous and
788 Jurassic deposits (van Kaam-Peters et al., 1997; Sinninghe Damsté et al., 1998; Van Kaam-Peters
789 et al., 1998; Kolonic et al., 2002; Kolonic et al., 2005; Böttcher et al., 2006; van Dongen et al.,
790 2006; Hetzel et al., 2009; Raven et al., 2018; Raven et al., 2019) d) observations that many fossil
791 fuels and their precursors have high levels of OSCs (Sinninghe Damsté et al., 1989a; Sinninghe
792 Damsté et al., 1989b) and e) laboratory studies (Krein and Aizenshtat, 1994; Schouten et al., 1994).

793 Sulfurization is thought to proceed in anoxic environments in which sufficiently high
794 concentrations of POC and H₂S coexist in the absence of metals such as reactive Fe (Gransch and
795 Posthuma, 1974; Werne et al., 2004; Amrani, 2014), although there is some evidence that
796 sulfurization can happen in the presence of reactive iron species since it can lead to the formation
797 of polysulfides which in turn seem to enhance the incorporation of S atoms into organic structures
798 (Kohnen and Sinninghe Damsté, 1989; Werne et al., 2004; Heitmann and Blodau, 2006).
799 Somewhat paradoxically, sulfurization is thought to be an abiotic process, yet the requisite sulfide
800 is attributed to microbial sulfate reduction, leading to the observation that high organic content is
801 sometimes required for its preservation (Quijada et al., 2016).

802 Sulfurization takes place in a variety of environments on a range of timescales. Although
803 it was traditionally thought to be a relatively slow process taking place in sediments and petroleum
804 reservoirs (Sinninghe Damsté and De Leeuw, 1990; Werne et al., 2004), more recent research has
805 shown that it can take place in hydrothermal systems (Gomez-Saez et al., 2016), in sinking marine
806 particles on a timescale of hours (Raven et al., 2016; Raven et al., 2019), and surface sediments
807 subjected to oscillating redox conditions (Jessen et al., 2017). It has been shown that such rapid
808 sulfurization of organic carbon likely exerted an important feedback on ocean redox geochemistry
809 and climate during the end of a major Cretaceous extinction event (OAE2), ultimately terminating
810 the extreme environmental conditions that caused it (Raven et al., 2019; Huelse et al., 2019).

811 **2.8 Terrestrial studies**

813 Investigations on the cycling of organic carbon in terrestrial settings offer valuable insights
814 to analogous processes within the marine subsurface. Moreover, terrestrial settings are easier to
815 access than deep marine environments, and thus they are more amenable to long term observations
816 and manipulation for field and laboratory-based experiments. Through such studies, the stability
817 of organic carbon has been found to be largely dependent on the complex interplay of the
818 physicochemical (e.g. OC-mineral interaction and aggregation, temperature, moisture, salinity,
819 etc.) and biological (e.g. microbial community composition, nutrient availability, extracellular
820 enzyme production, etc.) properties of the environment rather than on the molecular properties of
821 the OC itself (e.g. elemental composition, presence of functional groups, molecular conformation,
822 etc.). Given that a substantial fraction of POC buried in marine sediments is of terrestrial origin
823 (Burdige, 2007a), understanding the factors governing OC stability in terrestrial ecosystems
824 provides valuable insight into the marine carbon cycle.

825 Within soils, certain organic compounds such as lignin have classically been viewed as
826 resistant to biodegradation due to their large and complex molecular structures. However, lignin
827 and lignocellulose compounds are no more likely to persist in soils than other organics given the

828 proper conditions (Marschner et al., 2008b; Klotzbücher et al., 2011; Schmidt et al., 2011). This
829 is largely due to the activity of fungi, who play a critical role in the degradation of poorly reactive
830 organic substrates on land (Treseder and Lennon, 2015) and thus may also play a similar role in
831 marine sediments containing soil-derived organics. In fact, new experiments show that fungi living
832 in coastal marine sediments play a role in degrading lignocellulose at the land-sea interface
833 (Ortega-Arbulú et al., 2019).

834 The ability of microorganisms to degrade soil OC may, at times, also be restricted by
835 nutrient or energy limitations. This is especially pronounced in deep soil layers where turnover
836 times are on the order of thousands to tens of thousands of years (Schmidt et al., 2011). Recent
837 studies suggest that this long turnover time cannot be solely attributed to the chemical structure of
838 OC as there is not always a significant change in composition with depth (e.g. Fontaine et al.,
839 2007). However, amendments with fresh OC to subsoil via root exudates or decomposition (often
840 called priming) has been shown to stimulate increased degradation of the old OC, indicating that
841 the fresh OC may provide a needed energy source to promote the activity of existing microbial
842 degraders (Fontaine et al., 2007; Marschner et al., 2008b; Kuzyakov, 2010). This mechanism has
843 also been shown to occur to marine OC as well (Steen et al., 2016). The mechanism behind priming
844 effects, however, is unclear. Common root exudates such as oxalic acid may enhance organic
845 carbon degradation by removing organic carbon from mineral surfaces, thereby increasing its
846 reactivity (Keiluweit et al., 2015). In the case of permafrost, which is also primarily composed of
847 old organic carbon, temperature has been found to be a dominant factor governing its degradation.
848 While frozen, decreased water availability and microbial and enzymatic activity lead to an increase
849 in OC stability. With rising temperatures, these limitations are largely erased and OC degradation
850 rates increase (Schoor et al., 2009; Schmidt et al., 2011) and references therein).

851 Molecular biological tools have revealed that anoxic freshwater sediments contain similar
852 microbial groups that exist in their marine counterparts (Vuillemin et al., 2018). The presence of
853 the common phylum, Bathyarchaeota, in deep terrestrial sediments that contain high amounts of
854 unreactive plant derived organic matter (e.g. lignocellulose) is thought to be due to their ability to
855 use lignin as an energy source (Yu et al., 2018b). Bathyarchaeota might also be involved in the
856 turnover of terrestrially derived organic matter, such as lignin, in marine sediments in coastal
857 settings where land-derived OC is commonly deposited. Other bacterial “dark matter” groups that
858 are present in marine sediments such as the candidatus groups *Latescibacteria*, *Omnitrophica*, and
859 *Parcubacteria* have been shown to have similar rates of organic carbon turnover in freshwater
860 sediments relative to more well-studied groups such as the *Proteobacteria* (Coskun et al., 2018).
861 Given their transcriptional activities in marine sediments (Orsi, 2018), these groups could also be
862 important for benthic carbon cycling in the ocean.

863

864 **3. Old, hot and deep organic carbon**

865 Most studies concerning the rates of POC degradation in marine sediments focus on the
866 shallowest, most recently deposited material. However, it is becoming clear that deeply-buried
867 organic carbon is actively being consumed and that fluid circulation in the ocean basement can
868 impact OC reactivity through the modification of organic compounds as well as the composition
869 of sediment pore water.

870

871 **3.1 Ancient sediments**

872 Throughout Earth’s history there have been numerous periods of time when the deposition
873 flux of organic carbon into sediments has been much higher than the present day (Pedersen and

874 Calvert, 1990). A fraction of this ancient OC persists in modern marine sediments within layers of
875 elevated OC concentrations (Condie et al., 2001; Jenkyns, 2010; Ohkouchi et al., 2015). Although
876 the details vary depending on the time period, there is evidence that large-scale tectonic processes
877 and volcanism are ultimately responsible for the relatively high concentrations of OC deposited in
878 the past (Berry and Wilde, 1978; Condie et al., 2001; Jenkyns, 2010; Trabucho-Alexandre et al.,
879 2012; Ohkouchi et al., 2015). One such example is a section of Cretaceous-aged sediments located
880 in an area of the equatorial Atlantic known as the Demerara Rise, where drill cores from ODP Leg
881 207 have revealed shales that typically contain between 2 and 15 wt% POC in layers ranging from
882 56 to 94 meters thick (ShipboardScientificParty, 2004). Biogeochemical reaction transport
883 modelling has revealed that deep Demerara organic-rich strata likely host organisms that convert
884 the POC in these shales into CH₄ which is subsequently consumed by anaerobic methane oxidizing
885 microbial consortia using SO₄²⁻ as the oxidant (Arndt et al., 2006). Although data on microbial
886 abundance are not available, it is likely that biomass concentration is higher in POC-rich sediment
887 layers as well as the adjacent sulfate-reducing zone than in the hundreds of meters of sediment
888 separating these layers from the SWI, in which the POC content is far lower. Supporting this
889 notion, cell abundances in core sections 1,500 to 2,500 mbsf near the Shimokita Peninsula, Japan,
890 are orders of magnitude higher in organic-rich lignite layers than surrounding, organic-poor
891 sediments (Inagaki et al., 2015). Although much of this deeply-buried organic matter looks to have
892 escaped microbial degradation, it seems as if it is actually hosting a very slowly metabolizing
893 community. Observations and diagenetic modeling results show that the organic matter in ancient,
894 deeply buried organic carbon-rich strata still provides a suitable substrate for ongoing microbial
895 respiration (Krumholz et al., 1997; Coolen et al., 2002; Krumholz et al., 2002; Moodley et al.,
896 2005; Arndt et al., 2006; Arndt et al., 2009). Microbial biomass and cell activity have also been
897 shown to peak at redox transition zones, including at oxic-anoxic transition zones in North Pond
898 sediments (Zhao et al., 2019), and in deep (~90 m below the SWI) Peru Margin sediments
899 associated with ODP Leg 201 (site 1229) where there is a convergence of methane and sulfate, the
900 latter of which is diffusing upwards from a brine (Jørgensen et al., 2003).

901 The rate at which old, deeply buried organic carbon is metabolized by microorganisms in
902 marine sediments becomes extremely slow with depth (Middelburg, 1989), but as these organics
903 are exposed to sufficient pressure and temperature, they can be converted abiotically into
904 petroleum through a process known as catagenesis. Although it is thought that the principle zone
905 of oil formation in organic-bearing sediments occurs from ~ 50 - 160° C, with pressure playing a
906 lesser role, hydrocarbons and methane can be generated abiotically from complex organic matter
907 at lower temperatures (Tissot and Welte, 1984; Hunt, 1996). As noted by LaRowe et al. (2017a),
908 nearly 35% of the volume of marine sediments are above 60°C, and even if sediments do not
909 contain enough OC to be commercial sources of petroleum (TOC > 0.5% by weight), the remaining
910 organic carbon in them can still be converted to microbially accessible hydrocarbons through
911 abiotic processes. Some fraction of small-molecular weight hydrocarbons and CH₄ produced
912 abiotically in sedimentary basins could be expelled and migrate to regions that are more conducive
913 for life. Both petroleum and natural gas can migrate hundreds of kilometers from source rocks
914 (Selley, 1998), and there are certainly thermophilic anaerobes capable of oxidizing common
915 products of catagenesis such as alkanes and benzyl-compounds (Teske et al., 2014). In addition,
916 water, CO₂ and H₂S can also be produced in large amounts during the catagenesis of Type II
917 kerogens (Tissot and Welte, 1984), fueling microbial activities with carbon and electron acceptors
918 and donors. Furthermore, it has been estimated that more CH₄ has been produced by methanogens
919 degrading petroleum reservoirs than there is primary CH₄ produced from catagenesis (Milkov,

920 2011). In total, $1.97 - 3.94 \times 10^{13}$ kg of free CH₄ generated from the microbial degradation of
921 petroleum is estimated to exist in sedimentary basins (Milkov, 2011). Taken together, catagenesis
922 could be fueling microbial communities deep in marine sediments of unknown size.
923

924 **3.2 Hydrothermal sediments**

925 Sediments that are deposited in regions near spreading centers or volcanic hot spots are
926 subjected to advecting hot fluids that transform organic molecules. The effects are particularly
927 pronounced near continental settings, such as the Guaymas Basin in the Gulf of California
928 (Simoneit and Lonsdale, 1982) and at Middle Valley on the Juan de Fuca Ridge, off the coast of
929 Washington State (Cruse and Seewald, 2006). The transformations that occur have been compared
930 to the formation of petroleum on geologic time scales (Simoneit and Lonsdale, 1982), but with
931 important differences due to the presence of water (Seewald, 2001). In laboratory experiments,
932 sediments heated in the presence of water typically release a large pulse of organic matter into the
933 fluids, followed by a slow decline in overall organic concentrations, presumably due to the
934 formation of degradation products such as CO₂ and CH₄ (Seewald et al., 1990; Lin et al., 2017).
935 Organic acids, acetate in particular, are some of the most abundant degradation products (Eglinton
936 et al., 1987; Fisher, 1987; Lundegard and Kharaka, 1994; Kawamura et al., 1996; Shebl and
937 Surdam, 1996; Seewald, 2001), although reactive amino acids, polysaccharides, and small peptides
938 have also been found to be released from Guaymas Basin sediments by heating (Martens, 1990;
939 Lin et al., 2017). These ancient petroleum-derived substrates are further catalyzed by subsurface
940 microbes (Pearson et al., 2005). Acetate and other low molecular weight organic compounds
941 including formate, lactate, methanol and ethanol have been identified in Guaymas Basin sediments
942 and were found to have a microbial rather than thermal source (Zhuang et al., 2019). Hydrothermal
943 alteration of DOC begins at temperatures as low as 68 °C (Hawkes et al., 2016), suggesting that
944 the hydrothermal influence may be widespread (LaRowe et al., 2017a).
945

946 **3.3 Ocean basement fluids**

948 Scientific drilling into the seafloor has revealed that the chemical constituents of fluids
949 circulating in the ocean crust basement, such as oxygen, diffuse into overlying sediments (Orcutt
950 et al., 2013b; Wheat et al., 2013) (see Figure 4). The implications of this for POC degradation in
951 sediments is only just being explored. The oceanic basement is generally considered a net sink for
952 marine OC (Lang et al., 2006; Shah Walter et al., 2018) with both microbiological and abiotic
953 removal mechanisms. In addition to the sediment column, deep-ocean DOC, POC and sedimentary
954 particles enter the crust with oceanic bottom water through exposed outcrops. Most of this fluid
955 flux occurs away from active ridge axes in older, cooler crust and is equivalent to about one fifth
956 of the global riverine flux into the ocean (Johnson and Pruis, 2003).

957 Recent studies have described the concentration and isotopic composition of DIC and DOC
958 in ocean basement fluids from naturally outflowing fluids from the Dorado Outcrop (McManus et
959 al., 2019) and fluids recovered from IODP CORK observatories on the flank of the Juan de Fuca
960 Ridge (Lin et al., 2019) and North Pond (Shah Walter et al., 2018) - all relatively cool settings
961 away from mid-ocean ridge spreading centers. Although fluid chemistry is variable on the flanks
962 of ridges, ranging from warm, anoxic fluids recovered from near the Juan de Fuca Ridge (Lang et
963 al., 2006; Lin et al., 2019) to oxygenated fluids that resemble bottom seawater at North Pond
964 (Meyer et al., 2016), fluid temperatures are low enough to allow for microbial activity to influence
965 the OC reservoir (McCarthy et al., 2011; Shah Walter et al., 2018; McManus et al., 2019).

966 Heterotrophic activity has been identified in these environments (e.g. Furnes et al., 2001; Lin et
967 al., 2015; Robador et al., 2015; Russell et al., 2016) and DOC concentrations in circulating
968 basement fluids are lower than in overlying bottom water. Compared to 35-45 μM in deep
969 seawater, cool hydrothermal DOC concentrations can be $<15 \mu\text{M}$ (Lang et al., 2006; Lin et al.,
970 2012; Shah Walter et al., 2018; Lin et al., 2019). This DOC removal has been attributed to selective
971 oxidation on the basis of a concurrent loss of oxygen, the ^{14}C content of the remaining organic
972 matter and characterization by NMR and FT-ICR-MS (LaRowe et al., 2017b; Shah Walter et al.,
973 2018; Lin et al., 2019). The DOC removed in the crustal subsurface has a ^{14}C age of up to 4,300
974 years at North Pond, indicating a long residence time in the open ocean before oxidation by
975 basement microorganisms, underscoring the importance of treating OC degradation as an
976 ecosystem property. Chemoautotrophic DOC, isotopically and molecularly distinct from deep-
977 ocean DOC, has also been identified in cool hydrothermal fluids, although their concentrations are
978 lower than DOC in bottom water, implying a slow production rate (McCarthy et al., 2011; Shah
979 Walter et al., 2018).

980 Fluids that pass through high temperature black smoker hydrothermal systems have DOC
981 concentrations that are approximately one-third that of deep seawater (Lang et al., 2006). Abiotic
982 removal pathways are dominant in regions of active hydrothermal venting where fluids are
983 intensely heated and can reach temperatures of 400°C . Thermal decomposition of OC to volatile
984 gases, CO_2 , H_2 and CH_4 , has been demonstrated experimentally (Siskin and Katritzky, 1991;
985 Seewald, 2001; McCollom and Seewald, 2003b, a) and is known to be an important loss
986 mechanism that “scrubs” fluids of deep-ocean DOC in high temperature reaction zones (Lang et
987 al., 2006; Hawkes et al., 2015), although DOC sorption to crustal surfaces is also possible
988 (Schwarzenbach et al., 2005). In seafloor regions adjacent to high temperature venting,
989 oxygenated seawater can mix with reduced hydrothermal fluids, creating chemical disequilibria
990 that autotrophic microorganism can use to fuel primary production (McCollom and Shock, 1997).
991 These regions can be hot spots of organic matter production both within the fluids and within the
992 surrounding sediments (Karl et al., 1980; Lang et al., 2006; Wankel et al., 2011). DOC is seemingly
993 produced abiotically at vents hosted on ultramafic rocks, with elevated concentrations compared
994 to overlying bottom water (Lang et al., 2010). Most of this increase is thought to be due to the
995 abiotic formation of small organic acids (Lang et al., 2010; McDermott et al., 2015). A
996 combination of microbial, abiotic and sedimentary sources likely contributes to seafloor DOC
997 pools, which if circulated in the basement from the ridges, could diffuse into overlying sediments,
998 potentially fueling communities.

999

1000 **4. Computational models**

1001 A theoretical understanding of the carbon cycle in marine sediments underpins much of the
1002 present knowledge and constraints on the burial and transformation of organic carbon in this
1003 setting, both in the present day and throughout Earth’s history. Numerical models have been used
1004 for decades within this framework to quantify how POC drives sediment diagenesis at particular
1005 locations (Berner, 1964; Lerman, 1971; Berner, 1980; Boudreau, 1997). These models can include
1006 the role of particular electron acceptors, secondary redox reactions, sorption and desorption, and
1007 microbial dynamics while simultaneously accounting for transport processes such as sedimentation,
1008 bioturbation, bioirrigation and the diffusion of solutes. A comprehensive review of reaction
1009 transport models and their use in marine sediments is provided in (Arndt et al., 2013), covering
1010 the formulation of various reaction and transport networks, their application to natural and
1011 engineered systems across a wide range of temporal and spatial scales, and the challenges and

1012 limitations of implementing these models. The following sections highlight recent modeling
1013 advances with respect to marine sediments and new research directions that could further improve
1014 them.

1015

1016 **4.1 Representing pools of organic molecules**

1017 It is both infeasible and ineffectual to explicitly resolve the true complexity of organic
1018 carbon in marine sediments in numerical models. Rather, owing to its complexity and
1019 heterogeneity, OC is usually characterized by its apparent bulk reactivity. Therefore, numerical
1020 models for OC transformations in marine sediments must account for changes in both (1)
1021 concentration and (2) reactivity of the bulk substrate. If more specific information describing how
1022 the proportions of compound types are changing were available, ideally, this would be quantified
1023 as well. The concentration of organic carbon is usually defined in absolute terms as the sum of all
1024 of the various reactive fractions, and corresponds directly to conventional laboratory
1025 measurements of POC. Models of organic carbon reactivity can be broadly divided into two
1026 classes: discrete and continuum. Within discrete models, OC is attributed to either a single pool of
1027 concentration G (one- G) with a constant first-order degradation rate (Berner, 1980), or divided
1028 across a discrete number of pools representing various classes of reactivity (multi- G), where the
1029 apparent reactivity of the bulk organic matter is related to the reactivity of each class (Jørgensen,
1030 1978). Continuum models, alternatively, assume a continuous distribution of organic matter
1031 compounds across an infinite spectrum of reactivities (Aris, 1968; Ho and Aris, 1987; Boudreau
1032 and Ruddick, 1991). The choice of model formulation is generally governed by the overarching
1033 research question, the relevant spatial- and timescales, data availability, and mathematical
1034 expedience. Since these numerical formulations are abstracted from measurements, it can be
1035 challenging to constrain reaction rate constants based on experimental data. Consequently, organic
1036 matter reactivity is traditionally constrained by inverse modeling of comprehensive sets of
1037 sediment depth profiles.

1038

1039 **4.2 Organic molecular data**

1040 There are very few models describing the degradation of OC in sediments that use
1041 information about the molecular character of organic compounds. This is primarily because there
1042 are relatively few reports describing the chemical formulas and structures of marine sedimentary
1043 organic compounds in a way that could be parameterized in a model (see Section 2.2). The
1044 modeling studies that have used molecular information have only tangentially addressed how this
1045 information impacts rates of marine OC degradation. Reaction transport modeling (Niggemann et
1046 al., 2007; Freitas et al., 2017) and kinetic modeling studies (Schouten et al., 2010) have explored
1047 how different degradation rates of specific biomarker compounds could influence the
1048 interpretation of past sea surface temperatures. The abundance and proportion of certain types of
1049 amino acids in marine sediments has been used as an index for the degradation state of POC
1050 (Dauwe et al., 1999). In another study that evaluated the abundance of particular organic
1051 compounds, the Gibbs energy associated with the degradation of organic compounds was used to
1052 explain patterns of biomarker degradation in sediments from the Southeast Atlantic ocean
1053 (Hernández-Sánchez et al., 2014). The Gibbs energies in this study are estimated based on the
1054 oxidation state of the carbon in organic compounds, which is in turn calculated from the
1055 stoichiometry of the compounds (see LaRowe and Van Cappellen, 2011). LaRowe and Van
1056 Cappellen used this approach to argue that the rate of organic carbon degradation in anoxic marine
1057 sediments is retarded by the molecular character of the organic compounds. The rationale for this

1058 is based on the idea that the rate of microbial catabolism is proportional to the Gibbs energy of that
1059 metabolism: less exergonic reactions are catalyzed more slowly than more exergonic reactions (see
1060 Jin and Bethke, 2003; LaRowe et al., 2012).

1061

1062 **4.3. Microorganisms in models**

1063 Although the actions of microorganisms are implicitly accounted for within models of OC
1064 degradation in marine sediments, they are rarely explicitly resolved within the mathematical
1065 formulae, i.e. as a separate state variable. This is mostly due to (a) model applications that are
1066 focused on geochemistry or biogeochemistry rather than microbiology, and (b) the uncertainties
1067 concerning microbial growth, maintenance, death, and dormancy in marine sediments which must
1068 be resolved in order to accurately simulate microbial dynamics (Hoehler and Jørgensen, 2013;
1069 Jørgensen and Marshall, 2016; Kempes et al., 2017; Bradley et al., 2018a). Nevertheless,
1070 (Boudreau, 1999) was the first to couple microbial processes to organic carbon diagenesis, and
1071 derive a mathematical basis between previously observed microbial biomass and organic carbon
1072 concentrations in sediments (Bird and Duarte, 1989). Later work incorporated explicit
1073 mathematical representation of microbial processes into reactive transport frameworks linking
1074 sediment redox gradients and reaction rates to microbial processes (Wirtz, 2003; Thullner et al.,
1075 2005), the competition of different microbial groups for a common substrate (Thullner et al., 2007)
1076 and to assess the impact of transport processes on transient biomass distributions, anaerobic
1077 oxidation of methane rates and methane release fluxes from the sea floor (Dale et al., 2006; Regnier
1078 et al., 2011; Puglini et al., 2019). Formulations of microbial processes in sediment models have
1079 been developed further to account for the relative importance of growth versus maintenance, and
1080 variable physiological states (i.e. dormancy) (Bradley et al., 2018a, 2019).

1081

1082 **4.4 Application scale**

1083 Despite marine sediments comprising a significant volume of the Earth's surface (LaRowe
1084 et al., 2017a), playing a dominant role in the global carbon budget on long time scales (Arndt et
1085 al., 2013), and hosting a significant fraction of Earth's living biomass (Kallmeyer et al., 2012),
1086 their treatment in global-scale models of the Earth's climate and biogeochemistry may often be
1087 little more than a simple closure term for mass conservation (Soetaert et al., 2000; Hülse et al.,
1088 2017; Lessin et al., 2018). In case they are explicitly resolved, the interactions between marine
1089 sediments and the overlying water column, i.e. benthic-pelagic coupling, are often neglected or
1090 crudely implemented in such global-scale models (Soetaert et al., 2000; Gehlen et al., 2006;
1091 Munhoven, 2007; Hülse et al., 2017). Even relatively simple reaction-transport models are more
1092 typically applied to regional scales (Ruardij and Van Raaphorst, 1995; Luff and Moll, 2004; Arndt
1093 and Regnier, 2007) over idealized global ocean hypsometric transects or provinces (e.g. Soetaert
1094 et al., 1996; Thullner et al., 2009; Krumins et al., 2013) and over time-spans of thousands to
1095 millions of years (e.g. Arndt et al., 2009; Krumins et al., 2013; Orcutt et al., 2013b). Only a very
1096 small number of global scale biogeochemical or Earth System models employ an explicit,
1097 vertically resolved, multi-component description of diagenetic dynamics (e.g. Heinze et al., 1999;
1098 Munhoven, 2007; Shaffer et al., 2008; Palastanga et al., 2011; Ilyina et al., 2013; Tjiputra et al.,
1099 2013; Hülse et al., 2018a). Yet, due to the need to find computationally efficient analytical solutions
1100 to the diagenetic equations these descriptions generally rely on simplifying assumptions and/or are
1101 restricted to the upper few centimeters of the sediment. However, coupled models can provide
1102 important insights into ocean biogeochemical cycling and climate feedbacks. For instance, the
1103 recent coupling of a vertically resolved benthic model to the three-dimensional Earth System

1104 Model CGENIE (Hülse et al., 2018b) has revealed that organic matter sulfurization reduces the
1105 extent and intensity of toxic euxinic conditions, and accelerates climate cooling on a scale that is
1106 globally significant during ocean anoxic event recovery (Hülse et al., 2019). Alternatively, large
1107 ensemble runs of complex one-dimensional diagenetic models have also been used to derive
1108 transfer functions for specific target outputs such as benthic fluxes or benthic methane gas hydrates
1109 that have then been applied on a regional and global scale (Gypens et al., 2008; Dale et al., 2015;
1110 Capet et al., 2016). In another large-scale effort, (LaRowe et al., 2020) have developed a global-
1111 scale model based on the analytical solution of the one-dimensional conservation equation for
1112 benthic organic carbon dynamics that reveals the 3-D distribution of marine sediment POC for
1113 Quaternary-aged sediments (< 2.6 Ma) as well as rates of its degradation. Bradley et al. (in
1114 revision) have built on this model to quantitatively estimate the cell-specific power utilization of
1115 microorganisms transforming POC in global aerobic, sulfogenic and methanogenic sediment
1116 horizons.

1117

1118 **5. Outlook**

1119 Although it is well known that human activity is responsible for a rapid rise of atmospheric
1120 CO₂, it is unclear how this disturbance will impact the natural fluxes of carbon among major global
1121 reservoirs. In particular, it is still an open question how human-induced climate change will alter
1122 the strength of the marine sedimentary carbon sink, and therefore control of atmospheric CO₂.
1123 Recent observations and model projections suggest that the impact of climate change on marine
1124 POC is likely going to be regionally heterogeneous (Passow and Carlson, 2012), and will include
1125 warming waters, disappearing sea ice, increased DIC content, lowered pH and altered fluxes of
1126 organic carbon into and through the water column (Levin and Le Bris, 2015; Sweetman et al.,
1127 2017), particularly from terrestrial sources (Bauer et al., 2013b; Regnier et al., 2013). Each of these
1128 factors have potential implications for how organic carbon is delivered to and processed within
1129 sediments. Yet, because benthic carbon dynamics are first and foremost controlled by the quantity
1130 and quality of OC that settles onto the seafloor, perhaps the most important factor in controlling
1131 the response of deep ocean (< 200 m) benthic carbon dynamics to projected environmental change
1132 is the biological carbon pump, the process by which organic carbon produced in the euphotic zone
1133 is exported into the deep ocean. In addition, coastal benthic carbon cycling, in particular in
1134 nearshore depositional environments in the vicinity of large rivers such as, among others, the
1135 Arctic shelf, the Amazon shelf or the South China Sea, will also be affected by changes in
1136 terrestrial inputs.

1137 The geologic record includes numerous examples of such climate change induced
1138 perturbations in the functioning of the biological carbon pump (Arthur et al., 1985; Kohfeld et al.,
1139 2005; Ridgwell, 2011; John et al., 2014; Hülse et al., 2019). For instance, abundant black shales
1140 in the sedimentary record speak to periods when much or all of the world's bottom ocean waters
1141 were devoid of free O₂ (Jenkyns, 2010), likely due to a warmer climate, the paleogeography,
1142 enhanced nutrient supply and elevated marine primary productivity that in turn might have been
1143 maintained by benthic nutrient cycles perturbed by this bottom water anoxia (Ingall and Jahnke,
1144 1994; Van Cappellen and Ingall, 1994). Ultimately, the widespread anoxic and euxinic
1145 depositional conditions enhanced organic carbon preservation such that atmospheric CO₂ and,
1146 therefore, temperatures decreased and O₂ eventually returned to bottom waters, a process lasting
1147 tens to hundreds of thousands of years (Arthur et al., 1988; Kolonic et al., 2005; Jarvis et al., 2011;
1148 Hülse et al., 2019; Raven et al., 2019). Though there is a consensus that it is not currently possible
1149 to gauge how the biological pump will be altered in the next several decades (Pörtner et al., 2014),

1150 a number of studies are hinting at how climate change will impact the flux of carbon to marine
1151 sediments.

1152 As a master variable for biogeochemical reactions, temperature will have likely have a
1153 significant impact on the reactivity of organic carbon in marine sediments. Ocean warming has
1154 already led to the expansion of oxygen minimum zones in the water column over the last 50 years
1155 (Schmidtko et al., 2017; Bertagnolli and Stewart, 2018; Breitburg et al., 2018), disrupting the role
1156 of bioturbation on POC reactivity. Warmer water seems to select for smaller plankton altering the
1157 export flux of POC to the seafloor (Morán et al., 2010) since smaller particles tend to have longer
1158 transit times to the seafloor. In high latitudes, the disappearance of sea ice, an increase in the length
1159 of the growing season, fundamental changes to regional circulation (e.g. Atlantification) resulting
1160 in changing salinity, temperature and nutrient conditions will exert important, yet poorly known
1161 impacts on ecosystem structure. In general, temperature changes are known to influence the
1162 structure and function of marine microbial communities (Sunagawa et al., 2015b), and, in addition
1163 to other environmental forces, virus-host relationships (Danovaro et al., 2008; Danovaro et al.,
1164 2011), which in turn can alter patterns of carbon sequestration (Guidi et al., 2016) in sediments.
1165 The combination of warming, acidification, eutrophication and human activities such as bottom
1166 trawling (Hiddink et al., 2017) and seafloor mining (Orcutt et al., 2020) might lead to ecosystem
1167 destruction and/or many areas of the seafloor to become covered in microbial mats (de Bakker et
1168 al., 2017; Ford et al., 2018), rather than bioturbated sediments. In addition, lower than normal pH
1169 cause some marine bacterioplankton to express genes for maintenance rather than growth (Bunse
1170 et al., 2016), thus slowing the flux of C to sediments. Although it is difficult to predict how it will
1171 impact the reactivity of organic carbon in sediments, e.g. (Isla and DeMaster, 2018), it is clear that
1172 climate change is altering the physiochemical variables that govern microbial behavior. Therefore,
1173 attempts to better understand how carbon fluxes will respond to projected climate change and also
1174 how carbon fluxes have responded to past extreme climate and carbon cycle perturbations will
1175 require an ecosystem approach that includes the role of microorganisms (Cavicchioli et al., 2019).

1176 The information summarized in this contribution supports the emerging view that organic
1177 matter reactivity in marine sediments is a complex function of biological, geochemical and
1178 physical forces that vary from one part of the seafloor to another. Given the large variety of
1179 organic compounds, minerals, organisms, and environmental conditions found in marine
1180 sediments, it is undoubtedly true that all of the mechanistic hypotheses described in this review
1181 contribute in some way to the long-term preservation of organic carbon, with the relative
1182 importance of each changing with both time and space. Going forward, it will be critical that
1183 studies examining sedimentary organic carbon account for the whole array of biophysiochemical
1184 factors that impact reactivity, thus providing the much needed interdisciplinary data sets required
1185 to advance our quantitative understanding and predictive capabilities. Disentangling which
1186 mechanism operates under what set of environmental conditions is a complicated task requiring
1187 integration of measurements, laboratory experiments, quantitative modelling and an open mind. A
1188 community effort will be required to understand not only what determines organic carbon
1189 reactivity in marine sediments now, but how this will change in the future. Moreover, integrated
1190 approaches considering marine sediments in relation to the terrestrial and water column settings is
1191 needed to gain a truly global and comprehensive understanding of the carbon cycle.

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1215

1216 **Figure captions:**

1217

1218 Figure 1. Schematic of topics discussed in this review: ecosystem factors that influence the
1219 reactivity of particulate organic carbon, POC, in marine sediments. The bulleted
1220 processes/variables and four categories are not necessarily independent of one another.

1221

1222 Figure 2. Concentration of particular organic carbon (POC) at a) the sea floor, b) 1 meter below
1223 the sea floor and c) 10 meters below the seafloor, based on calculations by LaRowe et al. (2020)
1224 and data summarized in Wallmann et al (2012), which, for Holocene sediments, is taken from a
1225 compilation by (Seiter et al., 2004). Grey areas in c) indicate regions where Quaternary sediments
1226 (i.e. sediments deposited throughout the last 2.59 million years) are less than 10 m thick. The
1227 Quaternary cutoff is the temporal limit for the model used by LaRowe et al. (2020).

1228

1229 Figure 3. Estimated a) regions of the seafloor where dissolved O₂ is modeled to be present
1230 throughout the sediment to the underlying oceanic basement and b) depth of the sulfate-methane
1231 transition (SMT) zone. The dark shading in a) refers to the minimum extent of modeled O₂-
1232 penetrating regions while the light shading, together with the dark shading, indicate the maximum
1233 extent, based on D’Hondt et al (2015). The white regions in b) denote regions where there is no
1234 SMT. All data for b) from Egger et al (2018).

1235

1236 Figure 4. Oxygen concentration profiles as a function of depth in marine sediments and ocean
1237 basement crust from three IODP drill cores located on ~ 8 Ma flank of the mid-Atlantic Ridge
1238 (also known as North Pond – see Orcutt et al., 2013). The bottom panel contains a cross section
1239 schematic of what is thought to be the mechanism of O₂ delivery to basal sediments – upward
1240 diffusion from oxygenated fluid flowing rapidly in the basement. This fluid is chemically very
1241 similar to local bottom seawater and is likely introduced to the subsurface from locally outcropping

1242 basalt (see Meyer et al., 2016). Oxygen loss in flowing fluids is thought to result from both
1243 diffusion into sediments and consumption during microbial oxidation of DOC.

1244
1245 Figure 5. Calculated cell concentrations in marine sediment at a) the seafloor, b) 1 meter below
1246 the sea floor and c) 10 meter below the seafloor using the data compilation and approach described
1247 by Kallmeyer et al. (2012).

1248
1249 Figure 6. Phylogenetic tree showing microbial groups containing genes encoding putatively
1250 secreted enzymes capable of degrading proteins and carbohydrates in anoxic marine sediments
1251 (modified from Orsi et al, 2018). The term CAZymes refers to carbohydrate-active enzymes
1252 (Lombard et al., 2013).

1253
1254 **References**

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2706

Figure 1

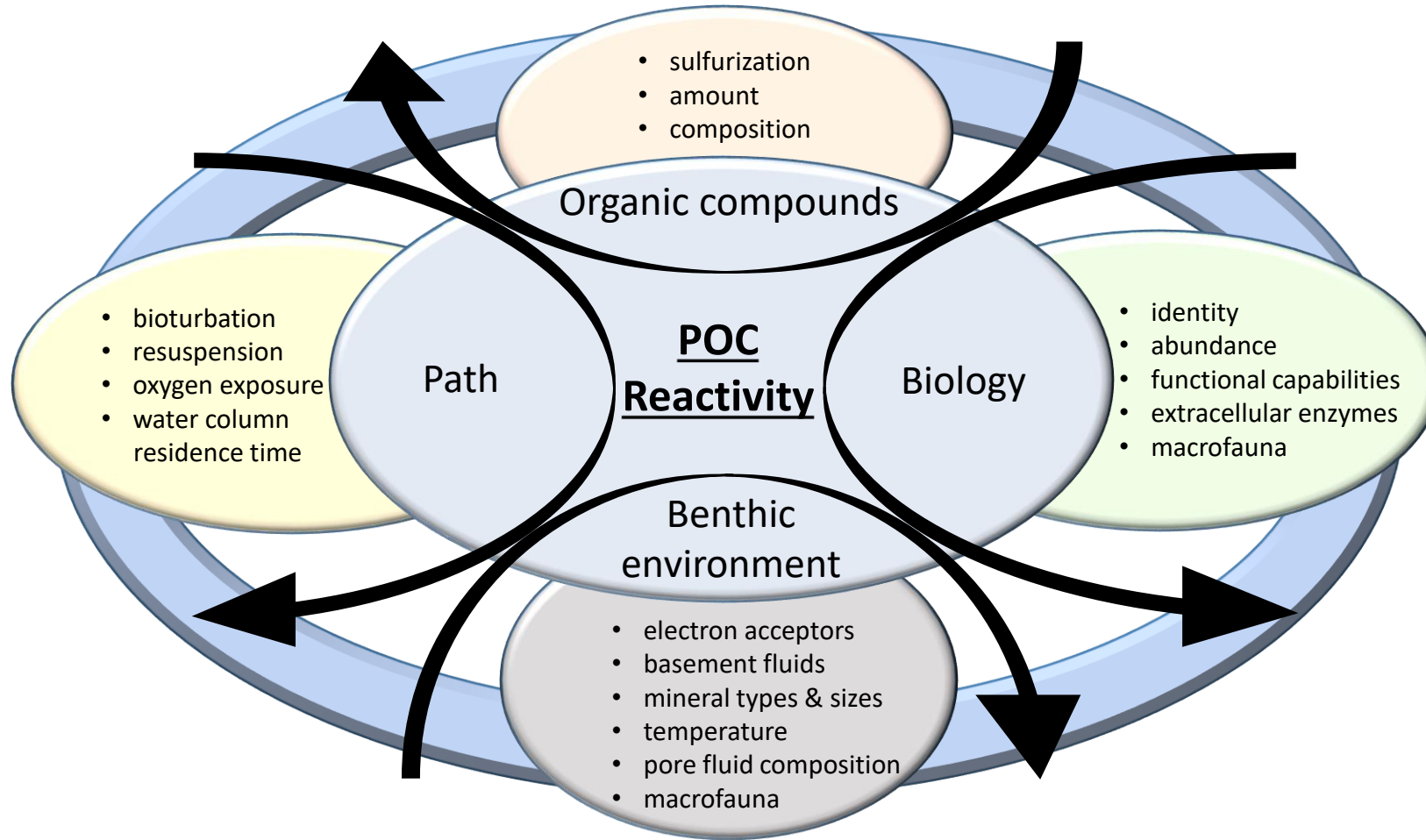


Figure 2

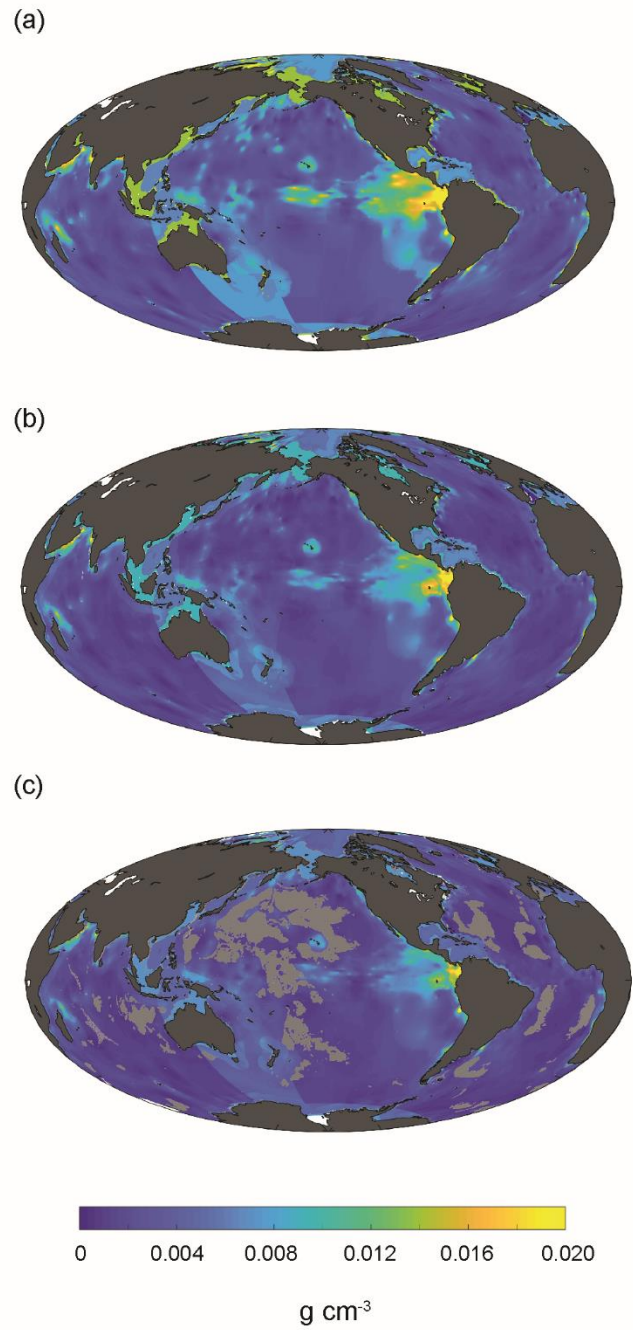


Figure 3

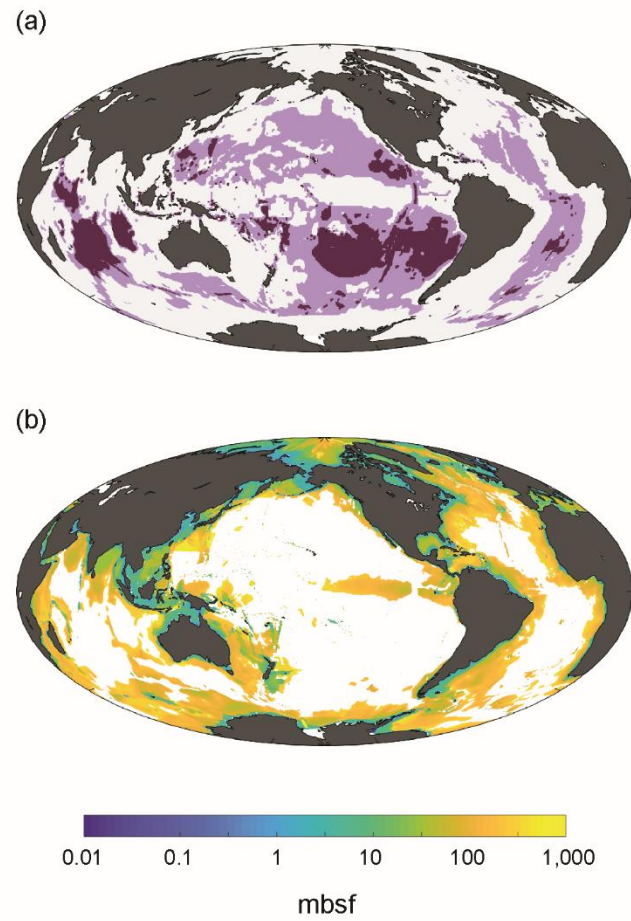


Figure 4

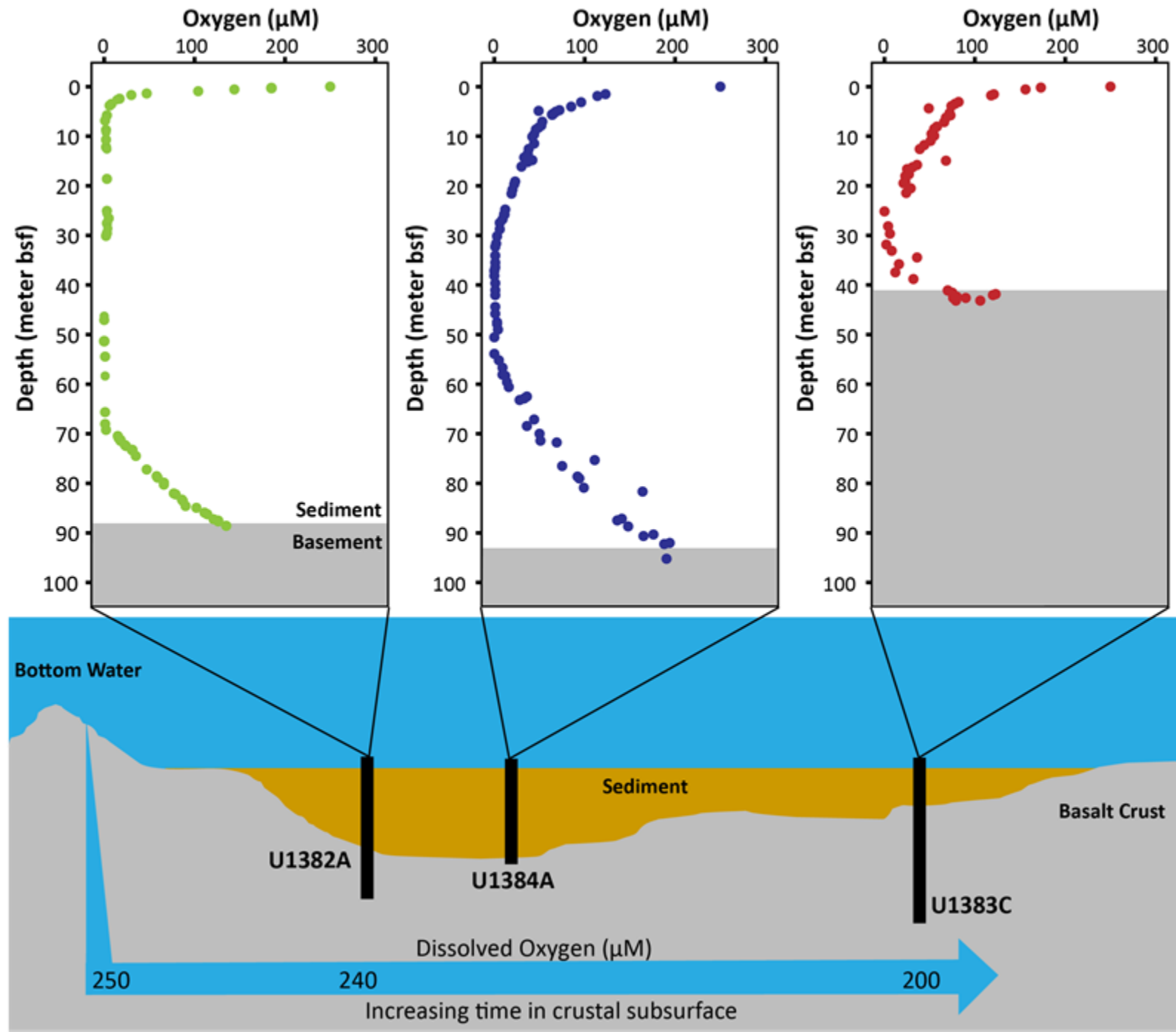


Figure 5

