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► **To cite this version:**

Gretchen L Früh-Green, Deborah S Kelley, Marvin D Lilley, Mathilde Cannat, Valérie Chavagnac, et al.. Diversity of magmatism, hydrothermal processes and microbial interactions at mid-ocean ridges. *Nature Reviews Earth & Environment*, 2022, 3, pp.852-871. 10.1038/s43017-022-00364-y . hal-04285383

HAL Id: hal-04285383

<https://hal.science/hal-04285383v1>

Submitted on 14 Nov 2023

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1 Accepted version 30. Sept. 2022

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3 **Diversity of magmatism, hydrothermal processes and microbial interactions**
4 **at mid-ocean ridges**

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17

18

19 **Abstract**

20 Hydrothermal circulation and alteration at mid-ocean ridges and ridge flanks have a key role
21 in regulating seawater chemistry and global chemical fluxes, and support diverse ecosystems
22 in the absence of light. In this Review, we outline tectonic, magmatic and hydrothermal
23 processes that govern crustal architecture, alteration, and biogeochemical cycles along mid-
24 ocean ridges with different spreading rates. In general, hydrothermal systems vary from
25 those that are magmatic-dominated with low pH fluids >300 °C, to serpentinizing systems
26 with alkaline fluids <120 °C. Typically, slow-spreading ridges (rates <40 mm yr⁻¹) have greater
27 variability in magmatism, lithology, and vent chemistry, which are influenced by detachment
28 faults that expose lower crustal and serpentinized mantle rocks. Hydrothermal alteration is
29 an important sink for Mg, Na, sulphate and bicarbonate, and a net source of volatiles, iron
30 and other nutrients to the deep ocean and vent ecosystems. Magma-hosted hydrothermal
31 systems host a vast, hot and diverse microbial biosphere that represents a deep organic
32 carbon source to ocean carbon budgets. In contrast, high pH serpentinizing hydrothermal
33 systems harbour a more limited microbial community consisting primarily of methane-
34 metabolizing Archaea. Continued advances in monitoring and analytical capabilities coupled
35 with developments in metagenomic technologies will guide future investigations and new
36 discoveries in hydrothermal systems.

37

38 **Website summary:**

39 Oceanic spreading centres are sites of extensive tectonic, magmatic and hydrothermal
40 activity that provide nutrients to the ocean and multifaceted habitats for life. This Review

41 explores processes governing variations in hydrothermal vents, microbial ecosystems, and
42 global fluxes from ocean ridges.

43

44 **Key points**

- 45 1. Spreading rates control variations in heat sources, magma input, and tectonic processes
46 along mid-ocean ridges and influence crustal architecture and hydrothermal processes,
47 providing multifaceted habitats for life.
- 48 2. Approximately one third (7×10^{12} to 11×10^{12} W) of the global oceanic heat flux (32×10^{12} W)
49 occurs through hydrothermal convection at ridges and ridge flanks. Seawater circulation,
50 hydrothermal alteration, and microbial interactions regulate seawater chemistry and
51 change the composition and physical properties of the lithosphere.
- 52 3. Roughly 50% of the global mid-ocean ridges are spreading at rates $< 40 \text{ mm yr}^{-1}$, where
53 major detachment faults expose lower crustal and upper mantle rocks, creating
54 asymmetric ridge segments with large variability in structure, hydrothermal processes
55 and vent fluid chemistry.
- 56 4. Serpentinization decreases bulk density ($< 2.9 \text{ g cm}^{-3}$) and seismic velocities ($V_p < 6 \text{ km s}^{-1}$)
57 of mantle rocks and weakens the oceanic lithosphere along detachment faults.
58 Serpentinization reactions produce highly reduced fluids with high H_2 , CH_4 and other
59 organic molecules that provide energy for microbial life.
- 60 5. Hydrothermal processes govern global chemical fluxes (such as Mg, Fe, Mn, and volatiles)
61 and provide nutrients (for example, Fe flux $\sim 4\text{-}6 \times 10^9 \text{ mole yr}^{-1}$) to the deep ocean.

62 Approximately 0.05 GtCyr^{-1} of organic carbon are estimated to be produced through
63 microbial interactions and oxidation of organic compounds within hydrothermal plumes.
64 6. Magma-hosted systems host a vast, hot and diverse microbial biosphere in contrast to
65 serpentinizing systems that sustain more limited microbial communities primarily
66 dominated by methane-metabolizing Archaea. Advanced technologies allow better
67 characterization of the genetic makeup and metabolism of microbes and the role of
68 viruses in shaping diversity.

69

70 **[H1] Introduction**

71 Mid-ocean ridge (MOR) systems extend approximately 60,000 km around the globe and are the
72 most dynamic and continuous tectonic feature on the planet (FIG. 1). On average, about 3.3 km^2
73 yr^{-1} of new oceanic crust is generated at global spreading centres¹, which account for >70% of
74 the total volcanism and where about 60-70% of the Earth's surface has been produced over the
75 last 160-180 Myr REF.². Mantle melting, volcanism and faulting at MORs drive hydrothermal
76 circulation that allows the transfer of heat, chemical compounds, metals and volatiles [G] from
77 the asthenosphere [G] to the hydrosphere and biosphere. Approximately 75-80% of the Earth's
78 total heat flux occurs as the oceanic crust ages³⁻⁵ and is most pronounced at ridge flanks⁶, where
79 low temperature fluid flow continues off-axis for millions of years and contributes to global
80 biogeochemical cycles^{4,7}. It is estimated that the volume of the ocean circulates through the
81 oceanic ridge system in much less than 1 Myr⁶.

82 Spreading centres are one of the most extreme environments on Earth that can support
83 oases of life at high temperatures and thriving in perpetual darkness. Microorganisms obtain
84 energy from magmatic gases and chemical compounds of altered oceanic crust rather than from

85 light through a process called chemosynthesis [G]⁸⁻¹⁰. In turn, many of these microorganisms
86 symbiotically sustain macrofaunal communities that populate hydrothermal vent environments⁸.
87 The microorganisms with the highest known growth temperature on Earth are found within MOR
88 hydrothermal systems^{11,12}, and investigation of their genetic diversity has changed the current
89 view of the tree of life^{13,14}.

90 Only a small percentage of the global seafloor has been investigated, and as such, the deep
91 ocean remains one of the last frontiers on Earth to be explored and directly sampled. Diffuse,
92 low-temperature (6-17°C) hydrothermal vents were first discovered in 1977 at the Galápagos
93 Spreading Centre in the equatorial Pacific¹⁰. In early 1979, high temperature (> 350°C), low pH
94 [G] fluids discharging from sulphide structures were found on the East Pacific Rise at 21°N, ref.¹⁵,
95 and demonstrated for the first time that seafloor hydrothermal fluids could transport high
96 concentrations of ore-forming elements¹⁶. Diffuse springs associated with these vents were
97 found to support exotic benthic communities of giant tube worms, clams, and crabs similar to
98 those found at the Galápagos Ridge, which survive through symbiotic relationships with bacteria
99 that oxidize reduced sulphur¹⁷. These exciting discoveries inspired subsequent multidisciplinary
100 research into MOR systems that brought to light the complex interplay of magmatism, tectonics,
101 hydrothermal circulation and fluid-rock interaction linked to seawater chemistry and life.

102 Since the first discoveries, more than 500 sites of hydrothermal venting on the seafloor
103 have been identified¹⁸ (FIG. 1). Integrated approaches of targeted drilling, sampling,
104 biogeochemical analyses, seismic experiments, modelling, and real-time observations at ocean
105 observatories (Box 1) are providing fundamental insights about Earth and the evolution of life,
106 and offer unlimited opportunities for new discoveries. In addition to the pivotal discoveries in the
107 late 1970's of exotic ecosystems around hydrothermal vents^{8,19}, advances have been made in

108 monitoring earthquakes and volcanic eruptions in real-time and in understanding the extent of
109 the subsurface biosphere. Advanced analytical and microbiological techniques are helping
110 constrain the role of submarine volcanoes in controlling ocean chemistry and give new insights
111 about novel life forms, their metabolic and genetic diversity, and evolution.

112 This Review provides an overview of tectonic, magmatic and hydrothermal processes that
113 govern variations in crustal architecture, water-rock-microorganism interactions, and
114 hydrothermal fluxes in MOR systems. We summarise key differences among ridges with differing
115 spreading rates that have experienced varying degrees of magmatism and tectonism. This
116 Review is not intended as a comprehensive compilation of all major sites. Instead, we focus on a
117 few well-studied examples from the East Pacific Rise (EPR), Juan de Fuca Ridge (JdF) and Mid-
118 Atlantic Ridge (MAR), highlighting variations in geological and biogeochemical processes that
119 result in a diversity of hydrothermal environments and associated ecosystems.

120

121 **[H1] Variations in MOR spreading**

122 A wide range of geological features form at ocean rifts as lithospheric plates diverge and
123 new crust is created (FIG. 2). The morphology and **oceanic crustal architecture [G]** of MORs, and
124 the hydrothermal systems they host, are governed by differences in magmatic, tectonic and
125 alteration processes, which are directly a function of spreading rates and vary in response to
126 regional tectonic stresses and magma supply. These magmatic and tectonic variations at MORs
127 are discussed in this section alongside how they are monitored.

128

129 **[H2] Fast-spreading ridges**

130 Fast-spreading ridges (80-120 mm yr⁻¹) generally have high magmatic budgets and erupt
131 voluminous basaltic lavas that accommodate extension, forming a smooth central, raised axial
132 ridge with little faulting. The EPR (FIG. 1) is the fastest spreading MOR, currently reaching rates >
133 100 mm yr⁻¹ near 10° N and 150 mm yr⁻¹ near 30° S, Refs.^{20,21}. Regions with a continuous input of
134 magma are thought to result in a relatively uniform, layered crustal structure, with volcanic and
135 plutonic rocks that are similar to lithostratigraphy found in some ophiolites [G] (such as in Cyprus
136 and Oman). Typically, this general layer-cake stratigraphy, referred to as Penrose-type crust²²,
137 consists of a sequence of pillow basalt and lava flows, sheeted-dykes, and gabbros [G] that
138 commonly contain ultramafic cumulates, overlying variably tectonized upper mantle sequences
139 (Fig. 2a).

140 Most conceptual models of fast-spreading ridges are based on geophysical studies of the
141 EPR. These models predict that sub-Moho [G] melts feed sills through small dykes and
142 accumulate in a shallow axial melt lens (AML), 1–2 km beneath the ridge axis (FIG. 2a)^{23,24}. There
143 are contrasting conceptual models for the formation of the gabbroic lower crust at fast-
144 spreading ridges that predict differences in lower crustal structure and which have different
145 implications for thermal and magnetic properties and hydrothermal cooling. Two leading models
146 invoke either: crystallization of multiple stacked magmatic sills (referred to as the sheeted sill
147 model; FIG. 2a); or the presence of one small sill at the base of the sheeted dyke complex from
148 which gabbro cumulates crystallize and subside to form the lower crust (referred to as the
149 gabbro glacier model; see review in REF.²⁵).

150 Sheeted sill models predict an axial heat flux of ~15 MW km⁻¹ and require extensive, fast
151 hydrothermal cooling along a mush zone to remove latent heat of crystallization at the ridge

152 axis²⁵. In contrast, gabbro glacier models predict that most crystallization occurs within the
153 shallow magma sill, with slow cooling and higher axial heat fluxes of $\sim 30 \text{ MW km}^{-1}$ through
154 hydrothermal circulation²⁵. Microstructural, crystallographic, and petrological data from the
155 lower crust at Pito Deep on the EPR^{26,27} support both models and document regional and
156 temporal variations in crystallization, magmatic flow and faulting with depth in the gabbroic
157 sequences but at relatively constant and fast spreading rates²⁶. The magnetic structure preserved
158 at Pito Deep also suggests that crustal temperatures remained around 500°C up to $\sim 8 \text{ km}$ off
159 axis²⁷. The continuous release of latent heat over this broad region would delay the onset of
160 conductive cooling in the lower crust.

161 High temperature hydrothermal vents at the EPR are fuelled by small, shallow magma
162 chambers (FIG. 2a) and are influenced by frequent volcanic eruptions that occur every 10-20
163 years (see overview in Ref.²⁸). Frequent eruptions can bury young vents and biological
164 communities and result in smaller sulphide structures and fewer vents along the ridge axis.
165 Eruptive fissures and margins of the EPR axial graben provide well-established permeable
166 pathways for hot fluids to ascend through the crust²⁸. The EPR 9°50' N area was the first
167 documentation of a seafloor eruption in 1991 and the impact it can have on both vent fluid
168 chemistry and the surrounding water column^{29,30}. For example, time-series analyses of vent
169 fluids sampled within a month of the 1991 eruption documented changes in chloride contents,
170 which were dominated by a vapour phase directly after the eruption but showed an increase in
171 chlorinity to greater than seawater values in 3 years or less³¹. Prediction of a repeat eruption in
172 the same area and observation of the microearthquake character of the eruption was recorded
173 by ocean-bottom seismometers in mid-2005 and documented an intense but brief inferred diking
174 event in early 2006^{32,33}. Seismic monitoring at the 9°50' N area between 2003 and 2004 also

175 provided a regional picture of the distribution of tectonic and hydrothermal stresses that control
176 permeability and promote along-axis flow above the axial magma chamber³⁴.

177

178 **[H2] Intermediate-spreading ridges**

179 Mid-ocean ridges with intermediate-spreading rates (40-80 mm yr⁻¹) exhibit transitional
180 morphologies, crustal structure, and variations in hydrothermal output. Temporal and spatial
181 variations in magmatism along these ridges result in both magma-rich regions around axial highs
182 and magma-poor regions more influenced by faulting. The best-studied examples are the Juan de
183 Fuca and Gorda Ridge system (900 km in length) and the Galapagos Rift (1700 km in length).
184 Seismic imaging of the Juan de Fuca indicates stacked subaxial **magma lenses [G]** at depths of
185 ~1.7–4.5 km, extending ~1-8 km along axis and which underlie the majority of high temperature
186 vent sites²³.

187 Axial Seamount on the JdF is the most magmatically active submarine volcano in the NE
188 Pacific (Supplementary Movie 1), where an extensive cabled network of multidisciplinary
189 instruments has been installed and dedicated for 25 years of operation (Regional Cabled Array;
190 BOX 1). It is the first site where stacked magmatic sills were imaged and where the full evolution
191 of an eruption in real-time was captured³⁵⁻³⁷. Long-term measurements of summit inflation and
192 deflation prior to and following seafloor eruptions at Axial led to the first forecasting model for a
193 submarine eruption^{38,39}.

194 The Endeavour Segment of the JdF is one of the most vigorously active hydrothermal areas
195 on the global MOR system and has been the subject of numerous multidisciplinary research since
196 the early 1980's⁴⁰⁻⁴⁴. Similar to Axial, it is monitored by a cabled array of instruments,
197 implemented by Ocean Networks Canada (BOX 1). Unlike Axial, no historical seafloor eruptions

198 have been detected at Endeavour. However, widespread venting has produced abundant large
199 sulphide chimneys, some of which are the largest sulphide structures ever discovered^{44,45}
200 (Supplementary Movie 2).

201

202 **[H2] Slow- and ultraslow-spreading ridges**

203 Roughly 50-60% of the global MOR system is spreading at rates $<40 \text{ mm yr}^{-1}$ and extends
204 from the Arctic Ocean, along the entire Atlantic Ocean, and into the southwest Indian Ocean^{46,47}.
205 Slow ($20\text{-}40 \text{ mm yr}^{-1}$) and ultraslow ($<20 \text{ mm yr}^{-1}$) spreading ridges have rugged topographies and
206 a large variability in exposed and subsurface rock types, magma supply, and tectonic extension.
207 Plate separation is partly accommodated by faulting, resulting in asymmetric axial valleys and
208 large-offset normal faults, called **oceanic detachment faults [G]**, similar to structures in
209 continental extensional settings (FIG. 2b)⁴⁸. In these environments, the interplay of discontinuous
210 magma supply and tectonic processes results in highly heterogeneous oceanic **lithosphere [G]**
211 and exposure of lower crustal and upper mantle rocks, leading to major variations in geophysical
212 properties, structure and geochemistry along and across ridge axes.

213 **Oceanic detachment faults [G]** are recognized as a distinct mode of oceanic accretion and
214 have a key role in fluid circulation⁴⁹. Serpentinized mantle **peridotite [G]** and lower-crustal
215 plutonic rocks exposed through detachment faults represent on average 25% of the seafloor^{47,50}.
216 Long-lived (>1 million years) detachment systems result in dome-shaped massifs, with spreading-
217 parallel undulations (corrugations) of the seafloor. These corrugated domes, termed oceanic
218 core complexes (OCCs) or megamullions^{51,52}, are common along the Mid-Atlantic and Southwest
219 Indian Ridges (SWIR)⁵³⁻⁵⁵. OCCs form in the footwall of axial detachments during periods of
220 reduced and variable magma supply and are juxtaposed to more volcanic seafloor in the

221 opposite plate (FIG. 2b)^{56,57}. In some ultraslow-spreading locations, such as the easternmost
222 SWIR and regions of the Gakkel Ridge in the Arctic^{56,58,59}, very low melt supply results in more
223 extensive, widespread exposures of mantle rocks⁵⁶. Studies of OCCs have documented complex
224 histories of deformation^{54,60–62} and fluid circulation^{63,64} along the detachment fault zones leading
225 to active hydrothermal systems, such as the high temperature TAG (Trans-Atlantic
226 Geotraverse)^{69,72} and the serpentinite-hosted Lost City hydrothermal fields^{65,66}.

227 The northern MAR is the best studied slow-spreading environment and currently the site
228 of an uncabled seafloor and water-column observatory dedicated to long-term (>20 years)
229 monitoring of volcanic, tectonic, hydrothermal and biological activity at the basalt-hosted Lucky
230 Strike hydrothermal field⁶⁷ (BOX 1). Measurements at Lucky Strike have revealed an estimated
231 minimum total heat flux of 200 MW, REFS.^{68,69}, similar to heat flux estimated at the Costa Rica
232 Rift⁷⁰. Numerical modelling predicts along-axis hydrothermal flow at Lucky Strike⁷¹, which is
233 consistent with more recent seismic studies at 9°50'N on the EPR³⁴.

234 Multidisciplinary investigations of MORs continue to provide a better understanding of
235 variations in seafloor spreading processes as a function of spreading rate and highlight the
236 complex relationship between magmatic and tectonic processes that influence the formation of
237 volcanic and plutonic crust and exposure of mantle rocks on the seafloor. Differences in
238 magmatic activity and crustal architecture also control seawater circulation, hydrothermal
239 alteration and vent fluid chemistry, which impact hydrothermal fluxes and microbial interactions,
240 and are discussed in the following sections.

241

242 **[H1] MOR hydrothermal systems**

243 Contrary to early assumptions, hydrothermal circulation in the oceanic crust and the
244 distribution and composition of MOR vents are highly variable, and depend on the interplay of
245 tectonic, magmatic, geochemical and biological processes.

246 ***[H2] Hydrothermal circulation at MORs***

247 Penetration of seawater is limited in all settings to the depth of the brittle lithosphere,
248 which is a function of **spreading rate [G]** and thermal structure. Permeability in this brittle
249 domain likely decreases with depth, and hydrothermal circulation is expected to be restricted to
250 < 6 km, with the possible exception of the damage zone of axial detachment faults⁷². At fast-
251 spreading ridges, axial magma chambers at depths of 1-2 km drive shallow hydrothermal
252 circulation^{24,73,74}. Models of the thermal structure of MORs that fit multichannel seismic data and
253 axial earthquake centroid depths⁷⁵ suggest that a steady-state magma lens can only exist at
254 depths < 6 km at spreading rates greater than ~40-60 mm yr⁻¹. As spreading rates decrease,
255 persistent magma bodies are deeper and the permeability of the upper lithosphere becomes
256 more complex, with fluids channelled along normal faults that can reach 5-8 km into the oceanic
257 lithosphere⁷⁶. Therefore, at slower spreading ridges, only transient melt bodies can exist at
258 depth^{77,78} and hydrothermal circulation mainly occurs along faults. In the following section, the
259 main types of hydrothermal systems are discussed, but we emphasize that a strict categorization
260 of vent types is not always applicable.

261

262 ***[H2] Types of hydrothermal systems***

263 The type of rocks in the subsurface of hydrothermal systems together with variability in
264 heat sources and faulting have a profound influence on fluid circulation pathways, vent

265 distribution and fluid chemistry. At least three general classes of vent systems have been
266 distinguished⁷⁹ (FIG. 2): high-temperature (>300°C) hydrothermal systems driven by cooling
267 magmas and/or proximal gabbroic crust; high-temperature hydrothermal vents (>300°C) in
268 detachment settings where variable mixtures of gabbro and peridotite influence heat and mass
269 fluxes; and low- to moderate-temperature (<~120°C) hydrothermal activity driven by cooling of
270 mantle-dominated lithosphere resulting in **serpentinization [G]**, alkaline fluids and precipitation
271 of carbonate chimneys (BOX 2), exemplified by Lost City^{65,80} on the MAR and Old City on the
272 SWIR⁸¹ (FIG. 2f).

273 However, not all MOR hydrothermal systems fit directly into these general categories. For
274 example, the ultra-slow Mid-Cayman spreading centre in the Caribbean Sea is the deepest site
275 yet discovered that has multiple hydrothermal vents and likely different sources, all in close
276 proximity at varying water depths⁸². At Mid-Cayman, the vent fluid chemistry and temperatures
277 are intermediate between high and low temperature systems⁸²⁻⁸⁴ (Supplementary Data). The
278 most prominent feature is Mount Dent, a topographic high on the western flank of the axial
279 valley, which hosts multiple vent fields with abundant fauna, including the Von Damm and
280 Piccard vent fields at 2,300 m and 4,960 m, respectively⁸². Mount Dent is interpreted as an OCC
281 and the fluid geochemistry reflects the influence of both gabbroic and ultramafic rocks along the
282 flow and alteration pathways⁸⁵. In contrast to other high-temperature systems, hydrothermal
283 activity at the Von Damm vent field could be supported by deep fissuring on the OCC, allowing
284 heat to be mined from a deep crustal source rather than from cooling of magma at depth⁸².

285 The diversity of hydrothermal systems at MORs reflects variations in heat sources and
286 differences in subsurface rock types. In general, magmatism fuels high temperature
287 hydrothermal systems with variable chemistry that are found in all spreading environments,

288 whereas deep faulting promotes lithospheric cooling and drives medium to low temperature
289 systems with fluid compositions indicative of interaction with lower crustal and upper mantle
290 rocks exposed on, or close to, the seafloor.

291

292 **[H1] Vent distribution and chemistry**

293 Sampling and measurements over multiple months and years provide important
294 constraints on regional and temporal variations in seismic activity, hydrothermal circulation,
295 permeability, fluid-rock and microbiological interactions, and how these are affected by tectonic
296 and magmatic events^{31,40,86}. The key controls on the distribution of hydrothermal systems and
297 their vent chemistry are discussed in the following sections (FIG. 3).

298

299 ***[H2] Alteration along convection pathways***

300 As seawater-derived fluids penetrate the crust and are heated at depth, convection cells
301 are established, resulting in zones of hydrothermal upflow and fluid discharge onto the seafloor
302 that drive cold seawater downflow and recharge of the system (FIG. 3b). Water-rock reactions
303 along the convection pathway result in chemical exchange that alters the composition of the
304 host rocks and transforms seawater into hydrothermal fluids.

305 ***[H3] Basalt-hosted and high temperature systems***

306 The highest temperature and deepest portion of the hydrothermal circulation cell is known
307 as the reaction or root zone⁸⁷, although reactions occur over the entire circulation pathway and
308 continue on the ridge flanks. Hydrothermal alteration of the oceanic lithosphere at varying
309 temperatures is an important sink for seawater-derived Mg, sulphate and alkali elements (FIG.
310 3b), but a source for many others, such as Ca, Cu, Fe, Mn, Zn, Pb, Li, Rb, REE and Cs^{31,87}. Volatiles,

311 such as H₂, CO₂, H₂S and CH₄, can be released through magmatic degassing or form through fluid-
312 rock reactions and can be utilized or produced by microbial ecosystems at and beneath the
313 seafloor^{9,42}. At the deepest level of penetration in magmatic systems, water-rock reactions
314 produce greenschist-facies minerals in the reaction zone and acidic hydrothermal fluids, which
315 are enriched in metals and volatiles and are extremely hot: 350° to >400°C (Supplementary
316 Data). High temperature fluids are buoyant and rapidly rise to the seafloor through pipe-like
317 conduits. Mixing of superheated fluids with cold seawater at and near the seafloor causes
318 dissolved metals to precipitate and the formation of variably-sized edifices and sulphide deposits
319 forming black and less commonly white smoker chimneys that have become hallmarks for hot
320 marine hydrothermal systems^{28,88} (FIG. 3b).

321 ***[H3] Diffuse fluid flow at hydrothermal vents***

322 There are two types of low temperature or so-called diffuse vents that are integral
323 components of magma-hosted hydrothermal environments. One type of diffuse venting occurs in
324 basalts that are too fractured for the flow path to become sealed (as in high temperature vents),
325 and the rising hot fluid mixes with seawater to produce dispersed fluids with temperatures of 5 -
326 ~50°C (FIG. 3b, orange arrows). Geochemical data indicate that such diffuse fluids show a loss of
327 H₂S and H₂, and gain of CH₄ that are not simply dilutions of high temperature vent fluids but
328 point to subsurface microbial interactions^{89,90}. The microbial populations associated with such
329 diffuse sites can be spatially distinct but temporally stable^{91,92} and likely sustain a subsurface
330 biosphere⁹³⁻⁹⁵. The other type of low temperature fluid emission is diffuse flow directly within
331 sulphide structures where high temperature fluid mixes with seawater as it moves through the
332 porous walls of the mounds. Both types of diffuse flow support complex microbial and
333 macrofaunal communities that are different from those at vent sites with focussed flow^{10,96}.

334 Diffuse fluid flow is also important in slow-spreading environments and influences the alteration
335 of mantle rocks and serpentinization processes. Peridotite-hosted systems have highly complex
336 and variable vent chemistry, which we discuss in more detail in later sections.

337

338 **[H2] Phase separation**

339 In addition to water-rock reactions, two important processes – boiling and condensation of
340 brines – impact vent fluid compositions in all high temperature environments^{97–100} (FIG. 3c).
341 Because seawater contains 3.2 wt% (weight percent) NaCl, it behaves differently than pure water
342 as it is heated⁹⁷. As seawater migrates to depth, at temperatures above 407°C and pressures
343 above 298 bars (2980 m at hydrostatic pressure), the fluids separate into droplets of brine and a
344 lower salinity vapour phase. This process is called supercritical phase separation or brine
345 condensation. These processes partly govern gas concentrations (for example, CO₂, H₂S, and H₂)
346 and are important in partitioning chloride and metals. The development of low-salinity vapours
347 (< 3.2 wt% NaCl) and brines (up to 10 wt% NaCl) by phase separation is inferred to be an active
348 process throughout the oceanic crust and is documented in diverse magmatic rocks (FIG. 3c;
349 Supplementary Data). As hydrothermal systems wane and cool, the brines can be entrained into
350 upwelling fluids (for example, Endeavour fluids reach twice normal seawater salinities) or are
351 released during eruptive events^{101,102}. Brines in the subsurface support distinct, high-
352 temperature, anaerobic [G] microorganisms (halophiles) that tolerate very high NaCl
353 concentrations and metal-rich fluids¹⁰³.

354 Extreme phase separation was documented at the Turtle Pits and Comfortless Cove
355 hydrothermal fields at 5°S MAR, where 407°C black smoker chimneys were emitting gas bubbles
356 and chloride-depleted fluids (224 mM Cl) with respect to seawater values (545 mM Cl)^{104,105}. At

357 3000 m depth, venting was occurring at pressure-temperature conditions near the **critical point**
358 **of seawater [G]** salinity fluids. A short burst of fluid (20 seconds) in the Comfortless Cove field
359 was measured at 464°C, clearly above the critical point and far higher than previously measured
360 fluid temperatures (FIG. 3c)¹⁰⁵. The low-salinity fluids were enriched in Fe, Cu, Co and Mo¹⁰⁶,
361 reflecting the extremely high temperature of the fluids and importance of phase separation and
362 chloride-complexing in metal transport.

363 High-temperature fluids and their vapour-dominated nature are influenced by volcanic
364 activity^{40,107,108}. For example, following a diking event at the Main Endeavour Field in 1999, the
365 380°C edifice named Puffer at 2200 m was venting fluids with one of the lowest chlorinities ever
366 measured (19 mM Cl). In 1998, a temperature of 405°C was measured at the Brandon Vent on
367 the southern EPR with fluids that varied from below to above seawater salinities¹⁰⁹. At pressures
368 and depths greater than the critical point of seawater, all vent fluid temperatures fall far off the
369 two-phase curve, many of which occur along the MAR (FIG. 3c; Supplementary Data). Vent
370 temperatures and fluid chemistry suggest that substantial cooling occurs during ascent of the
371 fluids. On the Mid-Cayman Rise, 401°C fluids from the Piccard site are thought to have phase-
372 separated at temperatures in excess of 500°C and deeper within the crust⁸⁴.

373

374 ***[H2] Impact of magmatic events***

375 The large volume of melts at MORs is an important reservoir for volatiles and plays a key
376 role in transferring gases such as CO₂ and He from the mantle to the hydrosphere. Perhaps more
377 than any other factor, volatiles provide a common thread that link geodynamic, geologic, and
378 geobiological processes in submarine environments. Pronounced changes in seismic activity,
379 permeability, heat flux, temperature and vent fluid chemistry result from intermittent diking and

380 volcanic eruptive or tectonic events at MORs^{40,86,108,110}. Large increases in CO₂ could precede
381 volcanic events, as documented at the Main Endeavour Field following an earthquake swarm in
382 1999^{40,111,112}. Lava interacting with hydrothermal circulation cells produces extreme changes in
383 water-rock reactions and the nature and degree of phase separation. These events also provide
384 nutrients and energy to microbial populations¹¹³, alter macrofaunal communities, and produce
385 large deep-sea **hydrothermal plumes [G]** in the water column¹¹⁴.

386 An important feature of submarine dike-eruptive events is the formation of so-called
387 megaplumes, characterized by the sudden voluminous release of volatiles into the water column,
388 anomalous heat and He relationships, and elevated Mn and Fe that can persist 2-5 years (see
389 review in ref.⁴²). The buoyant megaplumes can rise 1000 metres or more above the surrounding
390 seafloor and can be 20 km across and 70 km in length^{114,115}. Estimates of the relative heat flux
391 indicate a sixfold increase during eruptions³⁶. Magmatic volatiles released during emplacement
392 of melt into water-saturated porous oceanic crust provide nutrients for massive microbial
393 blooms that accompany eruptions¹¹⁶⁻¹¹⁹. Expulsion of **microbial floc [G]** and formation of
394 **snowblowers [G]** was first documented at EPR 9°50' N²⁹ and has been observed at Axial
395 Seamount and on the CoAxial segment of the JdF³⁵. This snowblower phenomenon likely occurs
396 during and after most dike and/or eruptive events and is the result of explosive growth of
397 sulphide-oxidizing bacteria during mixing of large volumes of hydrothermal fluid with oxygenated
398 seawater below the seafloor. These observations and studies of microbes thriving within low- to
399 moderate-temperature diffuse flow fluids have been key in forming the hypothesis that there is a
400 vast, but largely unexplored, diverse microbial biosphere in the crust in close proximity to
401 volcanoes and active submarine hydrothermal systems^{94,121,122}.

402

403 **[H2] Sediment influence**

404 Where ridges are near continental margins, spreading centres can be covered by sediment
405 and are thus classified as sedimented ridges. The presence of a low permeability, insulating
406 blanket of sediment over more permeable volcanic basement directly influences heat and fluid
407 fluxes and the chemistry of the hydrothermal systems that are commonly rich in
408 hydrocarbons^{123–125}. The best-studied sedimented MORs are Middle Valley on the JdF^{126,127}, the
409 Escanaba Trough on the Gorda Ridge^{127–129}, and the Guaymas and Pescarado Basins in the Gulf of
410 California^{124,130,131}. The chemistry of hydrothermal fluids rising through the sediment cover is
411 metal-poor and enriched in CH₄, NH₄, and higher hydrocarbons as a consequence of thermogenic
412 decomposition of organic matter¹³² (Table 1; Supplementary Data).

413 High CH₄ and NH₄ and low values for $\delta^{13}\text{C}_{\text{CH}_4}$ ¹³³, as well as elevated B, $\delta^{11}\text{B}$, Br, I, Li, Rb, Cs,
414 distinguish Endeavour from many other black smoker systems and led to the concept of a bare-
415 rock, sediment-influenced hydrothermal system^{133,134}. The sedimentary component at Endeavour
416 has been hypothesized to be Pleistocene turbidite flows from the Vancouver Island continental
417 margin that are buried at depth¹³³. Such turbidite flows buried the Middle Valley hydrothermal
418 site under thick sediments and currently lap to within 200 m of the axial valley at the northern
419 end of the Endeavour segment. Stable and radiocarbon isotope studies¹³⁵ showed that sediments
420 also supply a portion of CO₂ to the vent fluids. Another known sediment-influenced vent system
421 is Loki's Castle on the ultraslow-spreading Arctic Ridge, which is also enriched in barium^{136,137}.

422 In summary, oceanic spreading centres are sites of variable but extensive hydrothermal
423 circulation that impacts exchange between seawater and the lithosphere and provides nutrients
424 for microbial activity on and below the seafloor. In addition to subsurface lithologies and water-
425 rock-microbe interactions, phase separation and magmatic events are important factors that

426 influence vent fluid compositions. Crustal architecture, magma supply and hydrothermal activity
427 are particularly diverse at the slow-spreading MAR, as discussed in the following sections.

428

429 **[H1] The impact of serpentinization**

430 A number of hydrothermal systems along the slow-spreading MAR are hosted in ultramafic
431 and gabbroic rocks. These include the Rainbow (36°N), Logatchev (14°45'N) and Ashadze vent
432 fields (12°58'N)^{138,139} and the off-axis Lost City hydrothermal field (30°07'N)^{65,80}. These systems
433 vary in venting temperature, fluid composition, and type of hydrothermal deposit, but all
434 characteristically have high CH₄ and H₂, attributed to seawater interaction with gabbroic and
435 ultramafic rocks along the circulation pathways^{65,140}. High H₂ concentrations especially mark the
436 influence of serpentinization processes on fluid chemistry^{141–144} (BOX 2, Supplementary Data).
437 Such systems with highly reducing H₂-rich fluids have gained particular interest because of the
438 potential for **abiotic [G]** reduction of dissolved inorganic carbon (DIC) to form organic
439 compounds and their potential role in prebiotic chemistry and the origin of life on Earth and
440 perhaps other planets^{145–147}.

441 **[H2] High temperature peridotite-hosted systems**

442 Key differences between high and low temperature peridotite-hosted systems are
443 observed in pH, temperature and CO₂ contents, which in addition to differences in trace element
444 concentrations and mantle $\delta^{13}\text{C}$ values of CO₂^{138,148}, point to magmatism as an important source
445 of heat and CO₂ at slow-spreading ridges (Table 1). The Rainbow, Logatchev, and Ashadze fields
446 are black smoker systems, in which sulphides are deposited from low-pH (pH ~3.3), high-
447 temperature (350 – 365 °C), metal-rich fluids with high concentrations of CO₂, CH₄, H₂, and higher
448 hydrocarbons^{138,140,149} (see figure in BOX 2). Rainbow vent fluids have high chlorinity (above

449 seawater concentrations) indicative of supercritical phase separation (FIG. 3c) and contain the
450 highest dissolved Fe of any MOR vent fluid yet studied¹⁵⁰ (Supplementary Data). Elevated CH₄
451 and H₂ in MAR high temperature vents likely reflect a gabbroic and ultramafic influence in the
452 subsurface^{140,151,152}. Heat output from Rainbow has been estimated at 1–5 GW¹⁵³, which is the
453 largest heat flux yet discovered. High heat and fluid output, the formation of sulphide deposits,
454 low pH, and high CO₂ and Fe concentrations in the fluids all suggest that hydrothermal circulation
455 in high-temperature peridotite-hosted systems is likely driven by crystallizing magma within the
456 lithospheric mantle. A magmatic heat source is consistent with seismically imaged magmatic sills
457 beneath the Rainbow hydrothermal field¹⁵⁴.

458

459 **[H2] Lost City**

460 The Lost City hydrothermal field on the Atlantis Massif (MAR 30°N) is the first discovered
461 end-member for serpentinite-hosted, hydrothermally active systems devoid of magmatic
462 activity^{65,80} and is likely an analogue for the Old City vent field on the SWIR⁸¹. Lost City is the
463 furthest off-axis submarine venting environment and is dominated by variably altered peridotite
464 with gabbroic lenses in the subsurface^{66,155}. The fluids are 40° – 116 °C and alkaline (pH 10 – 11),
465 with very low CO₂ and metal concentrations, and high CH₄, H₂, formate, and higher
466 hydrocarbons^{65,156–158} (BOX 2; Supplementary Data). Hydrothermal circulation is thought to be
467 driven by residual crustal heat and lithospheric cooling, with fluid compositions primarily
468 controlled by serpentinization reactions^{65,159}, and fluid discharge controlled by normal faults⁶⁶.
469 Mixing of the alkaline fluids with ambient seawater produces up to 60 m high, carbonate-brucite
470 towers within the field (FIG. 2f; Supplementary Movies) and carbonate deposits along pre-
471 existing, subparallel deformation structures in the detachment fault zone^{65,66,159,160}.

472 Because the hydrothermal carbonate structures are bright white (Figure 2f), the Lost City
473 vents have erroneously been referred to as white smokers. However, white smoker vents are
474 part of evolved, high temperature, basalt-hosted sulphide systems, located distal to the main
475 upflow zone (FIG. 3b) and emit lighter-hued minerals, rich in barium, calcium, sulphate or silicon,
476 leading to the precipitation of anhydrite at temperatures higher than 150°C and barite towards
477 lower temperature⁸⁸. In contrast, the Lost City fluids are clear, commonly diffuse, and essentially
478 devoid of mineral or metal particles (Table 1).

479

480 ***[H2] H₂ export and DIC uptake***

481 Serpentinization has consequences for H₂ fluxes in hydrothermal systems^{47,158,160} (BOX 2).
482 Water column studies and in-situ monitoring while drilling across the Atlantis Massif indicate
483 widespread release of H₂ (up to 44nM) into the water column and elevated H₂/CH₄ ratios which
484 are distinct from channelled flow at Lost City^{155,160,161}. In addition, radiocarbon data and distinctly
485 low concentrations of CO₂ in the fluids have been used to argue that modern seawater DIC must
486 be lost within the circulation paths, likely deposited as carbonate in the basement rocks^{156,162,163}.
487 A similar uptake of seawater bicarbonate was documented at Endeavour¹³⁵ and at 9°50'N,
488 suggesting that hydrothermal systems in general could be an important sink of DIC from
489 seawater, stored as carbonate in the rocks¹⁵⁶. Natural carbon uptake in thermodynamically
490 stable carbonate minerals has now been recognized as a potential mechanism of permanently
491 removing CO₂ from the atmosphere¹⁶⁴ and could help stabilize atmospheric greenhouse gas
492 concentrations.

493 Timescales on which such hydrothermal fluids circulate through the oceanic lithosphere
494 remain poorly constrained for most MOR environments, which has limited the understanding of

495 geochemical processes that depend on time. The short-lived radionuclide ^{223}Ra (half-life = 11
496 days) is abundant in Lost City fluids and has been used to constrain subsurface fluid residence
497 times to less than 0.5–2 years¹⁶⁵. These timescales are surprisingly similar to estimates from
498 seafloor vents in volcanic-hosted systems^{166,167} and are likely short enough to allow complex
499 organic molecules to be exported into the overlying water column before they are destroyed.
500 Short residence times also have important implications for understanding hydrothermal carbon
501 transformation reactions that could have led to the formation of the first biomolecules and
502 possibly early life on Earth¹⁶⁸.

503

504 **[H2] CH_4 formation**

505 Processes leading to reduced carbon species in marine hydrothermal systems and the role
506 of serpentinization in CH_4 formation have become controversial^{84,169,170}. Methane in peridotite-
507 hosted systems (BOX 2) has long been attributed to abiotic Fischer-Tropsch or Sabatier reactions
508 in ultramafic rocks^{156,171}, where hydration of olivine during serpentinization produces highly
509 reducing conditions and H_2 , leading to abiotic reduction of CO_2 to CH_4 . Based on studies of fluid
510 inclusions in SWIR gabbros^{172,173}, field and clumped isotope studies in the past decade suggest
511 that gabbroic intrusions are also a potential source of CH_4 in hydrothermal systems^{84,174,175}. Such
512 studies postulate that CH_4 possibly forms in olivine-rich rocks early in the system when
513 temperatures are hotter, is stored as fluid inclusions^{84,169}, and then is stripped from the rocks
514 into modern fluids during hydrothermal circulation. The origin and the importance of CH_4 for
515 microbial life on Earth and other planets are an active area of research and the processes of CH_4
516 production in marine ultramafic settings remain disputed^{169,170}.

517 Continued investigations of hydrothermal systems along the MAR and SWIR emphasise the
518 importance of discontinuous magmatism and faulting that result in asymmetric ridge segments,
519 exposure of gabbroic and ultramafic rocks, and marked differences in hydrothermal vent systems
520 at slow-spreading ridges. In contrast to high temperature systems, Lost City-type systems are
521 devoid of magmatic activity and driven by serpentinization processes.

522

523 **[H1] Microbial diversity at hydrothermal vents**

524 In this section, the marked differences in microbial communities between volcanic-hosted
525 and peridotite-hosted hydrothermal systems^{93,122,176} are discussed. Magma-driven systems
526 support a high diversity of Bacteria and Archaea due to pronounced physical, thermal and
527 chemical gradients that support a wide range of habitats (Fig. 4). In contrast, low-temperature,
528 serpentine-influenced systems devoid of magmatic activity, such as Lost City, support a low
529 diversity of microorganisms (and macrofauna) and are dominated by CH₄-metabolizing
530 archaea^{177–179}.

531

532 **[H2] Diversity at magma-driven vents**

533 Temperature and degree of seawater mixing between seawater and hydrothermal fluids
534 are important determinants of high microbial diversity at magma-driven vents, as these factors
535 affect the availability of electron acceptors and donors, and thus the energy-yielding microbial
536 metabolisms⁹⁶ (FIG. 4). Different groups of vent-associated Bacteria and Archaea have been
537 shown to grow over the temperature range of 2°C, in surrounding seawater and hydrothermal
538 vent plumes⁹⁶, to at least 122°C in hot subsurface fluids^{11,12,93}.

539 **[H3] Energy sources and redox reactions**

540 In general, above 40°–60°C, oxygen is limiting such that the majority of microorganisms are
541 anaerobic, using elemental sulphur, sulphate, nitrate and CO₂ as electron acceptors (FIG. 4a). CO₂
542 is the predominant source of carbon for all thermal groups of vent Bacteria and Archaea,
543 although **heterotrophs [G]** have also been detected, even among some of the thermophilic
544 archaea. In addition to sulphur, high levels of H₂ serve as the energy source for phylogenetically
545 and physiologically diverse groups of Bacteria and Archaea. H₂-utilizing microorganisms have
546 been identified in subsurface, black smoker and vent plume environments, and as animal
547 symbionts¹⁸⁰. H₂-utilizing proteobacteria dominate the cooler environments, whereas archaeal
548 methanogens dominate the most extreme of the high temperature environments. The latter are
549 limited in the availability of reduced or oxidized nitrogen sources, but **hyperthermophilic [G]**
550 methanogens have been isolated that fix N₂¹⁸¹. Abiotic reactions that can reduce N₂ have also
551 been identified under both volcanic-hosted and peridotite-hosted hydrothermal conditions^{182,183}.
552 Whether these reactions provide a source of reduced N for vent microorganisms is unknown.

553 Porous vent environments influenced by mixing with seawater – varying from subsurface
554 habitats to black smoker chimney structures, and hydrothermal vent plumes advecting through
555 the water column – support a markedly high diversity of Bacteria, including aerobes that utilize
556 seawater-derived electron acceptors such as oxygen, sulphur, CO₂, nitrate, nitrite and nitrous
557 oxide, and various metals including iron^{42,96,184,185} (FIG. 4). Many members of vent bacteria derive
558 energy from redox reactions involving electron acceptors such as nitrate and iron coupled to the
559 oxidation of reduced sulfur compounds and H₂^{184,186,187}. The dominant Archaea isolated from
560 magma-driven vent environments include species from both the Euryarchaeota and the
561 Crenarchaeota. Methanogens are dominant among Euryarchaeota, although Euryarchaeota also
562 include many of the commonly isolated heterotrophic hyperthermophilic (75 to >100°C) Archaea,

563 some of which were among the first hyperthermophilic species isolated from hydrothermal vent
564 environments in the 1980s.

565 ***[H3] Hydrothermal plumes and diffuse fluids***

566 High temperature hydrothermal vents produce buoyant plumes that harbour a wide range
567 of chemosynthetic microorganisms capable of oxidizing S, H₂, CH₄, Fe and Mn as energy sources
568 and using CO₂ as the carbon source (FIG. 4b). The source of plume microorganisms is the deep
569 ocean where they are ubiquitous. Active plume microbial communities comprise a substantial
570 fraction of the deep ocean carbon pool, estimated to be comparable to the particulate organic
571 carbon flux exported from pelagic sources¹⁸⁸.

572 Low temperature diffuse fluids at different vents within the same hydrothermal field
573 indicate that individual diffuse flow sites can maintain unique microbial populations over time
574 and have spatially distinct taxonomic, metabolic potential, and genetic characteristics^{91,92,94}. The
575 ability of an individual site to maintain an active seafloor population is intrinsically linked to
576 the geochemistry of the system, mixing conditions, and the geological characteristics of the
577 individual vent site^{92,176}.

578 Microbial ecology has been revolutionized by new bioinformatics methods that use
579 genome sequences to identify uncultivated microorganisms and viruses, which provide insight
580 into their physiology and evolutionary history and help advance culturing techniques.
581 Bioinformatic approaches have resulted in discoveries that not only have identified very high
582 diversity of microorganisms in hydrothermal vent and seafloor environments and the role of
583 viruses in shaping that diversity, but also have profoundly changed the understanding of the
584 evolutionary history of the microbial world¹⁸⁹. A key discovery was the identification of the
585 Lokiarchaeota in deep-sea sediments in the Arctic that had episodic hydrothermal input, likely

586 from the nearby basalt-hosted hydrothermal vents at Loki's Castle¹⁹⁰. Lokiarchaeota share many
587 characteristics previously thought to be found only in Eukaryotes, thus promising a better
588 understanding of the evolution of eukaryotes^{14,190,191} and supporting evidence for placing the
589 Eukaryotes as emerging from the archaeal branch of the tree of life^{192,193}.

590

591 **[H3] Growth rates of hydrothermal vent microorganisms**

592 Most information on growth rates of vent microorganisms comes from laboratory studies
593 of pure cultures and can vary with doubling times from minutes to hours. One of the major gaps
594 in understanding the microbial ecology of vent environments is determining *in situ* growth rates
595 and productivity of microbial communities. Determining *in situ* growth rates and productivity is a
596 difficult task, particularly in diffuse fluids, because of mixing of different physiological groups of
597 microorganisms from different depths that have marked gradients in temperature, electron
598 acceptors and energy sources. An attempt to circumvent these obstacles involved the incubation
599 of vent water samples from the EPR 9°50'N at *in situ* temperature and pressure with and without
600 supplements of electron acceptors¹⁹⁴. Microbial growth and carbon fixation rates were measured
601 using subsurface water incubated at *in situ* temperature of 24°C and 50°C with and without O₂,
602 NO₃⁻ and H₂. The results showed a production rate as high as those found in animal symbiosis
603 and with doubling times of 17-41 hours. The authors identified three genera of the
604 Campylobacteria group that included S and H₂ oxidizers as the dominant microbes.
605 Campylobacteria are common in vent environments and represent 85% of the biomass in sulfide
606 chimneys. Campylobacteria have also been identified as the dominant group in diffuse flow vents
607 and in the shallow seafloor⁹⁶. While this study was limited to just one group of the diverse

608 population in vent fluids, it emphasizes that something must limit the accumulation of microbial
609 biomass given the rapid growth rates.

610 One possible limit to growth could be the widespread diversity of viruses including both
611 free-living and lysogenic (associated with the host genome) that are present in specific vent
612 environments¹⁹⁵. The rate of virus lysis of vent microbes or the rate and specific genes
613 transferred by virus to bacteria is unknown. Moreover, there is evidence of protist grazing of
614 vent bacteria that appears to be particularly substantial in diffuse flow vent environments and
615 based on bacterial productivity rates¹⁹⁴, protists grazing could account for up to 22% of
616 chemosynthetic populations¹⁹⁶.

617

618 ***[H2] Diversity at serpentinite-hosted vents***

619 The microbial ecology of marine serpentinite-dominated vent environments is known
620 largely from Lost City. Less information is available from the more recently discovered site Old
621 City vent field at the SWIR⁸¹ or from Logatchev and Rainbow. Early microbiology studies at Lost
622 City showed a very low diversity of microorganisms, with CH₄-metabolizing archaea dominating
623 at active, moderate temperature, anaerobic carbonate chimneys, and sulphur-metabolizing
624 Proteobacteria occupying the lower temperature, oxic or anoxic chimney environments^{65,179,197}
625 (FIG. 4c). The CH₄-metabolizing archaea, which are related to the Methanosarcinales, exist as
626 complex biofilms within young, active carbonate chimneys. As the chimneys age and
627 hydrothermal input decreases, the dominance by Methanosarcinales shifts to complete
628 dominance by anaerobic CH₄-oxidizing archaea (ANME 1)¹⁹⁸. Rare microbial taxa in the youngest
629 samples are progressively more dominant in older samples, suggesting that the Lost City

630 microbial community and perhaps other similar serpentinization environments are preadapted
631 to reoccurring environmental changes as an example of long-term ocean memory¹⁹⁹.

632 Molecular (DNA-based) characterization of the Lost City Methanosarcinales biofilm has
633 shown their potential to fix N₂, and based on an extraordinary abundance of transposable
634 elements, a potential for a very high incidence of gene transfer^{200,201}. In laboratory experiments,
635 this biofilm has both produced and anaerobically oxidized CH₄, enhanced by H₂²⁰¹. Low
636 concentrations of CO₂ in Lost City fluids indicates that these Methanosarcinales might utilize
637 alternate sources of carbon for CH₄ production, such as formate or acetate¹⁵⁷ (FIG. 4c). The
638 observation that sulphate-reducing bacteria convert formate to CO₂¹⁷⁷ has led to the hypothesis
639 that this CO₂ is then converted to CH₄¹⁷⁸. The Lost City Methanosarcinales biofilm show multiple
640 morphologies, including cells with stacked, intracellular membranes similar to morphologies of
641 aerobic [G] methane-oxidizing bacteria, and might thus have some cells that oxidize methane
642 anaerobically²⁰¹. Many questions remain about the Lost City microbial community, particularly
643 regarding Methanosarcinales, including their in-situ growth and activity rates, their diversity in
644 physiologies and potential syntrophic interactions.

645 Summarizing, magma-hosted hydrothermal systems host a vast, hot and diverse microbial
646 biosphere that sustain thriving macrofaunal communities at vents and contributes a substantial
647 fraction of the deep ocean carbon pool. In contrast, high pH serpentinizing hydrothermal systems
648 harbour distinctly more limited microbial communities dominated by methane- metabolizing
649 archaea.

650

651 **[H1] Global fluxes and biogeochemical cycles**

652 Hydrothermal circulation at MORs and ridge flanks controls global heat fluxes and plays an
653 important role in regulating seawater chemistry, biogeochemical cycles, and input fluxes into
654 subduction zones^{87,202}. Although rates and directions of chemical exchange vary, hydrothermal
655 processes are an important sink for seawater Mg, sulphate, and P and a source of volatiles and
656 many elements, such as Fe and Mn and other metals²⁰³, that serve as energy sources for
657 microbial ecosystems at and beneath the seafloor.

658 **[H2] Heat Flux**

659 Most estimates of hydrothermal chemical fluxes combine convective heat output with
660 compositional differences between hydrothermal fluids and seawater. A problem with this
661 approach is to properly apportion heat flow between on-axis and ridge-flank regions. Current
662 estimates put this distribution at 1.8 ± 0.3 TW and 8.1 ± 2 TW⁷, respectively. Other estimates of
663 heat flux use magma input, which lead to an average value of 50 MW km^{-1} (~ 3 TW) for the entire
664 ridge system²⁰⁴ or combine hydrothermal fluid concentrations with the compositions of the rocks
665 in the subsurface²⁰⁵, both of which tend to be lower than those using heat flux. However, vent
666 fluid compositions can change dramatically with time, particularly following magmatic and
667 seismic events^{108,110}, and we do not yet have an adequate understanding of the role played by
668 these events relative to the steady-state flux.

669 **[H2] Magnesium and calcium**

670 The long standing Mg problem, which recognized that the riverine input of Mg was much
671 larger than the known sinks²⁰⁶, was notably improved by the discovery of Mg uptake in
672 hydrothermal systems²⁰⁷. It is estimated that high temperature vent systems take up $\sim 37\%$ of
673 the riverine Mg input and that low temperature alteration on ridge flanks accounts for another

674 ~14%⁶. Modern dolomite formation might account for a major fraction of the remaining Mg sink,
675 as indicated by Mg isotopes²⁰⁸. Although hydrothermal processes are both a sink and source of
676 Ca, the net flux of Ca is to the oceans²⁰³ and is ~20% of riverine input⁶. An extensive list of
677 elements and compounds is found in REF²⁰³.

678 **[H2] Organic carbon**

679 Hydrothermal systems contribute to global carbon budgets by providing a notable fraction
680 of organic carbon to the deep ocean through microbial activity and oxidation of organic
681 compounds¹⁸⁸. Heterotrophic microbial production rates are estimated to be up to $0.9 \text{ gCm}^{-2}\text{yr}^{-1}$
682 and could contribute 0.05 GtCyr^{-1} of the particulate organic carbon (POC) within hydrothermal
683 plumes, similar to POC export fluxes of $\sim 3 \text{ gCm}^{-2} \text{ y}^{-1}$ estimated for the deep Atlantic and Pacific
684 oceans¹⁸⁸. Hydrothermal processes also influence¹⁸⁸ the composition and fluxes of dissolved
685 organic carbon (DOC) to the ocean²⁰⁹. A large fraction of the deep ocean DOC is refractory²¹⁰ and
686 ranges from 4000 years old in the North Atlantic to 6000 years in the North Pacific²¹¹. High
687 temperature hydrothermal circulation alters and largely destroys DOC; however, diffuse vent
688 fluids contain higher DOC than deep seawater, which has been attributed to subsurface microbial
689 communities^{212,213}. Ridge flank fluids contain less DOC than deep seawater and can be as old as
690 17,000 years^{212,214,215}. DOC older than deep North Atlantic water was also found emanating from
691 cold oceanic crust at North Pond near the MAR²¹⁶. These data coupled with findings of 6900-
692 year-old DOC near the East Pacific Rise at 25°S²¹⁷ have led to the speculation that hydrothermal
693 venting could be an important source of old DOC to the deep ocean²⁰⁹.

694 Hydrothermal circulation can also lead to the incorporation of DOC in basement rocks;
695 total organic carbon could be up to ~1500 ppm in oceanic ultramafic and up to ~600 ppm in
696 gabbroic rocks^{218,219}. Stable isotope and radiocarbon studies of the Atlantis Massif¹⁶³ indicate

697 that organic carbon with an average radiocarbon age of 14,000 years is incorporated during
698 serpentinization and suggest that oxidation of organic compounds along circulation paths could
699 provide carbon for carbonates. REF¹⁶³ estimated annual storage rates of up to 1.7×10^{11} mol C yr⁻¹
700 of organic carbon and up to 6×10^{12} mol C yr⁻¹ of inorganic carbon in serpentinized oceanic
701 peridotites.

702 **[H2] Iron**

703 Hydrothermal Fe fluxes to the deep ocean and the impact they could have on primary
704 productivity and nitrogen fixation are currently an exciting area of research. Early studies had
705 assumed that Fe from high temperature systems would quickly precipitate out of the plumes as
706 sulphide or oxygenated particles. However, Fe can be transported thousands of kilometres
707 across ocean basins away from the hydrothermal source either as nanoparticles or as organically
708 chelated dissolved iron²²⁰. Current estimates of dissolved Fe flux are $4-6 \times 10^9$ mole yr⁻¹,
709 REFS^{220,221}. This flux is thought to be a notable source to the deep ocean that could eventually
710 upwell and promote primary production in the so-called High Nitrate Low Chlorophyll (HTLC)
711 regions where Fe is considered to be the limiting nutrient. The Southern Ocean is one of these
712 important HTLC regions, where Fe is thought to lead to phytoplankton blooms^{222,223}. Modelling
713 has shown that upwelling of hydrothermal Fe might be responsible for 15-30% of the primary
714 production in this region, thus linking the global biogeochemical cycles of iron and carbon. Fe
715 from shallow hydrothermal plumes [G] at the Tonga-Kermadec Arc is an important component of
716 increased nitrogen fixation and primary production in that region^{224,225}.

717 There is currently extensive research on the topic of Fe fluxes and much to be learned
718 regarding the importance of hydrothermal sources of Fe and other trace metals to the deep
719 ocean. To date, most hydrothermal chemical flux estimates are based on basalt-hosted MOR

720 systems. However, it is well accepted that hydrothermal circulation at all ridges and ridge flanks
721 contributes to global heat fluxes and has an important role in regulating seawater chemistry, the
722 composition of the oceanic crust and biogeochemical cycles. Release of many hydrothermally-
723 related compounds to the water-column has an immediate effect on chemoorganotrophic
724 activity within hydrothermal plumes, representing a substantial organic carbon export flux in the
725 deep ocean¹⁸⁸. A full understanding of hydrothermal fluxes requires further research of back-arc
726 spreading centres, island-arc and peridotite-hosted sites as well as tackling the difficult job of
727 quantifying temporal variability in vent fluids^{40,108}.

728

729 **[H1] Summary and future perspectives**

730 The theories of plate tectonics and seafloor-spreading revolutionized Earth and ocean
731 sciences and paved the way for new oceanographic, analytical and theoretical approaches to
732 understand how Earth works. However, fundamental gaps remain in understanding the interplay
733 among geological and biogeochemical processes and in quantifying the hydrogeology of
734 hydrothermal systems and the impact of fluid pathways at ridges and ridge flanks on heat,
735 chemical, and biological fluxes to the ocean.

736 The discovery of submarine hydrothermal vents supporting chemosynthetic communities
737 led to revolutionary understanding of the tree of life¹⁹⁰ and the conditions under which life can
738 thrive, survive, and die. Indeed, we are beginning to acquire a glimpse of the rare deep biosphere
739 within the lithosphere and hydrothermal vents⁹⁵ and have started to make progress towards
740 understanding the importance of viruses¹⁹⁵ and fungi²²⁶ in these systems. However, little is
741 known about how organisms and viruses evolve over time, how these communities interact, and
742 to what extent vents are sources for organisms in the overlying ocean.

743 Advanced sampling, spectroscopic and chromatographic techniques have also started to
744 unravel the compositions, sources and decomposition of DOC and complex organic compounds
745 in hydrothermal systems²²⁷⁻²³⁰. The continued development of compound specific radiocarbon
746 analyses and new sampling and analytical techniques are needed to further understand the
747 composition, age and fate of seawater and hydrothermally derived DOC and its potential
748 contribution to deep ocean DOC.

749 Technical innovation and installation of ocean observatories have advanced the ability for
750 monitoring and allows for rapid response to magmatic and tectonic activity, providing real-time
751 information on the development of dike-eruptive events from their inception (BOX 1).
752 Advancing these capabilities is vital for future research and will require more sophisticated
753 sensors, cabled and uncabled instrument networks and advanced underwater vehicles^{231,232}.
754 Future research will be guided by advances in robotic technologies together with miniaturization
755 and automation of sensor systems²³³. Development of in-situ chemical, physical and
756 metagenomic sensors for long-term deployments on the seafloor and in the overlying water
757 column will allow the detection of ephemeral processes that have been missed by traditional
758 oceanographic methods and will provide information on how these systems evolve over time.

759 Understanding the processes that control the dynamic interplay of geology, chemistry and
760 biology within the oceans and rocks beneath it will become increasingly important as humans
761 continue to influence the Earth's oceans and atmosphere. Continued exploration of
762 hydrothermal environments promises to offer new insights across multiple disciplines. It is vital
763 that these systems are not exploited in ways that could destroy or irreversibly alter them, which
764 would result in lost opportunities for new discoveries and limit future insight into the processes

765 that shape the planet. The deep sea holds many spectacular wonders, with many more to
766 discover – and much to protect.

767

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1452

1453 **Acknowledgements**

1454 G.F-G acknowledges support from the Swiss National Science Foundation (grant no. 200021-
1455 163187). Support to D.S.K. was provided by the US National Science Foundation grant no. OCE-
1456 0137206, the Management and Operation of the Ocean Observatories Initiative grant 1743430
1457 and the University of Washington. M.D.L. was supported by the US National Science Foundation
1458 (grants OCE-1037874 and 535962) and the W.M. Keck Foundation for Project NEPTUNE. The
1459 authors acknowledge the late Karen L. Von Damm, who pioneered and inspired decades of MOR
1460 hydrothermal vent research discussed in this article. We further acknowledge the enthusiastic
1461 and unwaning efforts of John R. Delaney, who was instrumental in driving the innovative ideas
1462 behind installing seafloor observatories at JdF.

1463

1464 **Author contributions**

1465 G.F-G coordinated and led the writing of this article; M.D.L. contributed to all aspects of writing,
1466 compiled data and led discussions on hydrothermal vent discoveries, distributions, fluid
1467 chemistry, volatiles and fluxes; D.S.K. led discussions on Axial, Endeavour, Ocean Observatories,
1468 phase separation and water-rock-microbe interactions, and together with her CEV team provided
1469 many of the figures; M.C. and V.C. provided input on slow- and ultraslow-spreading ridges and
1470 the EMSO observatory; J.A.B. wrote all sections on life in hydrothermal environments. All authors
1471 participated in discussions and edited multiple versions of the manuscript.

1472

1473 **Competing interests**

1474 The authors declare no competing interests.

1475 **Peer review information**

1476 *Nature Reviews Earth & Environment* thanks [Referee#1 name], [Referee#2 name] and the other,
1477 anonymous, reviewer(s) for their contribution to the peer review of this work.

1478 **Publisher's note**

1479 Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional
1480 affiliations.

1481 **Data availability statement**

1482 The compilation of vent distributions and fluid compositions are provided in the online
1483 Supplementary Data file.

1484

1485 **Supplementary information**

1486 Supplementary information is available for this paper at <https://doi.org/10.1038/s415XX-XXX-XXXX-X>

1487

1488 **Related Links**

1489 Interactive Oceans - <https://interactiveoceans.washington.edu>

1490 Ocean Networks - <https://www.oceannetworks.ca/observatories/>

1491 European Multidisciplinary Seafloor and water-column Observatory (EMSO) - <https://www.emso->

1492 [fr.org/EMSO-Azores](https://www.emso-fr.org/EMSO-Azores)

1493

1494 **Glossary**

1495 **Chemosynthesis** – The synthesis of organic compounds by microorganisms using energy
1496 derived from inorganic chemical reactions.

1497 **Oceanic crust** – The outermost layer of the lithosphere formed at mid-ocean ridge (MOR)
1498 spreading centres; it is 5-10 km thick, primarily composed of mafic lavas, dikes and gabbros.

1499 **Gabbro** – Igneous rock (formed from crystallization of magma) consisting primarily of varying
1500 proportions of the minerals plagioclase and pyroxene.

1501 **Peridotite** – The dominant rock type in the Earth’s upper mantle consisting primarily of the
1502 Mg-rich minerals olivine and pyroxene.

1503 **Lithosphere** – Outer solid layer of the Earth, consisting of the brittle crust and uppermost
1504 mantle.

1505 **Asthenosphere** – The viscous, mechanically weak and ductile region of the upper mantle
1506 between approximately 80 and 200 km depth that is involved in plate tectonic dynamics.

1507 **Spreading Rate** – The rate at which new oceanic lithosphere is created at mid-ocean ridge
1508 plate boundaries resulting in seafloor spreading.

1509 **Oceanic crustal architecture** – Rock types (lithologies), their distribution and structure of the
1510 oceanic crust.

1511 **Moho** – The Mohorovičić discontinuity, known as the seismic Moho, is a discrete change in
1512 seismic wave velocities used to define the boundary between the crust and the mantle.

1513 **Ophiolite** – Segments of oceanic crust and upper mantle tectonically exposed on land, often
1514 preserving features observed in different tectonic settings on the seafloor.

1515 **Oceanic detachment fault** – Extensional normal fault associated with asymmetric spreading
1516 that results in exposure of lower crustal and upper mantle rocks on the seafloor.

1517 **Serpentinization** – Hydrothermal process that transforms anhydrous Fe-Mg silicates into
1518 hydrous minerals, such as serpentine and brucite, producing magnetite and hydrogen.

1519 **Magma lens** – During periods of enhanced magma replenishment at MORs, magma
1520 accumulates in an axial melt lens overlying smaller stacked sills beneath sheeted dikes.

1521 **Volatiles** – Dissolved gases in hydrothermal fluids or exsolved from melts.

1522 **Hydrothermal plumes** – Upwelling and dispersal of buoyant hydrothermal fluids into the
1523 ocean at hydrothermal vents or after eruptions or diking events.

1524 **Microbial floc** – Microbial aggregates that appear as cloudy suspensions of cells floating in
1525 seawater rather than attached to a surface like most biofilms.

1526 **Snowblowers** – A distinct form of low-temperature hydrothermal venting with expulsion of
1527 copious amounts of white flocculent microbial material, reminiscent of snow.

1528 **Critical point of seawater** – Pressure and temperature conditions at which solid, liquid and
1529 vapour phases of seawater coexist in thermodynamic equilibrium.

1530 **pH** – A logarithmic scale from 0-14 to indicate the concentration of hydrogen ions in an
1531 aqueous solution and specifies the acidity ($\text{pH} < 7$) or basicity ($\text{pH} > 7$) of the solution.

1532 **Abiotic** – Formed or characterised by the absence of life or living organisms.

1533 **Aerobic** – Pertaining to or requiring the presence of free oxygen.

1534 **Anaerobic** – Occurring, living or active in the absence of free oxygen.

1535 **Heterotrophs** – Organisms incapable of making their own food from light or inorganic
1536 compounds but consume complex organic compounds or other organisms in a food chain.

1537 **Hyperthermophilic** – Pertaining to microorganisms that thrive in extremely hot environments
1538 and optimally grow above 80°C.

1539

1540

1541 **Display items**1542 **Table 1. | Summary of end-member hydrothermal system characteristics**

	Sulphide Systems		Sediment-hosted & Sediment-Influenced Systems	Carbonate Systems (Lost City Type)
Host rock	Hosted in basalt or gabbro	Hosted in gabbro and/or serpentinized peridotite	Hosted in basalt, sediment cover, or influenced by sediments at depth	Hosted in serpentinite (\pm gabbro)
Heat source	Driven by cooling of magma / volcanic crust or gabbroic bodies	Driven by cooling of magma or gabbroic bodies; influenced by serpentinization	Driven by cooling of magma / volcanic crust; interaction with sediments along flow path	Driven by lithospheric cooling & influenced by serpentinization processes
Fluid temperature	High T: up to 400° C	High T: 300 - 360°C	High T: 280° - 320°C	Low-moderate T <120°C
pH	Low pH: 2-5	Low pH: 3-4	Moderate pH: 5-6	High pH: 10-11
Element enrichments	Enriched in metals (Fe, Cu, Mn, Zn, Pb) & Si	Enriched in metals (Fe, Cu, Mn, Zn) & variable Si	Variably enriched in metals, enriched in organic C	Low metal concentrations
Volatiles	High CO ₂ ; variable H ₂ S, CH ₄ , H ₂	High CO ₂ , CH ₄ , H ₂ & organic compounds; variable H ₂ S	High CH ₄ , NH ₄ ⁺ ; variable H ₂ S, CO ₂ , H ₂	High H ₂ , CH ₄ , C2-C4's & organic acids; variable H ₂ S; negligible CO ₂
Type of hydrothermal deposits	Metal-sulphide chimneys & stockworks in basement	Metal-sulphide chimneys & stockworks in basement	Metal-sulphide chimneys & stockworks in basement	Carbonate-brucite chimneys & carbonate in basement
Venting characteristics	-> Black & white smokers	-> Black (& white) smokers	-> Black & white smokers	-> <i>Not "white" smokers</i> Clear "non-smoking" fluids

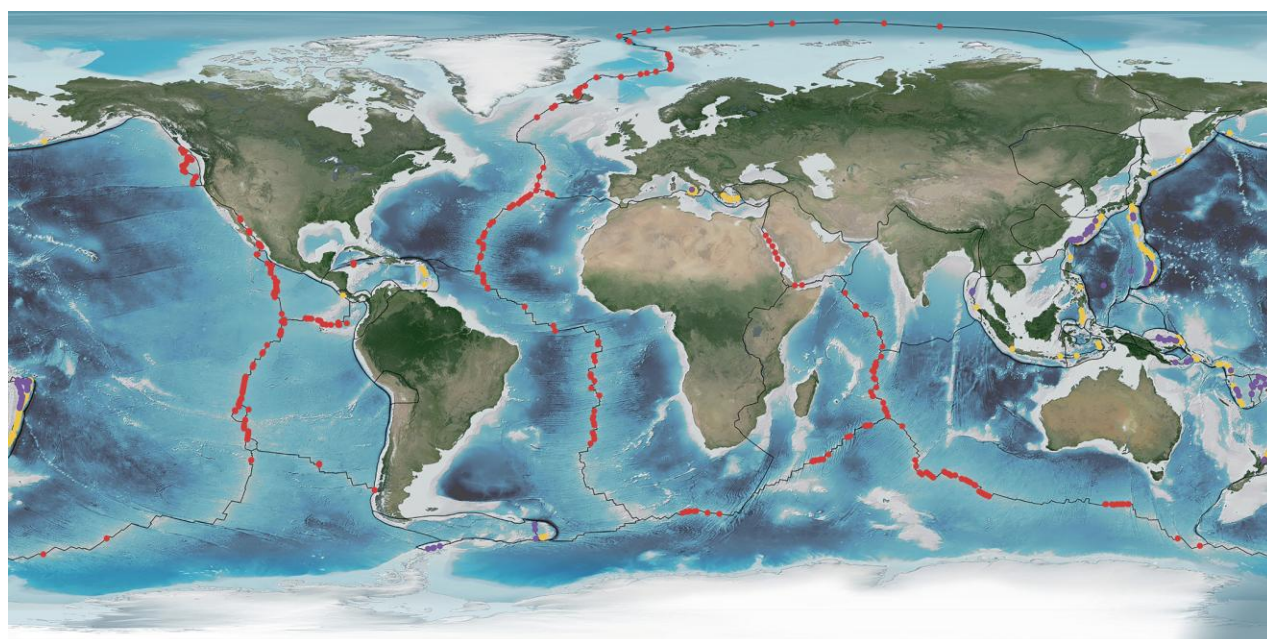
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Note: Compilation of vent distributions and fluid compositions in Supplementary Data.

1545 **Figures**

1546 Fig. 1 | **Global distribution of hydrothermal vents on the seafloor.** Map of the global ridge
1547 system with distribution of known sites of hydrothermal venting and sites inferred to be present
1548 from water column studies. Hydrothermal vents occur at MORs (red dots, 65% of known sites),
1549 back arc spreading centres (purple dots, 22%), and submarine arc volcanoes (yellow dots, 1%).
1550 Data from the InterRidge Vents Database. Map produced by the Center for Environmental
1551 Visualization, University of Washington (CEV, UW).



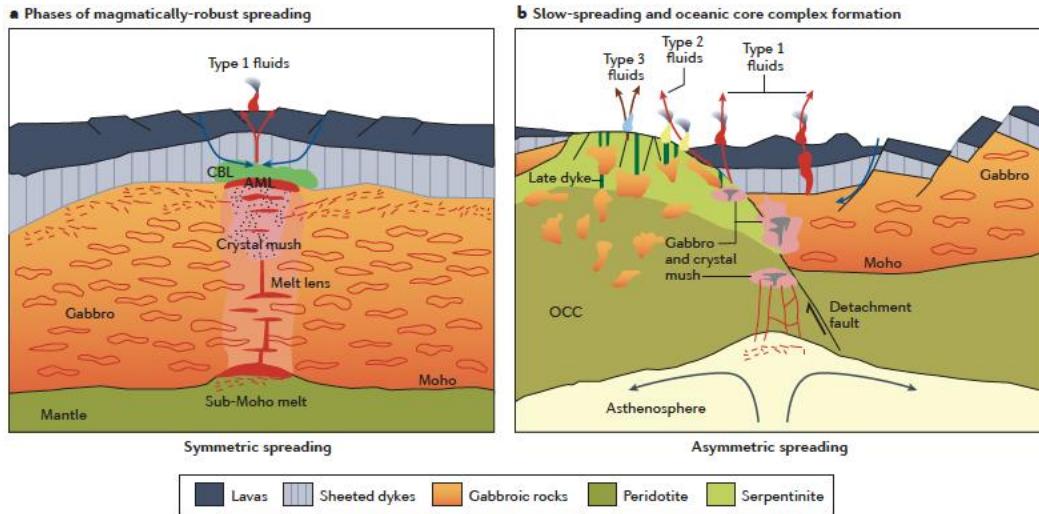
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1553

1554 Fig. 2 | **Variations in magmatism, structure and hydrothermal systems with varying spreading**
1555 **rates.** Conceptual, across-axis comparison with variations in magmatism and spreading rate. **a** |
1556 Regions with phases of robust magmatism, characteristic of fast spreading MORs, produce a rela-
1557 tively homogeneous layered crust. Geophysical models predict that sub-Moho melts feed sills
1558 through small dikes and accumulate in a shallow axial melt lens (AML), producing stacked sills
1559 and a crystal mush zone (high melt %; stippled region) surrounded by hot gabbroic rock²³. A
1560 conductive boundary layer (CBL) separates the AML from hydrothermal circulation where
1561 focused fluid flow produces high temperature Type-1 vent fields. Depth of profile ~6 km. **b** |
1562 Slow-spreading ridges are heterogenous and influenced by discontinuous magmatism leading to
1563 detachment faults, asymmetric ridge segments, and oceanic core complexes (OCC). Detachment
1564 faults can channel high-temperature Type 1 fluids (such as at TAG^{63,76,148}) and drive flow in
1565 gabbro- and peridotite-influenced Type 2 hydrothermal systems (such as at Logatchev and
1566 Rainbow^{139,140,234}). Late normal faults can focus low-temperature, alkaline fluids (Type 3 fluids,
1567 blue arrows) leading to large carbonate deposits, as at Lost City^{65,80}. Depth of profile ~9 km. **c** |
1568 Types of hydrothermal vents types described in panels **a** and **b**. **d** | The structure named Sully on
1569 the Endeavour Segment, Juan de Fuca ridge, overgrown with *Ridgeia piscesae* tubeworms
1570 venting 380°C Type 1 black smoker fluids after a diking event in 1999-2000. **e** | The black smoker
1571 structure named Candelabra, venting Type 2 fluids at a water depth of 3,300 metres in the
1572 Logatchev Hydrothermal Field, MAR. **f** | Carbonate-brucite deposits at 845 m water depth at the
1573 Lost City hydrothermal field, MAR 30°N. Supplementary Videos. Panel a adapted with permission
1574 from REF.²³. Panel b modified with permission from REFS^{49,79,235}. Panel d credit: Delaney, J.R. and
1575 Kelley, D.S, University of Washington; Canadian Scientific Facility - ROV ROPOS, 2004; W.M. Keck
1576 Foundation. Panel e credit: MARUM – Center for Marine Environmental Sciences, University of

1577 Bremen (CC-BY 4.0). Panel f credit: D.S. Kelley, UW, URI-ROV Hercules, IFE, URI-IAO, Lost City

1578 Science Party 2005, & NOAA Ocean Exploration.



c Types of hydrothermal vent systems

Type 1 fluids

- High temperature vents with sulphide deposits in basalt
- T > 300°C
- Low pH (<5)
- High metals
- Low CO₂, variable H₂S
- Low but variable H₂, CH₄
- Abundant macrofauna

Sully (Endeavour)

d

Type 2 fluids

- High temperature vents with sulphide deposits in serpentinites and gabbro
- T > 300°C
- Low pH (<5)
- High metals
- High CO₂ (gabbroic input)
- High H₂, CH₄ (ultramafic input)
- Abundant macrofauna

Rainbow (MAR)

e

Type 3 fluids

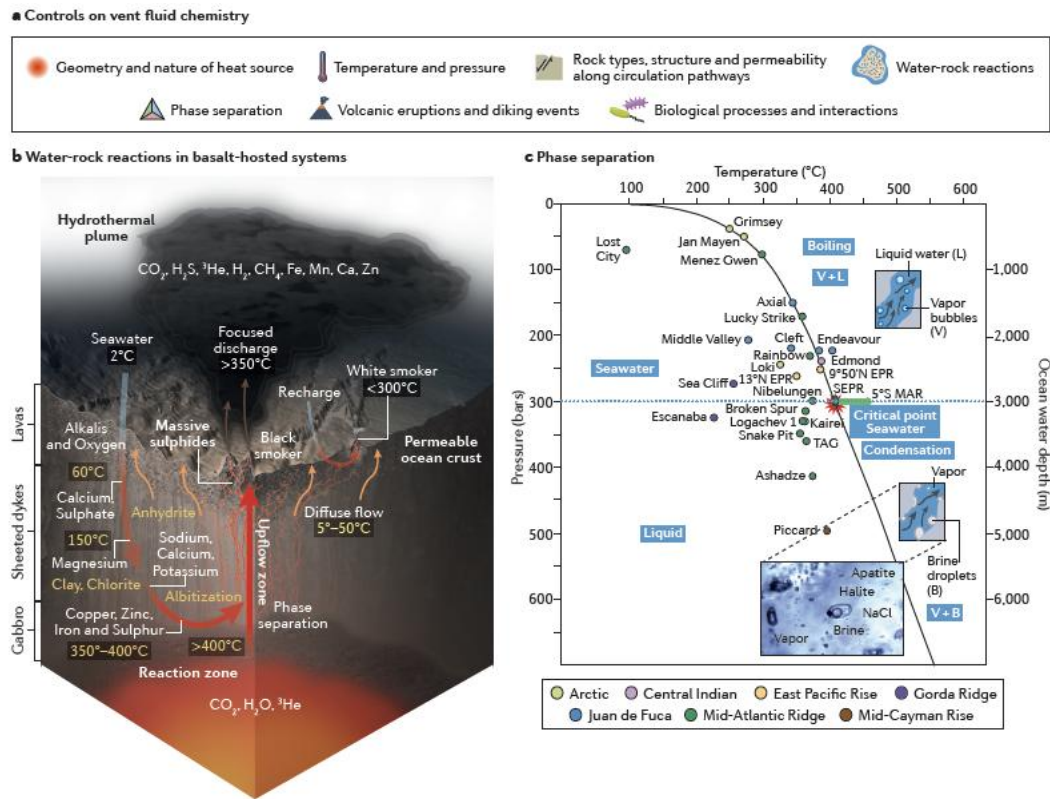
- Low temperature vents with carbonate deposits in serpentinite
- T < 120°C
- High pH (>9)
- Low metals
- Negligible CO₂
- High abiogenic H₂, CH₄, formate
- Limited macrofauna, diverse meiofauna

Lost City (MAR)

f

1579

1580 **Fig. 3 | Hydrothermal processes at mid-ocean ridges. a |** Summary of factors that influence
 1581 hydrothermal activity and fluid chemistry at MORs. **b |** Conceptual sketch of water-rock reactions
 1582 and flow paths in an idealised basalt-hosted seafloor hydrothermal system^{31,87}. Hot fluids rise
 1583 buoyantly to the seafloor, where metal-rich, superheated fluids are expelled into the ocean,
 1584 precipitating metals and forming black and white smoker edifices. **c |** Plot of maximum measured
 1585 temperatures and pressures of fluids issuing from hydrothermal vents (Supplementary Data). The
 1586 two-phase boundary (black line) and critical point (large red dot at 407°C, 298 bar) of seawater⁹⁷
 1587 are shown with labels indicating the boiling and condensation fields. Inset diagrams show how
 1588 volatiles partition preferentially into the less dense phase^{31,97}. Inset image is of magmatic fluid
 1589 inclusions (700°C) in gabbros from the MARK area⁹⁸. Panel b credit: D.S. Kelley, J.R. Delaney, CEV,
 1590 UW.



1591

1592

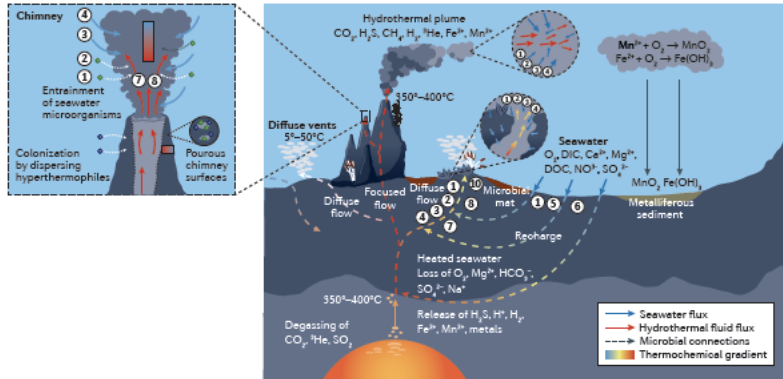
1593 Fig. 4 | **Mid-ocean ridge hydrothermal fluxes and life. a** | Variations in availability of electron
1594 donors and electron acceptors under varying temperature and redox conditions and their
1595 potential metabolic energy sources. Examples of general inorganic redox reactions along
1596 thermochemical mixing gradients in vent environments that support diverse microbial
1597 communities, with potential locations along subsurface flow paths in basalt-hosted systems
1598 shown as circled numbers on panel **b**. **b** | Representation of fluid flow paths and fluid-rock
1599 interactions that govern chemical fluxes, redox reactions and microbial ecosystems at
1600 magmatically robust black smoker systems with circulation limited to the upper crust (<2-3 km)
1601 above axial magma lenses. Reactions 1–4 take place in the shallow subsurface and zones of
1602 mixing with seawater and are not restricted to any particular distance from the ridge axis. **c** |
1603 Same as **b**, but for a Lost City-type system controlled by faults and serpentinization processes
1604 (BOX 2). Light blue anastomosing network depicts early interconnected fluid pathways leading to
1605 the onset of serpentinization^{162,236}. Reactions between gabbro lenses and peridotite cause
1606 localised silica metasomatism (lightest green patches in serpentinized domains)^{155,237}. Panel b
1607 modified after REF²³⁸. Inset in 4b modified after REF⁹⁶. Panel c modified after REFS^{155,162,237}; inset
1608 modified after REF²³⁹.
1609

a Potential metabolic energy sources and reactions in hydrothermal vent environments

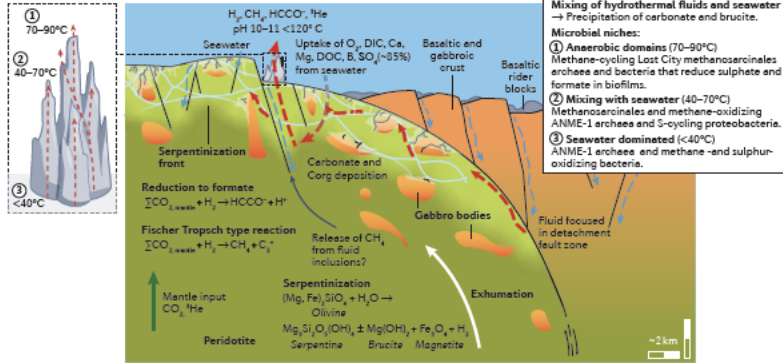
Electron donors	Electron acceptors	
$H_2, H_2S, CH_4, NH_4^+, S_2O_8^{2-}, Mn^{2+}, NO_2^-$	$+ O_2$	Oxidizing
$H_2, H_2S, S^0, S_2O_8^{2-}, Fe^{2+}$	$+ NO_3^-$	Increasing T General trend of decreasing energy yield
H_2S, S^0	$+ MnO_2$	
H_2	$+ Fe^{3+}$	Reducing
H_2	$+ S^0$	
H_2, CH_4	$+ SO_4^{2-}$	
H_2	$+ CO_2$	

Aerobic reactions	Anaerobic reactions
① Metal (iron II) oxidation $4Fe^{2+} + O_2 + 10H_2O \rightarrow 4Fe(OH)_3 + 8H^+$	⑤ Anaerobic iron oxidation $8Fe^{2+} + 10H^+ + NO_3^- \rightarrow 8Fe^{3+} + NH_4^+ + 3H_2O$ $10Fe^{2+} + NO_2^- + 12H^+ \rightarrow 10Fe^{3+} + N_2 + 8H_2O$
② Sulphide oxidation $H_2S + 2O_2 \rightarrow SO_4^{2-} + 2H^+$ $5HS^- + 8NO_3^- + 3H^+ \rightarrow 5SO_4^{2-} + 4N_2 + 4H_2O$	⑥ Nitrate reduction $H_2 + NO_3^- \rightarrow NO_2^- + H_2O$
③ Methane oxidation $CH_4 + 2O_2 \rightarrow CO_2 + 2H_2O$ $CH_4 + 2O_2 \rightarrow HCO_3^- + H^+ + H_2O$	⑦ Sulphate reduction $4H_2 + 2H^+ + SO_4^{2-} \rightarrow H_2S + 4H_2O$
④ Hydrogen oxidation $2H_2 + 2O_2 \rightarrow 2H_2O$ $5H_2 + 2NO_3^- \rightarrow N_2 + 4H_2O + 2OH^-$	⑧ Methanogenesis with CO_2 $4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$
	⑨ Methanogenesis with formate $4HCCO^- + H_2O^- \rightarrow 3HCO_3^- + CH_4$
	⑩ Anaerobic methane oxidation $CH_4 + 2H^+ + SO_4^{2-} \rightarrow H_2S + CO_2 + 2H_2O$

b Black smoker flow paths, fluid-rock interaction and ecosystems



c Lost City-type hydrothermal systems



1610

1611

1612 **Boxes**

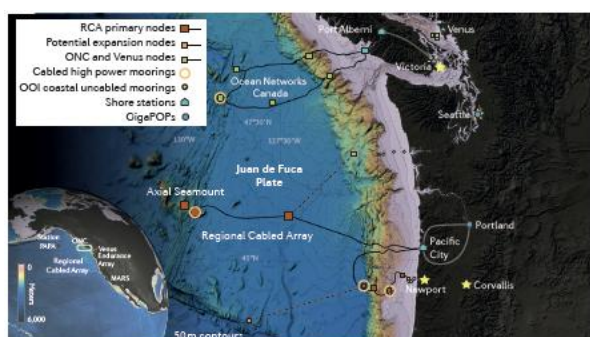
1613 **[B1] BOX 1 | Ocean observatories**

1614 Ocean floor observatories have advanced the ability to study interactions of seafloor
1615 deformation, volcanism, hydrothermal circulation and microbial activity during ocean crust
1616 evolution. Below we provide a brief overview of three ocean observatories currently installed to
1617 study MOR processes:

1618 ***Regional Cabled Array (RCA) and Ocean Networks Canada (ONC)*** – combined, these two
1619 instrumented networks on the Juan de Fuca Ridge form the first submarine cabled observatories
1620 to monitor an entire tectonic plate. The mid-ocean ridge components of the two observatories
1621 focus on both the magmatically robust Axial Seamount (RCA, operated by the U.S.), which
1622 erupted in 1998, 2011, and 2015, and the tectonically active Endeavour Segment (ONC, operated
1623 by Canada)^{231,240} (see figure). These two networks are linked to the global internet and provide
1624 data and imagery in real- to near-real time. Continuous monitoring of the oceanic plate is made
1625 possible through ~1700 km of fibre optic cable and 14 subsea terminals that provide 8-10 kW
1626 power and 10 Gbs two-way communications to hundreds of instruments on the seafloor and in
1627 the water column. A highlight of the networked RCA was the live detection of the 2015 Axial
1628 Seamount eruption, marked by a seismic crisis of >8,000 earthquakes coincident with 2.4 m of
1629 seafloor subsidence over a 24 hour period²⁴¹. Hydrophones detected acoustic activity delineating
1630 more than 30,000 volcanic explosions as lava spilled onto the seafloor²⁴², culminating in a 127 m-
1631 thick submarine lava flow. Three months later the summit of the flow was covered by kilometres
1632 of microbial mats fed by nutrient-rich, warm fluids circulating through the cooling lava¹¹⁹.

1633 ***European Multidisciplinary Seafloor and water-column Observatory (EMSO)*** – is located
1634 on the Mid-Atlantic Ridge south of the Azores. The principal target of the uncabled EMSO is to

1635 understand shorter-term variations of the Lucky Strike hydrothermal system in a tectonically
1636 complex framework, and their impact on life at and beneath the seafloor, similar to the JdF sites.
1637 One observatory node of the EMSO infrastructure is dedicated to long-term (>20 years)
1638 monitoring of volcanic, tectonic, hydrothermal and biological activity at Lucky Strike⁶⁷. The
1639 observatory includes arrays of autonomous instruments and two stations that communicate
1640 acoustically to a surface-relay buoy which transmits data to shore every 6 hours. Two stations
1641 monitor seismic activity, pressure at the seafloor, and key environmental parameters; one of
1642 these stations also connects to a camera that records daily videos of the hydrothermal fauna.
1643 Monitoring of variable responses to tidal forcing has revealed changes in the subseafloor
1644 permeability structure^{243,244} and episodic increases in microseismic activity. Changes in
1645 earthquake locations through time indicate that the main heat extraction is to the north of the
1646 hydrothermal field and moved by about 800m to the east between late 2013 and late 2015²⁴⁵.



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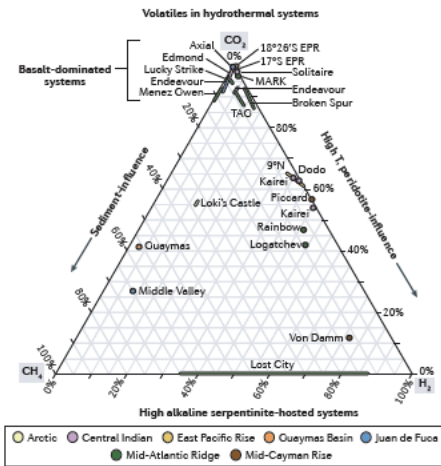
1649 [B2] Box 2 | **Serpentinization and volatiles in the oceanic lithosphere**
1650 The discovery of hydrothermal vents influenced by serpentinized ultramafic upper mantle
1651 rocks – and in particular, the discovery of the off-axis Lost City vent field – has had a key impact
1652 on the overall understanding of the role of slow-spreading ridges in global hydrothermal fluxes
1653 and the potential impacts of serpentinization²¹⁸ (FIG. 4c).

1654 **Serpentinization** involves hydration of mantle olivine and pyroxene, which produces
1655 hydrogen and incorporates up to 14 wt. % H₂O. Serpentinization decreases bulk density (to 2.5-
1656 2.9 g cm⁻³) and seismic velocities ($V_p < 6 \text{ km s}^{-1}$), and directly affects the strength and physical
1657 properties of the mantle, and the magnetic and gravity signatures of the oceanic
1658 lithosphere^{246,247}. The depth to which serpentinization can occur is controlled by the depth to
1659 which seawater can penetrate into the oceanic lithosphere and is largely controlled by tectonic
1660 processes and fracture permeabilities. The depth and spatial extent of serpentinized oceanic
1661 peridotites has direct consequences for the interpretation of seismic velocity data and can
1662 influence where geophysicists estimate the location of the seismic Moho. In addition, the
1663 presence of gabbroic intrusions in mantle peridotites leads to Si mobility and talc formation
1664 during alteration, which can influence the strength of the lithosphere along detachment faults
1665 and aid in uplift and emplacement of mantle sequences at the seafloor.

1666 **Serpentinization reactions** are associated with the uptake or release of many components,
1667 such as H₂O, Mg, Ca, Si, Cl, Li, B, C, and S^{218,237,248,249}, which can be recycled through subduction
1668 and affect subduction zone dynamics and the compositions of arc magmas²⁰². In addition,
1669 serpentinization reactions lead to highly reduced fluids with high concentrations of H₂, which
1670 distinguishes peridotite-hosted systems from basalt-dominated or sediment-influenced systems
1671 (see figure and Supplementary Data). Hydrogen production is linked to oxidation of ferrous iron

1672 in mantle minerals to produce magnetite during serpentinization, which is limited by brucite
1673 formation and incorporation of Fe in other alteration phases in oceanic serpentinites^{218,250,251}.

1674 **Fluids** in serpentinizing environments characteristically have elevated concentrations of
1675 methane, formate, ethane, propane, and other straight chain hydrocarbons^{152,156,177}. H₂
1676 production and the formation of organic molecules and reduced C-species have been considered
1677 to form through abiotic reactions, catalysed by Fe-, Ni-, and Cr-bearing minerals, and have
1678 important consequences for global chemical cycles and biological activity on and within the
1679 seafloor²¹⁸. The geochemical reactions that occur during serpentinization could have been key in
1680 early biochemical evolution, which potentially has major implications for the origin and evolution
1681 of life on Earth and other planets¹⁴⁵⁻¹⁴⁷.



1682