MICROBIAL PROVINCES IN THE SUBSEAFLOOR

INVEST: White Paper
CT1: Co-evolution of Life and Planet
WG1.1: Extent and habitability of subseafloor life and the biosphere

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ABSTRACT

The rocks and sediments of the oceanic subsurface represent a diverse mosaic of environments potentially inhabited by microorganisms. Understanding microbial ecosystems in subseafloor environments confounds standard ecological descriptions in part because we have difficulty elucidating and describing the scale of relevant processes. Habitat characteristics impact microbial activities and growth, which in turn affect microbial diversity, net production, and global biogeochemical cycles. Herein we provide descriptions of subseafloor microbial provinces, broadly defined as geologically and geographically coherent regions of the subseafloor that may serve as potential microbial habitats, as recently presented in a review article (Schrenk et al., in press, *Annual Reviews in Marine Science*). The criteria we outline are aimed at developing a unified framework to improve our understanding of subseafloor microbial ecology, enable quantification of geomicrobial processes, and facilitate their accurate assimilation into biogeochemical models. Subseafloor biosphere studies would benefit from careful comparisons between sites, further investigation of understudied sites, and elucidation of poorly understood physiological adaptations. Herein we summarize the most salient points of this review that may be useful for INVEST discussions.

1. INTRODUCTION

The exploration of the subseafloor biosphere has grown significantly in the past several decades from sampling the uppermost layers of deep-sea sediments by Zobell and colleagues in the 1950's (ZoBell 1952), to the first enumeration of microbial cells in newly discovered deep-sea hydrothermal vents in 1977 (Corliss et al 1979), to the detection of living cells in marine sediments hundreds of meters beneath the seafloor (Parkes et al 1994, Schippers et al 2005). The field has evolved from opportunistic sampling during geology-focused oceanographic expeditions to embrace, very recently, microbiology-focused initiatives in a range of deep-sea environments. Subseafloor microbial processes may exert fundamental influences on the biogeochemistry of the oceans and atmosphere but to date, there have been relatively few observations of subseafloor microbial communities and the picture of what defines the ecology of the deep marine biosphere is just emerging. In the oceanographic literature, different regions of the ocean are divided into distinct provinces based upon their general physical and chemical characteristics. We will explore the concept of provinces through the eye of ecologically relevant environmental factors (or biomes) and suggest common themes controlling the composition and dynamics of subseafloor microbial communities.

2. ROCKY SUBSEAFLOOR PROVINCES

Hard rock-hosted subseafloor microbial habitats begin with the emplacement of new ocean crust at the mid-ocean ridges, where they are exposed at the seafloor, eventually becoming overlain by marine sediments prior to their subduction and recycling (**Figure 1**). The following discussion highlights some of the characteristics of these systems, from the mid-ocean ridges (MOR) to continental margins.

2.1 Mid-Ocean Ridges

Rocks exposed at and near the ridge axes are typified by shallow geothermal gradients and extensive, hydrothermally driven fluid circulation (Fisher et al 2004). High-temperature fluid-rock reactions create highly reduced, metal rich fluids that are in disequilibrium with the surrounding seawater, and may result in mineral precipitation and/or dissolution that alter fluid flow on local scales (Bach et al 2003). This hot, dynamic environment undergoes perpetual renewal due to volcanic eruptions and associated earthquake activity. The ecology of microbial communities must be specifically adapted to this chaotic, ephemeral regime and the geothermal gradient, near axis, is likely to be prohibitive within several meters of the seafloor, by comparison to what could potentially be sustained in ridge flanks and marine sediments.

2.2 Ridge Flanks

The ridge flank environment begins at ~1 Ma crust (~5 km off the ridge axis) and extends as long as hydrothermal circulation continues, to ~80 Ma (Embley et al 1983). Hydrothermal circulation is driven by latent heat in cooling oceanic crust, and circulation is controlled by distribution and connectivity of pore spaces in the subsurface. Two major biomes can be considered within ridge flanks: (1) young ridge flanks (<10 Ma) adjacent to the mid-ocean ridges, and (2) older, cooler ridge flanks (>10 - 65 Ma). Young ridge flanks near the MORs are characterized by vigorous fluid flow, and generally low temperatures (<40°C) by comparison to ridge axis environments. Potential energy sources driving an ecosystem during low-temperature circulation derive less from the products of water-rock reactions, and more so from the primary alteration reactions themselves (Edwards et al 2005). When the young ridge flanks are sedimented, they are generally warmer, with less heat loss owing to the insulating characteristics of sedimentary cover, and characterized by more sluggish fluid flow. Samples for microbiological study have been accessed in actively producing seamounts and boreholes (Cowen et al 2003, Huber et al 2006). In the cooler, older ridge flank biome, petrographic observations of rock that has been recovered during geological surveys suggest microbial weathering of volcanic glass in numerous subseafloor settings (Banerjee & Muehlenbachs 2003, Fisk et al 1998).

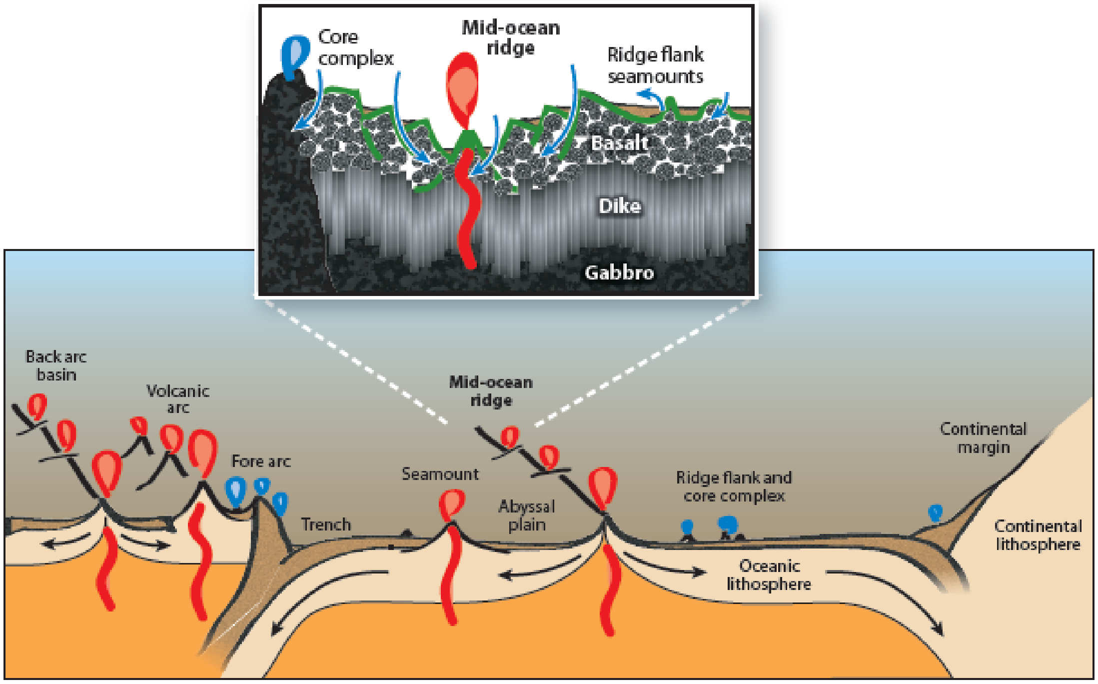

Figure 1 Diagram depicting the major provinces that make up the potential subseafloor biosphere. To date, most studies of the subseafloor have focused on sediment-hosted habitats associated with continental margins. Subseafloor biomes associated with the mid-ocean ridges, ridge flanks, volcanic arcs, and the abyssal plain each represent significantly different habitats in terms of their physical and chemical properties. Understanding the complex combination of physical, chemical, and biological factors that control the biogeochemistry of these various environments requires an appreciation of the diversity of these habitats and the different approaches required for their study.

2.3 Island Arc Environments

Diverse subseafloor environments are formed at subduction zones where one oceanic plate moves beneath another. During subduction, rocks and sediments melt, forming highly complex and variable magmas, and ultimately, hydrothermal systems. Volcanoes can be formed from both island arc and back-arc settings, as exemplified in the western Pacific by the Mariana Arc and the back-arc system associated with the subduction of the Pacific Plate beneath the Philippine Plate. It is estimated that there are over 20,000 km of volcanic and back-arc systems globally; however, exploration of these systems has only just begun (de Ronde et al 2003, Ishibashi &

Urabe 1995). Volcanic arcs have highly variable magmas and rock compositions, and as a result, individual volcanoes along an arc can occur at a wide range of depths (from less than 100 m to greater than 1500 m) and host extremely different intensities of venting and fluid chemistry (Embley et al 2004). Spreading axes in back-arc basins are structurally akin to the mid-ocean ridges and examples include the Manus and Lau Basins in the western Pacific. Both volcanic and back-arcs systems are impacted by recycling of volatiles (and solutes) in the subducted plate, which leads to more oxidizing fluid compositions and subsequently acidic pHs (between 1 and 3) with higher concentrations of gases and metals than MOR systems (Lupton & al. 2006).

2.4 Ocean Island Volcanoes

Mid-plate seamounts are topographic structures of the deep abyssal plain, formed by hotspot volcanism and the buildup of oceanic basalt. Volcanically active (e.g., Loihi Seamount, part of the Hawaiian Island chain in the central Pacific) and extinct (e.g., New England Seamounts in the western Atlantic) seamounts represent ubiquitous outcroppings of rock at the seafloor. While there are a few examples of isolated seamounts, most are found in chains and associated with either past or current hotspot volcanism. The unifying feature of seamounts, whether active or extinct, is that the extrusive basaltic rock that forms them creates a permeable and porous ocean crust outcropping ideal for fluid circulation and, potentially, microbial communities. Ocean island volcanoes are typified by melting of deeper, less degassed mantle rock, and their magmas have correspondingly more moderate gas contents. It is predicted that approximately 39,000 seamounts exist in the deep sea, more than half of which remain to be discovered (Hillier & Watts 2007).

3. MARINE SEDIMENT PROVINCES

Marine sediments cover nearly the entire extent of the deep seafloor and range in thickness from a few centimeters near newly formed oceanic crust to >10 km in the deep sea trenches (Fry et al 2008). They provide a snapshot into both past depositional processes and contemporary biogeochemistry. The defining physicochemical characteristic of these systems is that chemical transport is dominated by diffusion, which has profound influences upon the rate and extent of biotic versus abiotic reactions. Our knowledge of sedimentary microbial communities, while larger than that of crustal communities, is highly skewed toward shallow (<1 m depth) and continental margin sites. Collectively, continental margin sediments represent just one part of the range of subseafloor conditions that exist globally, from extremely low-nutrient and -carbon regimes to extremely high-productivity regimes near the coasts (**Figure 1**).

3.1 Active Continental Margins

Subduction zones at convergent plate margins are typified by the formation of deep trenches, the accumulation of thick accretionary prisms on the overriding plate, and a series of complex water-rock reactions. In contrast to open ocean sites, the subseafloor province at actively subducting continental margins has been relatively well studied. The microbiology of deep-sea sediments has been covered extensively in several recent reviews (Fry et al 2008, Jørgensen & Boetius 2007). The sole microbiology-focused leg of the Ocean Drilling Program (ODP Leg 201) to date, which explored the Peru Margin and eastern equatorial Pacific off the coast of South America, has contributed a wealth of information to our understanding of the subseafloor biosphere in marine sediments (Biddle et al 2008, Parkes et al 2005). Subseafloor microbial ecosystems in these settings appear to be stratified with regard to the chemistries used for growth and are stimulated at interfaces between seawater sulfate and methane (referred to as the sulfate-methane transition zone). Comparative analyses between methane hydrate zones in numerous continental margin environments (Cascadia Margin, Nankai Trough, Peru Margin) are beginning to build a coherent picture of the biogeography of continental margin sediments (Inagaki et al 2006). So far, microbes have been found as deep as we have looked in continental margin systems---the absolute depths of the subseafloor biosphere in this biome has not yet been found.

3.2 Abyssal Plains

Abyssal plains are flat, deep regions of the seafloor that extend from the continental margins to the MOR. They account for as much as 79% of the seafloor worldwide and are generally at depths greater than 4000 m (4500 - 6000 m). These oligotrophic regions are by area the largest sedimentary habitats on Earth. Most organic matter in abyssal sediments derives from surface primary production. In extremely nutrient-deprived regions such as the South Pacific Gyre (SPG), the subseafloor biosphere is characterized by low biomass and very low metabolic activity (D'Hondt et al 2009). Here, the organic content of the sediment is so low that sometimes anoxia never occurs and oxidants have even been observed entering the base of the sediment column via basement rocks. This discovery raises questions about the ubiquity of potentially inverted electron acceptor profiles at the bottom of open ocean sediment packages. In contrast to the energy-rich hydrothermal systems, open ocean sedimentary systems like the SPG may be limited by electron donors. The carbon- and nutrient-starved open ocean gyres such as the SPG and the Tropical North Atlantic Gyre (North Pond) are poorly represented in deep sedimentary biosphere studies to date.

3.3 Passive Margins: Continental Shelves and Slopes

Continental margins along passive plate boundaries are important for linking the flow of nutrients and energy between the oceans and the continents. The continental shelves are typically considered an extension of the continents because they are underlain by continental not oceanic lithosphere. Passive margins generally have high levels of terrestrial organic matter and nutrient input, which is reflected in the high productivity of phytoplankton in this region. These systems are considered very stable, with predictable geotherms and isobars. The water depth in such regions is fairly shallow (<150 m), and the shelves merge into continental slopes, which represent the transition between continental and oceanic crust.

4. CHALLENGES TO HABITABILITY

A range of parameters can influence the success of microbial communities, from physical controls such as temperature and pressure, to chemical controls such as nutrient availability, pH, and free energy flux, to biological influences upon productivity and community structure. In theory, physiological constraints derived from laboratory investigations of microbial isolates can be used to impose strict boundary conditions upon the potential for life in the subsurface. In reality, it is well recognized that the most abundant microorganisms in many natural environments have not been obtained in pure laboratory cultures; thus the extrapolation of the physiology of few should be taken with extreme caution.

4.1 Temperature

What limits life in sediments and the crust? High temperature is a likely candidate for the ultimate limit to life in subseafloor sediment. While the highest temperature for life presently accepted by a significant fraction of the scientific community is ~122°C, in all likelihood the limits are closer to 150°C (Holden & Daniel 2004). While this temperature is exceeded at shallow depths at the MOR, in most subseafloor provinces, the thermally prohibitive isotherm is not crossed until considerable depths into the ocean floor (**Table 1**).

4.2 Organic Matter

If temperature is not the ultimate factor constraining the proliferation of life in most of the subseafloor, perhaps the composition and availability of organic matter is. Organic carbon content in subseafloor provinces varies from 0.09 to >12 wt% (**Table 1**), derived primarily from the deposition of terrigenous sediments and in some cases from primary productivity in overlying surface waters. Correspondingly, the highest in situ cell densities and deepest known extent of the subseafloor biosphere are associated with organic-rich habitats along the continental margins. Chemoautotrophy is also a common characteristic among microbial isolates from subsurface environments. These isolates range from anaerobic hyperthermophiles from the mid-ocean ridges, to aerobic mesophilic and psychrophilic sulfide oxidizers from off axis environments. The extent to which primary production occurs, along with its constraints, is an important topic worthy of further detailed exploration.

4.3 Free Energy

Whether the energy sources are organic or inorganic, life in the absence of light in the subseafloor biosphere is dependent upon chemical energy in the form of red-ox disequilibria. In some sedimentary environments, the very low availability of electron donors may limit life. In the ocean crust, electron donors may not be a limiting factor, as chemosynthetic reactions between the reduced crust and oxidizing advecting fluids may support the base of the crustal food web. However, at certain highly reducing sites, such as the Lost City Field near the Mid Atlantic Ridge, the presence of electron acceptors (oxidants) may be limiting to the subseafloor biosphere (Kelley et al 2005). End-member fluids at this site are so reducing that even the least energetically favorable electron acceptors are not present.

4.4 Pressure

An infrequently considered parameter in deep biosphere studies is the physiological effect of high hydrostatic pressure. The oceans have an average depth of ~3800 m (pressures of 38 MPa), and most of the subseafloor habitats discussed in this review reside at depths greater than this (pressures increase at a rate of 10 MPa/km for hydrostatic and 30 MPa/km for lithostatic pressure). The deepest parts of the ocean are at >11,000 m below the sea surface, or at approximately 110 MPa. Studies of pressure effects upon microbial biochemistry have shown changes in the composition of membrane lipids and proteins, which appear to be correlated with the depth of habitat isolation (DeLong & Yayanos 1985). Other studies have shown that in situ hydrostatic pressures increase the optimum and maximum growth temperatures of hyperthermophiles in laboratory cultures (Marteinsson et al 1997).

4.5 Nutrients

Another factor that may dictate the habitability of the subseafloor biosphere is the availability of raw materials required by all life, including carbon, the nutrients nitrogen and phosphorous, and trace elements (e.g., Ni, Mo, V). The crust and rocks of the subsurface are the largest reservoir of carbon on the planet (>99.9%). However, the fluxes, feedbacks, and linkages within this deep carbon cycle and the surface environment are poorly understood. The oxidation state of subsurface ecosystems is closely tied to the reactivity of carbon pools. The presence of organic carbon and the nutrients nitrogen and phosphorous are controlled, to a first order, by the occurrence of terrestrially derived sediments, which impacts productivity in continental margin environments. Whether nutrient deprivation absolutely controls productivity in the open ocean and in deep subsurface environments remains to be determined.

5. RECOMMENDATIONS

Deep marine biosphere studies seek to answer questions that range in nature from exploratory and census-level to the most complex and fundamental in the Earth and life sciences. Deep marine biosphere habitats are vast in scale- it is estimated that 1/3 to 1/10 of biomass on Earth is found in the deep marine subsurface- and in the range of physical and chemical conditions that are represented among them. A common feature among all deep marine biosphere habitats is that they exist in the dark, one or more steps removed from the photosynthetic activity that fuels the surface biosphere. Energy and carbon cycling in the deep marine subseafloor are potentially important issues in solving global red-ox and carbon budgets. However, quantification of the magnitude and activity of this dark biosphere and its organic versus inorganic energy and carbon sources is difficult, owing to a dearth of data concerning the nature of these deep ecosystems. Focused studies of the deep marine biosphere may potentially answer fundamental questions that have far-reaching consequences for life on Earth and beyond. These questions are diverse and demand an interdisciplinary approach. Through research targeted at quantifying geographic distributions of subseafloor sedimentary respiration, rates and magnitude of microbial crustal alteration, energy sources and carbon flow, robust analyses linking subseafloor processes to global scales and to biogeochemical cycles will be possible.

Deep marine biosphere research has grown dramatically within the last decade; state-of-the art molecular and microscopic tools are being applied to challenging environmental settings, and there is greater coordination among engineers, biologists, geochemists, and geophysicists. We are on the verge of going beyond isolated observations to quantifying biogeochemical processes in the deep subsurface, understanding the physiological capabilities of uncultured organisms, and using the seafloor as our laboratory. While such efforts can be resource-intensive, they represent a tremendous opportunity for discovery. We should conscientiously and carefully focus our resources in this regard. This review is intended to frame the key ecological influences upon subseafloor microbial populations, in order to aid in the investigation of this highly important yet highly challenging ecosystem.

Table 1 Physical and chemical characteristics of potential biomes in the subseafloor

Province/biome	**Examples**	**120° C isotherm mbsf**[a]	**TOC**[b] **Wt %**	**electron donors**	**TEA**[c]
Mid-ocean ridges					
fast and intermediate spreading	East Pacfic Rise, Juan de Fuca Ridge, Axial Seamount, Central Indian Ridge	< 10	low	H_2, H_2S, CH_4	O_2, NO_3^-, SO_4^{2-}
slow and ultraslow spreading	Mid Atlantic Ridge, Gakkel Ridge Southwest Indian Ridge	10 - 1000	low	H_2, Fe^{2+}, CH_4	O_2, NO_3^-, SO_4^{2-}
sedimented	Guaymas Basin, Middle Valley	<100	high	OM[d], H_2, H_2S, CH_4, NH_4^+	NO_3^-, SO_4^{2-}
Ridge flank					
young crust (<10 Ma)	Baby Bare Seamount	10 - 1000	low	OM, H_2, NH_4^+	O_2, NO_3^-, SO_4^{2-}
old crust (10 - 65 Ma)	various	<1000	low	H_2, H_2S, Fe^{2+}	O_2, NO_3^-, SO_4^{2-}
core complexes	Lost City Field	<1000	low	H_2, H_2S	SO_4, Fe^{3+}
Island arc system					
deep-sea trench	Marianas Trench	>3000	mod.	OM	O_2, NO_3^-
forearc/volcanic arc	Suiyo Seamount; Chamorro Seamount; Nankai Trough	10 - 1000	mod.	H_2, H_2S, CH_4	O_2, NO_3^-, SO_4^{2-}
backarc spreading center	Lau Basin, Manus Basin	<100		H_2, H_2S	NO_3^-, SO_4^{2-}
Abyssal plain					
open ocean-sediments	South Pacific Gyre, Equatorial Pacific	>1000	0.09 - 0.52	H_2	O_2, NO_3^-, SO_4^{2-}
open ocean- crustal	North Pond, South Pacific Gyre	>1000	low	Fe^{2+}, Mn^{2+}	NO_3^-
Ocean island volcanoes					
	Loihi Seamount, Vailulu'u Seamount	<100	low	Fe^{2+}, Mn^{2+}	O_2, NO_3^-
Active continental margin					
accretionary wedge	Cascadia Margin, Peru Margin	>3000	1.5	OM, H_2, CH_4	O_2, NO_3^-, SO_4^{2-}, CO_2
Passive continental margin					
continental slope	Newfoundland Margin, Namibia	>1700	high	OM, CH_4	O_2, NO_3^-, SO_4^{2-}, CO_2
continental shelf	Gulf of Mexico, Blake Ridge	>3000	0.8 - 1.4	OM, CH_4	O_2, NO_3^-, SO_4^{2-}, CO_2

[a] meters below the seafloor; [b] Total Organic Carbon; [c] terminal electron acceptor; [d] organic matter

REFERENCES

Bach W, Humphris SE, Fisher AT. 2003. Water-rock reactions and fluid flow in the oceanic crust: reconciling geological, geochemical and geophysical observations. In *The Subseafloor Biosphere at Mid-Ocean Ridges, Geophysical Monograph Series*, ed. WD Wilcock, DS Kelley, EF DeLong, C Cary. Washington, DC: AGU

Banerjee NR, Muehlenbachs K. 2003. Tuff life: Bioalteration in volcaniclastic rocks from the Ontong Java Plateau. *Geochemistry, Geophysics, Geosystems* 4: 1037

Biddle JF, Fitz-Gibbon S, Schuster SC, Brenchley JE, House CH. 2008. Metagenomic signatures of the Peru Margin subseafloor biosphere show a genetically distinct environment. *Proceedings of the National Academy of Sciences of the United States of America* 105: 10583-88

Corliss JB, Dymond J, Gordon LI, Edmond JM, von Herzen RP, et al. 1979. Submarine thermal springs on the Galapagos Rift. *Science* 203: 1073-83

Cowen JP, Giovannoni SJ, Kenig F, Johnson HP, Butterfield D, et al. 2003. Fluids from aging oceanic crust that support microbial life. *Science* 299: 120-23

D’Hondt S, Spivack AJ, Pockalny R, Ferdelman T, Fischer J, et al. 2009. Subseafloor sedimentary life in the South Pacific Gyre. *Proceedings of the National Academy of Sciences of the United States of America* in press

de Ronde EJ, G.J.Massoth, E.T.Baker, J.E.Lupton. 2003. Submarine hydrothermal venting related to volcanic arcs *Soc.Econ.Geol.Spec.Pub.* 10: 91-110

DeLong EF, Yayanos AA. 1985. Adaptation of the membrane lipids of a deep-sea bacterium to changes in hydrostatic pressure. *Science* 228: 1101-03

Edwards KJ, Bach W, McCollom TM. 2005. Geomicrobiology in oceanography: microbe-mineral interactions at and below the seafloor. *Trends in Microbiology* 13: 449-56

Embley R, Baker E, Chadwick W, Lupton JE, Resing JA, et al. 2004. Explorations of Mariana arc volcanoes reveal new hydrothermal systems. *EOS, Transactions of the American Geophysical Union* 85

Embley RW, Hobart MA, al. e. 1983. Anomalous heat flow in the northwest Atlantic: A case for continued hydrothermal circulation in 80-M.Y. crust. *Journal of Geophysical Research* 88: 1067-74

Fisher AT, Urabe T, Klaus A, and the Expedition 301 Project Team. 2004. Juan de Fuca Hydrogeology—The hydrogeologic architecture of basaltic oceanic crust: compartmentalization, anisotropy, microbiology, and crustal-scale properties on the eastern flank of Juan de Fuca Ridge, eastern Pacific Ocean. *IODP Sci Prosp* 301: doi:10.2204/iodp.sp.301.004

Fisk MR, Giovannoni SJ, Thorseth IH. 1998. Alteration of oceanic volcanic glass: textural evidence of microbial activity. *Science* 281: 978-80

Fry JC, Parkes RJ, Cragg BA, Weightman AJ, Webster G. 2008. Prokaryotic biodiversity and activity in the deep subseafloor biosphere. *FEMS Microbiology Ecology* 66: 181-96

Hillier JK, Watts AB. 2007. Global distribution of seamounts from ship-track bathymetry data. *Geophysical Research Letters* 34: L13304

Holden JF, Daniel RM. 2004. Upper temperature limit of life based on hyperthermophile culture experiments and field observations. In *The Subseafloor Biosphere at Mid-ocean Ridges*, ed. WSD Wilcock, EF DeLong, DS Kelley, JA Baross, SC Cary, pp. 13-24. Washington, D.C.: American Geophysical Union

Huber JA, Johnson HP, Butterfield DA, Baross JA. 2006. Microbial life in ridge flank crustal fluids. *Environmental Microbiology* 8: 88-99

Inagaki F, Nunoura T, Nakagawa S, Teske A, Lever M, et al. 2006. Biogeographical distribution and diversity of microbes in methane hydrate bearing marine sediments on the Pacific Ocean Margin. *Proceedings of the National Academy of Sciences of the United States of America* 103: 2815-20

Ishibashi J-I, Urabe T. 1995. Hydrothermal activity related to arc-backarc magmatism in the western Pacific. In *Backarc Basins;Tectonics and Magmatism*, ed. B Taylor, pp. 451-95. New York: Plenum Press

Jørgensen BB, Boetius A. 2007. Feast and famine - microbial life in the deep-sea bed. *Nature Reviews in Microbiology* 5: 770-81

Kelley DS, Karson JA, Früh-Green GL, Yoerger DR, Shank TM, et al. 2005. A serpentinite-hosted ecosystem: The Lost City Hydrothermal Field. *Science* 307: 1428-34

Lupton J, al. e. 2006. Submarine venting of liquid carbon dioxide on a Mariana Arc volcano, . *Geochemistry, Geophysics, Geosystems* 7: Q08007

Marteinsson VT, Moulin P, Birrien J-L, Gambacorta A, Vernet M, Prieur D. 1997. Physiological responses to stress conditions and barophilic behavior of the hyperthermophilic vent archaeon *Pyrococcus abyssi*. *Applied and Environmental Microbiology* 63: 1230-36

Parkes RJ, Cragg BA, Bale SJ, Getliff JM, Goodman K, et al. 1994. Deep bacterial biosphere in Pacific Ocean sediments. *Nature* 371: 410-13

Parkes RJ, Webster G, Cragg BA, Weightman AJ, Newberry CJ, et al. 2005. Deep sub-seafloor prokaryotes stimulated at interfaces over geological time. *Nature* 436: 390-94

Schippers A, Neretin LN, Kallmeyer J, Ferdelman TJ, Cragg BA, et al. 2005. Prokaryotic cells of the deep sub-seafloor biosphere identified as living bacteria. *Nature* 433: 861-64

ZoBell CE. 1952. Bacterial life at the bottom of the Phillippine Trench. *Science* 115: 507-08