

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Inagaki, F., and A. Taira. 2019. Future opportunities in scientific ocean drilling: Illuminating planetary habitability. *Oceanography* 32(1):212–216, <https://doi.org/10.5670/oceanog.2019.148>.

DOI

<https://doi.org/10.5670/oceanog.2019.148>

PERMISSIONS

Oceanography (ISSN 1042-8275) is published by The Oceanography Society, 1 Research Court, Suite 450, Rockville, MD 20850 USA. ©2019 The Oceanography Society, Inc. Permission is granted for individuals to read, download, copy, distribute, print, search, and link to the full texts of *Oceanography* articles. Figures, tables, and short quotes from the magazine may be republished in scientific books and journals, on websites, and in PhD dissertations at no charge, but the materials must be cited appropriately (e.g., authors, *Oceanography*, volume number, issue number, page number[s], figure number[s], and DOI for the article).

Republication, systemic reproduction, or collective redistribution of any material in *Oceanography* is permitted only with the approval of The Oceanography Society. Please contact Jennifer Ramarui at info@tos.org.

Permission is granted to authors to post their final pdfs, provided by *Oceanography*, on their personal or institutional websites, to deposit those files in their institutional archives, and to share the pdfs on open-access research sharing sites such as ResearchGate and Academia.edu.

Future Opportunities in Scientific Ocean Drilling

ILLUMINATING PLANETARY HABITABILITY

By Fumio Inagaki and Asahiko Taira

ABSTRACT. Over the past several decades, scientific ocean drilling has significantly expanded our knowledge of life and Earth. The discovery of deep microbial life and its ecosystems beneath the ocean floor suggests that subseafloor microbial ecosystems may have uniquely co-evolved in association with Earth dynamics, and this inevitable interrelationship has shaped planetary habitability for more than 3 billion years. In the future, scientific ocean drilling—from the surface to drilling’s accessible limit in the upper mantle—will permit a better understanding of what is life, why we are here, and what are the possible trajectories of our planet’s habitability and its sustainability as well as that of other celestial bodies in the universe.

INTRODUCTION

Despite several catastrophic perturbations during its history, Earth has nevertheless remained habitable. There are many unknowns and mysteries about the origins and evolution of life and Earth. No less mysterious is how Planet Earth and its life will co-evolve and develop sustainably in the future. How will life (from microbes to humans) adapt and transform in response to future environmental changes? How will life continue to shape Earth? How can we decipher “planetary habitability” and illuminate the sustainability of life on our planet and beyond?

To date, we recognize through challenging missions to many frontiers of Earth’s extreme environments that even in dark and energetically challenging conditions, intraterrestrial ecosystems have adapted and evolved and persisted over billions of years. One of the main tools for deciphering this past co-evolution is analysis of samples collected at deeply drilled sites. Expanding our knowledge of the ocean-Earth-life system through scientific ocean drilling

inspires new insights into the essence of planetary habitability—down to Earth’s upper mantle, which for today’s drilling technology is the deepest accessible limit. Such explorations will lead to an understanding of how and why life emerged on our planet, as well as an estimate (prediction) of the possible trajectories of life on Earth. They will also provide hints as to whether life persists on other celestial bodies, and which ones are the most likely to be habitable and even inhabited.

DEEP BIOSPHERE FRONTIERS

Over recent decades, materials recovered through scientific ocean drilling have led to the discovery of microbial life in deep-sea sediment and in Earth’s oceanic crust. The latest estimate of global subseafloor microbial abundance is $\sim 10^{29}$ cells, accounting for 4 Gt of carbon biomass on Earth (Lipp et al., 2008; Hinrichs and Inagaki, 2012; Kallmeyer et al., 2012; Parkes et al., 2014; [Figure 1](#)). DNA-based molecular investigations have revealed that diverse, but previously unknown, microbial species (in three domains of life: Bacteria, Archaea, and Eukarya) are

present in the deep subseafloor sedimentary biosphere, where they have evolved differently from microbes living in Earth’s surface biosphere (e.g., Biddle et al., 2006, 2008; Inagaki et al., 2006; Fry et al., 2008; Orsi et al., 2013; Ciobanu et al., 2014). Using a microfluidic digital polymerase chain reaction (PCR) technique applied to 300 deep-frozen sediment core samples, Hoshino and Inagaki (2019) demonstrated that archaeal cells constitute 37.3% of total subseafloor sedimentary cells (i.e., 1.1×10^{29} archaeal cells). This comprises a biomass comparable to the estimated archaeal biomass in the global ocean of 41.9% (Karner et al., 2001).

The activity of subseafloor microbial communities is generally extraordinarily low (Hoehler and Jørgensen, 2013; D’Hondt et al., 2004, 2015). In fact, extensive research into deep life using culture-dependent as well as culture-independent molecular and isotopic analyses demonstrates that many sedimentary microbes are alive and can be revived after persisting in low-energy subseafloor habitats over geologic time (Morono et al., 2011; Trembath-Reichert et al., 2017). Their “ultra-slow life” processes and strategies for long-term survival beneath the ocean—and even below its thick ocean sediment blanket—may have affected global biogeochemical element cycles (D’Hondt et al., 2002; Lever et al., 2013; Bowles et al., 2014).

Biogeographical models and simulation studies show that up to 37% of the global subseafloor sedimentary

environment is completely oxic, and thus that aerobic microbial life inhabits the entire sediment column from the seafloor down to the sediment-basement interface. These microbes have not fully consumed the available organic matter or the dissolved oxygen (D'Hondt et al., 2015; Estes et al., 2019; see also Orcutt et al., 2012), suggesting that there are no limits to subseafloor life in open-ocean sedimentary environments, and that the subseafloor sedimentary microbial ecosystems have developed an eco-physiological mode of persistence and survival over geologic time. In addition, ultra-slow metabolic activities (although we don't know the details yet), as well as their end products—dead biomass (i.e., necromass, detrital proteins), spores, and even viruses—may play significant ecological and evolutionary roles in Earth's deep biosphere (Lomstein et al., 2012; Lloyd et al., 2013; Engelhardt et al., 2014; Wörmer et al., 2019). Consequently, the deep subseafloor biosphere is possibly an important driver of element transformation and cycling between Earth's lithosphere, hydrosphere, and atmosphere.

THE LIMITS OF DEEP LIFE AND THE BIOSPHERE

To date, microbial life has been observed down to ~2.5 km below the seafloor on Pacific margins in organic-rich anaerobic sedimentary environments (Ciobanu et al., 2014; Inagaki et al., 2015). Multiple lines of analytical evidence from samples recovered in 2012 by the riser drilling vessel *Chikyu* during Integrated Ocean Drilling Program Expedition 337 “Deep Coalbed Biosphere off Shimokita” revealed that deeply buried microbial communities have played biogeochemical roles in carbon and other elemental cycling for millions of years, despite their extraordinarily slow metabolic activity. For example, using a stable isotope-probing nanometer-scale secondary ion mass spectrometry technique (SIP-NanoSIMS), it was demonstrated that indigenous bacteria slowly utilize methyl compounds in 20-million-year-old coal and shale beds at 2 km depth (Inagaki et al., 2015; Trembath-Reichert et al., 2017; Figure 2). Interestingly, the diversity of microbial communities in these deeply buried coal-associated habitats

was found to be very different from commonly observed subseafloor sedimentary microbes. In fact, they resemble anaerobic terrestrial communities living in peat or forest soil and can be cultivated by using down-hanging sponge bioreactors (Inagaki et al., 2015; Imachi et al., 2019). Furthermore, diverse fungal species of both Ascomycota and Basidiomycota isolated from the lignite coal and shale samples resemble terrestrial wood-rotting fungal communities (Liu et al., 2017). These discoveries indicate that some of the active and revivable microorganisms are derived from the original depositional environments (referred to as “paleome”; Inagaki et al., 2006, 2012; Coolen et al., 2013; Kirkpatrick et al., 2016; Orsi et al., 2017) and persist in energy-limited sedimentary habitat over geologic time periods (Walsh et al., 2016; Jørgensen and Marshall, 2016; Starnawski et al., 2017). In addition, the deeply buried microbial cells could be transported back toward the surface through mud volcanism, which occurs globally along convergent margins, and dispersed as “deep-biosphere seeds” into the ocean (Hoshino et al., 2017; Ijiri et al., 2018). These natural seeding pipelines may be important for sustainability of deep subseafloor microbial ecosystems. But what factors limit the size, diversity, functionality, and extent of the deep subseafloor biosphere?

Recent advances in scientific ocean

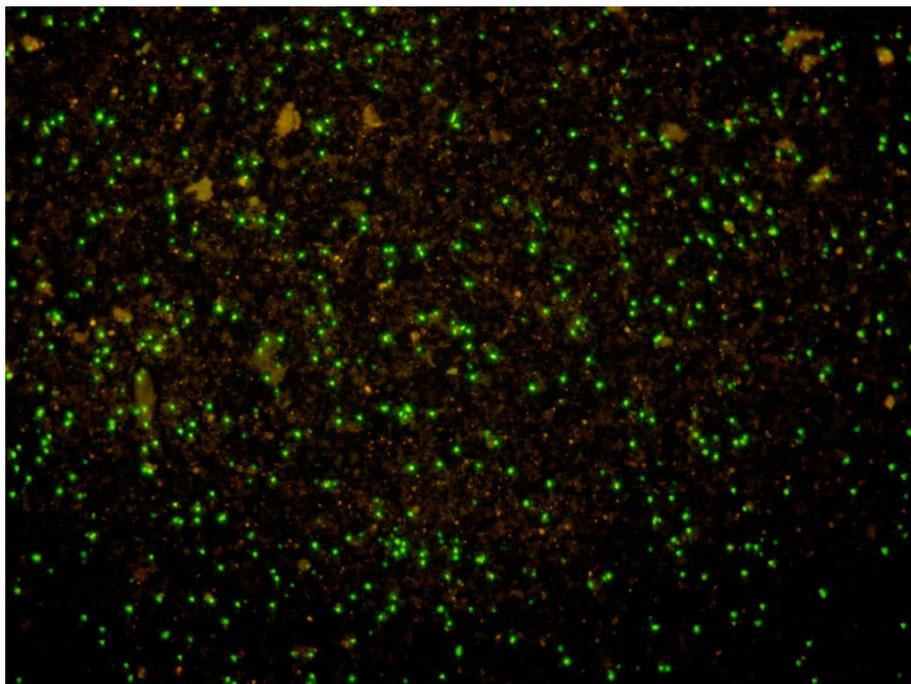


FIGURE 1. A microscopic view of microbial life in a subseafloor sediment core sample obtained during drilling vessel *Chikyu*'s shakedown expedition CK06-06 off Shimokita Peninsula, Japan. Green particles represent microbial cells, in which intracellular DNA is stained with a green fluorescent dye (Morono et al., 2009). The average cell is 200–500 nanometers in diameter. Photo credit: JAMSTEC

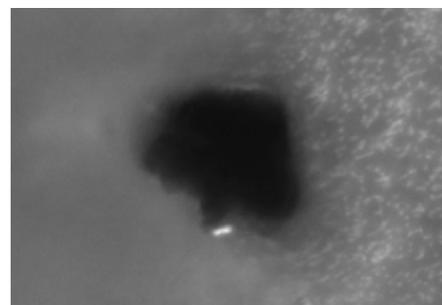


FIGURE 2. A microscopic image of a microbial cell (light blue) on a 2 km deep, 20-million-year-old lignite (coal) particle (black) obtained during *Chikyu*'s Integrated Ocean Drilling Program Expedition 337 (Site C0020; Inagaki et al., 2015; Trembath-Reichert et al., 2017). The microbial cell is approximately 500 nm in length. Photo courtesy of Elizabeth Trembath-Reichert, Caltech

drilling during the International Ocean Discovery Program (IODP), coupled with super-clean geomicrobiology facilities both at sea and on shore and with novel high-precision isotope geochemistry and microbiological techniques, will greatly enhance our knowledge of the limits and functionality of deep microbial life (e.g., IODP Expedition 370 “Temperature Limit of the Deep Biosphere off Muroto”; Heuer et al., 2017). To maintain essential life functions, not only geophysical constraints, such as temperature, but also the supply of water and bio-available nutrients and energy sources are crucial (Hoehler and Jørgensen, 2013; Lever et al., 2015; Jørgensen and Marshall, 2016; LaRowe et al., 2017; Ijiri et al., 2018; Tanikawa et al., 2018; Parkes et al., 2019). It may follow that this geosphere-biosphere interaction must be the essential driving force not only for Earth’s deep biosphere but also for any possible ecosystems on Mars and other celestial bodies (Dzaugis et al., 2018; Yung et al., 2018; Stamenković et al., 2019).

PLANETARY HABITABILITY AND SUSTAINABILITY

Exploring biosphere frontiers through scientific ocean drilling will elucidate how the habitable world has been established and co-evolved with Earth’s other subsystems and how the biosphere has responded to some drastic environmental changes during Earth history (see Challenge 7 in the IODP science plan for 2013–2024, available at <https://www.iodp.org/about-iodp/iodp-science-plan-2013-2023>). Traditionally, biological evolution and geological evolution have been studied separately, and as a consequence were considered to be different from each other. More recent views in geobiology and astrobiology make it clear that these two “spheres” (the biosphere and the geosphere) have systematically cooperated to evolve together for more than 3 billion years, with each adapting to and shaping the other. When rapid geological changes have occurred (e.g., asteroid impacts, oceanic anoxic events), life

has responded with mass extinctions and (sometimes a quick) recovery, and over the course of Earth history, it is estimated that 99% (or more) of all species that ever existed have gone extinct (Barnosky et al., 2011; Lowery et al., 2018). Nevertheless, it remains uncertain whether environmental perturbations have historically occurred in the deep seafloor biosphere and whether any life has ever gone extinct there.

In principle, life evolves with energy flow in Earth’s many entropy-increasing systems. But, it remains a matter of debate as to whether such co-evolution of Earth’s systems will be (more) resilient and sustainable in the future. For example, is plate tectonics absolutely required for the origin and long-term evolution of life on Earth (and other planets)? Sleep et al. (2011, 2012) suggest that CO₂ sequestration in the mantle during the Hadean was a necessary condition for making Earth’s surface environment habitable by increasing O₂ in the atmosphere through photosynthesis. But, within this context, how did Earth generate unstable forms of prebiotic molecules that polymerized and that developed the ability to recognize surroundings (and even itself) in multiple dimensions and time?

It is worth noting here that such evolutionary multisphere interactions may have occurred and likely will occur repeatedly in the future. Since the Industrial Revolution in the eighteenth century—thus, within the Anthropocene—humanity and associated economic development have resulted in serious global issues, including global warming, ocean acidification, and the subsequent ecosystem changes that will be preserved in the geologic record (Steffen et al., 2015; Waters et al., 2016). Human influences are forcing the ocean and Earth’s surface environment more than ever before, possibly with greater impacts than astronomical and geological factors like asteroids and super-volcano eruptions. What environmental factors constrained or forced co-evolution of life and Earth in the past and will do so in the present and the

future? How is Earth’s deep biosphere energetically connected to the dynamics of other subsystems? And how does humanity understand these (developing) threats to our planetary habitability and utilize this knowledge for developing a sustainable ocean-Earth-life system in the future?

EXPLORING EARTH’S MANTLE THROUGH SCIENTIFIC OCEAN DRILLING

Understanding and predicting the evolution of life (including humanity) and its effect on the ocean-Earth-life system has long been challenging. To tackle these issues important to science and human society, we need to strengthen both basic and applied sciences in a transdisciplinary and global manner. Our core understanding of planetary habitability can be enhanced only by collecting multidisciplinary observations and by finding patterns through scientific exploration. Core-log-seismic-observatory-experimentation plays an integral part in this mission to help unravel anticipated natural behaviors as well as any possible global anthropogenic consequences in the future. For example, during Earth history, biosphere activity (including surface photosynthesis and subsurface microbial activity) has significantly modified the redox state of the crust and mantle (Sleep et al., 2012; Bell et al., 2015; D’Hondt et al., 2015). These geosphere-biosphere interactions may have created various redox-sensitive minerals in the surface and subsurface and at any major boundary, which may be necessary for the diversification of both life and minerals (Hazen et al., 2008). CO₂ in both the hydrosphere and the atmosphere has been continuously sequestered in (ultra) mafic rocks, and the carbonates trapped within the oceanic crust are expected to return to the deep mantle at subduction zones. Even though the modern Earth is much cooler than the ancient, such systematic natural reactions and recycling of elements still continuously occur and evolve along with humanity and the

biosphere. Deep drilling into the ocean's thick accumulations of sediment and into other ocean regions provides an opportunity to study the vast history of and potential for the development of sustainable ocean-Earth-life systems.

Large gaps in our knowledge of the habitability of our own planet remain. Systematic understanding of “habitability dynamics” on Earth can only be addressed by scientific ocean drilling and through collecting long-term observations of the interactions of these multi-spheres. Scientific ocean drilling using *Chikyu* to drill down to the upper mantle—all the way through the Mohorovičić discontinuity (or Moho) as recognized in geophysical data—will deepen our knowledge of planetary habitability and its sustainability (Figure 3). Other example targets include geosphere-biosphere co-evolution along a transect from mid-ocean spreading ridge hydrothermal systems to the aerobic and stable open ocean lithosphere, as well as co-evolution in subduction zones where seawater penetrates the overriding plate and serpentinization occurs with increasing temperature and pressure. Continued international, transdisciplinary collaborations among the scientific ocean drilling community will help us to illuminate the trajectory of life and humanity with Earth's planetary system from deep geologic time to the present, and into the near future, and the deep future. 📷

REFERENCES

- Barnosky, A.D., N. Matzke, S. Tomiya, G.O.U. Wogan, B. Swartz, T.B. Quental, C. Marshall, J.L. McGuire, E.E. Lindsey, K.C. Maguire, and others. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471(7336):51–57, <https://doi.org/10.1038/nature09678>.
- Bell, E.A., P. Boehnke, T.M. Harrison, and W.L. Mao. 2015. Potentially biogenic carbon preserved in a 4.1 billion-year-old zircon. *Proceedings of the National Academy of Sciences of the United States of America* 112(47):14,518–14,521, <https://doi.org/10.1073/pnas.1517557112>.
- Biddle, J.F., J.S. Lipp, M.A. Lever, K.G. Lloyd, K.B. Sørensen, R. Anderson, H.F. Fredricks, M. Elvert, T.J. Kelly, D.P. Schrag, and others. 2006. Heterotrophic Archaea dominate sedimentary subsurface ecosystems off Peru. *Proceedings of the National Academy of Sciences of the United States of America* 103(10):3,846–3,851, <https://doi.org/10.1073/pnas.0600035103>.
- Biddle, J.F., S. Fitz-Gibbon, S.C. Schuster, J.E. Brenchley, and C.H. House. 2008. Metagenomic signatures of the Peru Margin subsurface biosphere show a genetically distinct environment. *Proceedings of the National Academy of Sciences of the United States of America* 105(30):10,583–10,588, <https://doi.org/10.1073/pnas.0709942105>.
- Bowles, M.W., J.M. Mogollón, S. Kasten, M. Zabel, and K.-U. Hinrichs. 2014. Global rates of marine sulfate reduction and implications for sub-sea-floor metabolic activities. *Science* 344(6186):889–891, <https://doi.org/10.1126/science.1249213>.
- Ciobanu, M.-C., G. Burgaud, A. Dufresne, A. Breuker, V. Rédou, S.S. Maamar, F. Gaboyer, O. Vandenabeele-Trambouze, J.S. Lipp, A. Schippers, and others. 2014. Microorganisms persist at record depths in the subsurface of the Canterbury Basin. *The ISME Journal* 8(7):1,370–1,380, <https://doi.org/10.1038/ismej.2013.250>.
- Coolen, M.J., W.D. Orsi, C. Balkema, C. Quince, K. Harris, S.P. Sylva, M. Filipova-Marinova, and L. Giosan. 2013. Evolution of the plankton paleome in the Black Sea from the Deglacial to Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America* 110(21):8,609–8,614, <https://doi.org/10.1073/pnas.1219283110>.
- D'Hondt, S., S. Rutherford, and A.J. Spivack. 2002. Metabolic activity of subsurface life in deep-sea sediments. *Science* 295(5562):2,067–2,070, <https://doi.org/10.1126/science.1064878>.
- D'Hondt, S., B.B. Jørgensen, D.J. Miller, A. Batzke, R. Blake, B.A. Cragg, H. Cypionka, G.R. Dickens, T. Ferdelman, K.-U. Hinrichs, and others. 2004. Distributions of microbial activities in deep subsurface sediments. *Science* 306(5705):2,216–2,221, <https://doi.org/10.1126/science.1101155>.
- D'Hondt, S., F. Inagaki, C.A. Zarikian, L.J. Abrams, N. Dubois, T. Engelhardt, H. Evans, T. Ferdelman, B. Gribsholt, R.N. Harris, and others. 2015. Presence of oxygen and aerobic communities from seafloor to basement in deep-sea sediment. *Nature Geoscience* 8:299–304, <https://doi.org/10.1038/ngeo2387>.
- Dzaugis, M., A.J. Spivack, and S. D'Hondt. Radiolytic H₂ production in Martian environments. *Astrobiology* 18(9):1,137–1,146, <https://doi.org/10.1089/ast.2017.1654>.
- Engelhardt, T., J. Kallmeyer, H. Cypionka, and B. Engelen. 2014. High virus-to-cell ratios indicate ongoing production of viruses in deep subsurface sediments. *The ISME Journal* 8:1,503–1,509, <https://doi.org/10.1038/ismej.2013.245>.
- Estes, E.R., R. Pockalny, S. D'Hondt, F. Inagaki, Y. Morono, R.W. Murray, D. Nordlund, A.J. Spivack, S.D. Wankel, N. Xiao, and C.M. Mansel. 2019. Persistent organic matter in oxic subsurface sediment. *Nature Geoscience* 12(2):126–131, <https://doi.org/10.1038/s41561-018-0291-5>.
- Fry, J.C., R.J. Parkes, B.A. Cragg, A.J. Weightman, and G. Webster. 2008. Prokaryotic biodiversity and activity in the deep subsurface biosphere. *FEMS Microbiology Ecology* 66(2):181–196, <https://doi.org/10.1111/j.1574-6941.2008.00566.x>.
- Hazen, R.M., D. Papineau, W. Bleeker, R.T. Downs, J.M. Ferry, T.J. McCoy, D.A. Sverjensky, and H. Yang. 2008. Mineral evolution. *American Mineralogist* 93:1,693–1,720, <https://doi.org/10.2138/am.2008.2955>.
- Heuer, V.B., F. Inagaki, Y. Morono, Y. Kubo, L. Maeda, and the Expedition 370 Scientists. 2017. *Expedition 370 Preliminary Report: Temperature Limit of the Deep Biosphere off Muroto*. International Ocean Discovery Program, College Station, TX, <https://doi.org/10.14379/iodp.pr.370.2017>.
- Hinrichs, K.-U., and F. Inagaki. 2012. Downsizing the deep biosphere. *Science* 338(6104):204–205, <https://doi.org/10.1126/science.1229296>.
- Hoehler, T.M., and B.B. Jørgensen. 2013. Microbial life under extreme energy limitation. *Nature Reviews Microbiology* 11:88–94, <https://doi.org/10.1038/nrmicro2939>.
- Hoshino, T., T. Toki, A. Ijiri, Y. Morono, H. Machiyama, J. Ashi, K. Okamura, and F. Inagaki. 2017. *Atribacteria* from the subsurface sedimentary biosphere disperse to the hydrosphere through submarine mud volcanoes. *Frontiers in Microbiology* 8:1135, <https://doi.org/10.3389/fmicb.2017.01135>.
- Hoshino, T., and F. Inagaki. 2019. Abundance and distribution of Archaea in the subsurface sedimentary biosphere. *The ISME Journal* 13:227–231, <https://doi.org/10.1038/s41396-018-0253-3>.
- Ijiri, A., F. Inagaki, Y. Kubo, R.R. Adhikari, S. Hattori, T. Hoshino, H. Imachi, S. Kawagucci, Y. Morono, Y. Ohtomo, and others. 2018. Deep-biosphere



FIGURE 3. The deep-Earth drilling research vessel *Chikyu*. Photo credit: JAMSTEC

- methane production stimulated by geofluids in the Nankai accretionary complex. *Science Advances* 4(6):eaao4631, <https://doi.org/10.1126/sciadv.aao4631>.
- Imachi, H., E. Tasumi, Y. Takaki, T. Hoshino, F. Schubotz, S. Gan, T.-H. Tu, Y. Saito, Y. Yamanaka, A. Ijiri, and others. 2019. Cultivable microbial community in 2-km-deep, 20-million-year-old subseafloor coalbeds through ~1000 days anaerobic bioreactor cultivation. *Scientific Reports* 9:2305, <https://doi.org/10.1038/s41598-019-38754-w>.
- Inagaki, F., T. Nunoura, S. Nakagawa, A. Teske, M. Lever, A. Lauer, M. Suzuki, K. Takai, M. Delwiche, F.S. Colwell, and others. 2006. Biogeographical distribution and diversity of microbes in methane hydrate-bearing deep marine sediments on the Pacific Ocean Margin. *Proceedings of the National Academy of Sciences of the United States of America* 103(8):2,815–2,820, <https://doi.org/10.1073/pnas.0511033103>.
- Inagaki, F., H. Okada, A.I. Tsapin, and K.H. Nealson. 2012. The paleome: A sedimentary genetic record of past microbial communities. *Astrobiology* 5(2):141–153, <https://doi.org/10.1089/ast.2005.5.141>.
- Inagaki, F., K.-U. Hinrichs, Y. Kubo, M.W. Bowles, V.B. Heuer, W.-L. Long, T. Hoshino, A. Ijiri, H. Imachi, M. Ito, and others. 2015. Exploring deep microbial life in coal-bearing sediment down to ~2.5 km below the ocean floor. *Science* 349(6246):420–424, <https://doi.org/10.1126/science.aaa6882>.
- Jørgensen, B.B., and I.P. Marshall. 2016. Slow microbial life in the seabed. *Annual Review of Marine Science* 8:311–332, <https://doi.org/10.1146/annurev-marine-010814-015535>.
- Kallmeyer, J., R. Pockalny, R.R. Adhikari, D.C. Smith, and S. D'Hondt. 2012. Global distribution of microbial abundance and biomass in subseafloor sediment. *Proceedings of the National Academy of Sciences of the United States of America* 109(40):16,213–16,216, <https://doi.org/10.1073/pnas.1203849109>.
- Karner, M.B., E.F. DeLong, and D.M. Karl. 2001. Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature* 409(6819):507–510, <https://doi.org/10.1038/35054051>.
- Kirkpatrick, J.B., E.A. Walsh, and S. D'Hondt. 2016. Fossil DNA persistence and decay in marine sediment over hundred-thousand-year to million-year time scales. *Geology* 44(8):615–618, <https://doi.org/10.1130/G37933.1>.
- LaRowe, D.E., E. Burwicz, S. Arndt, A.W. Dale, and J.P. Amend. 2017. Temperature and volume of global marine sediments. *Geology* 45(3):275–278, <https://doi.org/10.1130/G38601.1>.
- Lever, M.A., O. Rouxel, J.C. Alt, N. Shimizu, S. Ono, R.M. Coggon, W.C. Shanks III, L. Lapham, M. Elvert, X. Prieto-Mollar, and others. 2013. Evidence for microbial carbon and sulfur cycling in deeply buried ridge flank basalt. *Science* 339(6125):1,305–1,308, <https://doi.org/10.1126/science.1229240>.
- Lever, M.A., K.L. Rogers, K.G. Lloyd, J. Overmann, B. Schink, R.K. Thauer, T.M. Hoehler, and B.B. Jørgensen. 2015. Life under extreme energy limitation: A synthesis of laboratory- and field-based investigations. *FEMS Microbiology Review* 39(5):688–728, <https://doi.org/10.1093/femsre/fuv020>.
- Liu, C.-H., X. Huang, T.-X. Nie, N. Duan, Y.-R. Xue, T.-X. Zhao, M.A. Lever, K.-U. Hinrichs, and F. Inagaki. 2017. Exploration of cultivable fungal communities in deep coal-bearing sediments from ~1.3 to 2.5 km below the ocean floor. *Environmental Microbiology* 19(2):803–818, <https://doi.org/10.1111/1462-2920.13665>.
- Lipp, J.S., Y. Morono, F. Inagaki, and K.-U. Hinrichs. 2008. Significant contribution of Archaea to extant biomass in marine subsurface sediments. *Nature* 454:991–994, <https://doi.org/10.1038/nature07174>.
- Lloyd, K.G., L. Schreiber, D.G. Petersen, K.U. Kjeldsen, M.A. Lever, A.D. Steen, R. Stepanauskas, M. Richter, S. Kleindienst, S. Lenk, and others. 2013. Predominant archaea in marine sediments degrade detrital proteins. *Nature* 496(7444):215–218, <https://doi.org/10.1038/nature12033>.
- Lomstein, B.A., A.T. Langerhuus, S. D'Hondt, B.B. Jørgensen, and A.J. Spivack. 2012. Endospore abundance, microbial growth and necromass turnover in deep sub-seafloor sediment. *Nature* 484:101–104, <https://doi.org/10.1038/nature10905>.
- Lowery, C.M., T.J. Bralower, J.D. Owens, F.J. Rodríguez-Tovar, H. Jones, J. Smit, M.T. Whalen, P. Claeys, K. Farley, S.P.S. Gulick, and others. 2018. Rapid recovery of life at ground zero of the end-Cretaceous mass extinction. *Nature* 558(7709):288–291, <https://doi.org/10.1038/s41586-018-0163-6>.
- Morono, Y., T. Terada, N. Masui, and F. Inagaki. 2009. Discriminative detection and enumeration of microbial life in marine subsurface sediments. *The ISME Journal* 3(5):503–511, <https://doi.org/10.1038/ismej.2009.1>.
- Morono, Y., T. Terada, M. Nishizawa, M. Ito, F. Hillion, N. Takahata, Y. Sano, and F. Inagaki. 2011. Carbon and nitrogen assimilation in deep subseafloor microbial cells. *Proceedings of the National Academy of Sciences of the United States of America* 108(45):18,295–18,300, <https://doi.org/10.1073/pnas.1107763108>.
- Orcutt, B.N., C.G. Wheat, O. Rouxel, S. Hulme, K.J. Edwards, and W. Bach. 2012. Oxygen consumption rates in subseafloor basaltic crust derived from a reaction transport model. *Nature Communications* 4:2539, <https://doi.org/10.1038/ncomms3539>.
- Orsi, W., J.F. Biddle, and V. Edgcomb. 2013. Deep sequencing of subseafloor eukaryotic rRNA reveals active fungi across marine subsurface provinces. *PLoS ONE* 8(2):e56335, <https://doi.org/10.1371/journal.pone.0056335>.
- Orsi, W.D., M.J.L. Coolen, C. Wuchter, L. He, K.D. More, X. Irigoien, G. Chust, C. Johnson, J.D. Hemingway, M. Lee, and others. 2017. Climate oscillations reflected within the microbiome of Arabian Sea sediments. *Scientific Reports* 7:6040, <https://doi.org/10.1038/s41598-017-05590-9>.
- Parkes, R.J., B. Cragg, E. Roussel, G. Webster, A. Weightman, and H. Sass. 2014. A review of prokaryotic populations and processes in sub-seafloor sediments, including biosphere:geosphere interactions. *Marine Geology* 352:409–425, <https://doi.org/10.1016/j.margeo.2014.02.009>.
- Parkes, R.J., S. Berlandis, E.G. Roussel, H. Bahruji, G. Webster, A. Oldroyd, A.J. Weightman, M. Bowker, P.R. Davies, and H. Sass. 2019. Rock-crushing derived hydrogen directly supports a methanogenic community: Significance for the deep biosphere. *Environmental Microbiology Reports*, <https://doi.org/10.1111/1758-2229.12723>.
- Sleep, N.H., D.K. Bird, and E. Pope. 2011. Serpentinite and the dawn of life. *Philosophical Transactions of the Royal Society B* 366:2,857–2,869, <https://doi.org/10.1098/rstb.2011.0129>.
- Sleep, N.H., D.K. Bird, and E. Pope. 2012. Paleontology of Earth's mantle. *Annual Review of Earth and Planetary Sciences* 40:277–300, <https://doi.org/10.1146/annurev-earth-092611-090602>.
- Stamenković, V., L.W. Beegle, K. Zacny, D.D. Arumugam, P. Baglioni, N. Barba, J. Baross, M.-S. Bell, R. Bhartia, J.G. Blank, and others. 2019. The next frontier for planetary and human exploration. *Nature Astronomy* 3(2):116–120, <https://doi.org/10.1038/s41550-018-0676-9>.
- Starnawski, P., T. Bataillon, T.J.G. Ettema, L.M. Jochum, L. Schreiber, X. Chena, M.A. Lever, M.F. Polz, B.B. Jørgensen, A. Schramm, and K.U. Kjeldsen. 2017. Microbial community assembly and evolution in subseafloor sediment. *Proceedings of the National Academy of Sciences of the United States of America* 114(11):2,940–2,945, <https://doi.org/10.1073/pnas.1614190114>.
- Steffen, W., W. Broadgate, L. Deutsch, O. Gaffney, and C. Ludwig. 2015. The trajectory of the Anthropocene: The Great Acceleration. *The Anthropocene Review* 2(1):81–98, <https://doi.org/10.1177/2053019614564785>.
- Tanikawa, W., O. Tadai, Y. Morono, K.-U. Hinrichs, and F. Inagaki. 2018. Geophysical constraints on microbial biomass in subseafloor sediments and coal seams down to 2.5 km off Shomokita Peninsula, Japan. *Progress in Earth and Planetary Science* 5:58, <https://doi.org/10.1186/s40645-018-0217-2>.
- Trembath-Reichert, E., Y. Morono, A. Ijiri, T. Hoshino, K.S. Dawson, F. Inagaki, and V.J. Orphan. 2017. Methyl-compound use and slow growth characterize microbial life in 2-km-deep subseafloor coal and shale beds. *Proceedings of the National Academy of Sciences of the United States of America* 114(44):E9206–E9215, <https://doi.org/10.1073/pnas.1707525114>.
- Walsh, E.A., J.B. Kirkpatrick, S.D. Rutherford, D.C. Smith, M. Sogin, and S. D'Hondt. 2016. Bacterial diversity and community composition from seafloor to subseafloor. *The ISME Journal* 10(4):979–989, <https://doi.org/10.1038/ismej.2015.175>.
- Waters, C.N., J. Zalasiewicz, C. Summerhayes, A.D. Barnosky, C. Poirier, A. Gałuszka, A. Cearreta, M. Edgeworth, E.C. Ellis, M. Ellis, and others. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351(6269):aad2622, <https://doi.org/10.1126/science.aad2622>.
- Wörmer, L., T. Hoshino, M.W. Bowles, B. Viehweger, R.R. Adhikari, N. Xiao, G.-I. Uramoto, Y. Morono, F. Inagaki, and K.-U. Hinrichs. 2019. Microbial dormancy in the marine subsurface: Global endospore abundance and response to burial. *Science Advances* 5(2):eaav1024, <https://doi.org/10.1126/sciadv.aav1024>.
- Yung, Y.L., P. Chen, K. Nealson, S. Atreya, P. Beckett, J.G. Blank, B. Ehlmann, J. Eiler, G. Etiope, J.G. Ferry, and others. 2018. Methane on Mars and habitability: Challenges and responses. *Astrobiology* 18(10):1,221–1,242, <https://doi.org/10.1089/ast.2018.1917>.

ACKNOWLEDGMENTS

The authors are grateful to the numerous people involved in the first 50 years of scientific ocean drilling. We thank Steven D'Hondt, Kai-Uwe Hinrichs, Tori M. Hoehler, Bo Barker Jørgensen, Anthony Koppers, Shinichi Kuramoto, Judith A. McKenzie, Takashi Nakagawa, Kenneth H. Nealson, Victoria J. Orphan, Donald Pan, Barbara Sherwood Lollar, Michiyo Shimamura, Mitch L. Sogin, Vlada Stamenković, Kiyoshi Suyehiro, Shino Suzuki, Elizabeth Trembath-Reichert, and Yasuhiro Yamada for constructive discussions that improved the manuscript.

AUTHORS

Fumio Inagaki (inagaki@jamstec.go.jp) is Principal Senior Scientist, and **Asahiko Taira** is President, both at the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Yokosuka, Japan.

ARTICLE CITATION

Inagaki, F., and A. Taira. 2019. Future opportunities in scientific ocean drilling: Illuminating planetary habitability. *Oceanography* 32(1):212–216, <https://doi.org/10.5670/oceanog.2019.148>.