


COMMENTARY

The heterogeneous abyss

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The abyssal seafloor, that is, ocean depths of ~3,000 to 6,000 m, is widely considered simply to be vast, featureless plains of sediment. For example, Wikipedia asserts that “abyssal plains cover more than 50% of the Earth’s surface” and “are among the flattest, smoothest, and least explored regions on Earth” (1). Featureless tracts of mud make intuitive sense since abyssal plains are formed by the deposition of thick blankets of fine-grained sediments sinking from the surface ocean or transported as turbidity currents down continental margins. In most of the abyss, especially on seafloors >10 My old, this sediment blanket is tens to thousands of meters thick (2) and seems likely to bury or smoothen most of the irregularities in seafloor crust (e.g., basalt pillows) formed at midocean spreading centers. Riehl et al. in PNAS (3) help to dispel this notion that the abyssal seafloor is featureless, providing evidence of extensive rocky habitats along transform faults in the abyss.

Scientists studying the deep sea have long known that rocky or hard substrates do occur on abyssal plains. Perhaps the best known are polymetallic (“manganese”) nodules that were discovered during the *Challenger* expedition (1872 to 1876) (4); nodules are widespread in the Pacific abyss and, to a much lesser extent, the Indian and the Atlantic Oceans (5). In some Pacific regions, nodules may cover 10 to >50% of the seafloor area, providing abundant rocky habitat (6, 7). Seamounts also provide rocky substrates at abyssal depths where their slopes and outcrops are too steep to hold sediments (8). With as many as 200,000 seamounts in the world ocean, seamounts too provide significant habitat area for hard-bottom faunas, but once again, seamounts are concentrated in the Pacific Ocean (8).

Surveys with lowered cameras, human-occupied vehicles, remotely operated vehicles, and autonomous underwater vehicles have also documented rocky outcrops at abyssal depths in all of the ocean basins, often far removed from seamounts and midocean ridges (e.g., refs. 9–11). However, the percentage of the seafloor containing these features has been difficult to quantify



Fig. 1. Hard substrates at the abyssal seafloor provide habitat for a poorly known fauna, including many new species of cnidarians. This image shows the cnidaria *Relicanthus* sp.—a new species from a new suborder photographed at 4,100 m in the Clarion–Clipperton Fracture Zone (CCZ) in the equatorial Pacific Ocean. This species has tentacles ~3 m long and lives on sponge stalks attached to polymetallic nodules and rock outcrops. The species has never been collected. Image credit: D. J. Amon and C. R. Smith (University of Hawaii, Honolulu, HI). Reprinted from ref. 7, which is licensed under CC BY 4.0.

because these types of surveys explore very small areas, and relatively little of the abyssal floor has been mapped with high-resolution, multibeam sonar to help distinguish scarps and other abrupt seafloor topography that can yield rocky outcrops.

To begin to fill this abyssal gap, Riehl et al. (3) used high-resolution multibeam sonar to survey a 2,700-km-long swathe of abyssal seafloor along the Vema Fracture Zone, a transform fault crossing the Mid-Atlantic Ridge between the Caribbean Sea and the bulge of Africa. The total area surveyed was ~94,000 km² and spans crustal ages of 0 to 100 Ma. Riehl et al. (3) then combined analyses of seafloor relief (using a ruggedness index) with acoustic backscatter strength to apportion the abyssal seafloor into habitat types; both high ruggedness and high acoustic backscatter are correlated with the occurrence of hard surfaces at the seafloor. Riehl et al. (3) then classified their survey area into

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Author contributions: C.R.S. designed research, performed research, and wrote the paper.

The author declares no competing interest.

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See companion article, “Discovery of widely available abyssal rock patches reveals overlooked habitat type and prompts rethinking deep-sea biodiversity,” [10.1073/pnas.1920706117](https://doi.org/10.1073/pnas.1920706117).

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First published July 10, 2020.

three general habitat types: "Sediment" with low hard-rock exposure potential, "Transitional" with moderate hard-rock exposure potential, and "Hard Rock" characterized by high hard-rock exposure potential. They then used bottom dredges, grab samplers, gravity corers, a towed camera sledge, and an autonomous underwater vehicle to ground-truth their habitat classification, verifying that rocky substrates such as outcrops and polymetallic nodules predictably occurred as indicated by ruggedness and backscatter indices.

Not unexpectedly, Riehl et al. (3) found that many areas near the Mid-Atlantic Ridge with young crustal ages of 0 to 5 Ma (the neovolcanic zone) had high hard-rock potential, with the Hard Rock habitat class covering 30% of the seafloor area. However, Hard Rock habitat continued to be found even in the areas of older crust (50 to 100 Ma), with 5% of the seafloor considered to have high hard-rock exposure potential. Areas classified as Transitional, which included patches of hard surface such as polymetallic nodules and rock outcrops, also occurred widely across the Vema Fracture Zone, covering 33% of the total survey area. Thus, even in areas of very old seafloor crust 1,000 km from the Mid-Atlantic Ridge, rock outcrops and polymetallic nodules may provide frequent rocky habitat in the abyssal Atlantic. The Mid-Atlantic Ridge is crossed by many fracture zones in addition to the Vema, so Riehl et al. (3) scaled up their results to estimate that ~264,000 km² (9%) of the millions of square kilometers of fracture zones in the Atlantic have high hard-rock exposure potential. Of course, the midocean ridges that girdle all of the ocean basins also have numerous fracture zones, and rocky habitats are likely to be common on these features as well.

Why care if rocky habitats and habitat heterogeneity are far more common in the abyssal Atlantic and other oceans than previously thought? First, abyssal ecosystems are the largest on our planet, constituting most of the biosphere, so quantifying the distribution of habitats in the abyss is fundamental to understanding the distribution of life on Earth (12). Second, as even the most casual observer in the marine intertidal zone quickly notices, rocky substrates harbor fundamentally different communities than soft sediments. In the deep sea, hard surfaces such as glacial drop stones, rock outcrops, and polymetallic nodules often harbor a diversity of sessile suspension feeders such as sponges, soft corals, and anemones (e.g., refs. 7, 8, 13–15), while soft-sediment faunal communities are typically characterized by mobile animals including deposit-feeding polychaete worms and sea cucumbers, as well as a diversity of crustaceans of various feeding types (15). Enhanced habitat heterogeneity, especially the occurrence of rocky substrates in largely soft-sediment ecosystems, is associated with enhanced biodiversity (e.g., refs. 7, 14, 16), by providing new ecological niches, enhancing the flux of suspended food through exposure to higher currents, yielding access to prey or protection from predators, as well as altering gene flow and speciation potential by creating habitat isolation and disjunct populations [see mechanisms outlined in Riehl et al. (3)]. For example, Amon et al. (7) found a remarkable species richness of seafloor megafauna

(~170 species) in a 30- × 30-km area of the abyssal equatorial Pacific, with half of these species occurring only on manganese nodules; thus, the availability of rocky habitat in the form of nodules appeared to dramatically enhance local and regional biodiversity (Fig. 1). As pointed out by Riehl et al. (3), if rocky habitats occur much more widely in the abyssal Atlantic and other abyssal regions than previously assumed, the undersampling of abyssal biodiversity is even more acute than currently recognized (12) and future biodiversity assessments must include the poorly known, and difficult-to-sample, rocky habitats of the abyss.

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A final reason to care about abyssal habitat structure and biodiversity, including the biota of rocky substrates, is that these ecosystems are increasingly threatened by anthropogenic impacts, including climate change, seafloor mining, and pollution (e.g., from plastics) (12, 17). Evaluation of the threats to biodiversity from human impacts requires understanding of the baseline conditions of these habitats, in particular the distribution of habitat types and the patterns and drivers of biodiversity in each habitat, including rock outcrops, manganese nodules, and various types of sediments. From the Riehl et al. study (3), as well as from many other recent publications (e.g., refs. 6, 7, 14, 18, 19), it is clear that the abyssal seafloor cannot be considered one vast, monotonous ecosystem such that the species and communities disturbed in one area (e.g., from seafloor mining) will necessarily persist in other, faraway, undisturbed locations. Abyssal habitats, and clearly abyssal biodiversity, are heterogeneous on scales of tens of kilometers and beyond due to the occurrence of rock outcrops, variability in polymetallic nodule abundance, and the presence/absence of nearby seamounts (e.g., refs. 3, 6, 7, 14, 18, 19). Other ecological parameters that drive deep-sea biodiversity also vary significantly across the abyss over scales of 100 to 1,000 km, including sediment type, the availability of food sinking from the euphotic zone, and bottom currents (5, 12, 20). As a consequence, distinct biodiversity is likely to occur on much smaller scales at the abyssal seafloor than previously appreciated. This heterogeneity must be considered as we evaluate biodiversity and the impacts of human activities, including the potential for species extinctions, in the largest and most poorly understood ecosystems on our planet.

Acknowledgments

C.R.S.'s research is supported by grants from the Gordon and Betty Moore Foundation, the Pew Charitable Trusts, the National Science Foundation, and the National Oceanic and Atmospheric Administration Office of Ocean Exploration and Research.

1 Anonymous, Abyssal plain. https://en.wikipedia.org/wiki/Abyssal_plain. Accessed 26 May 2020.

2 E. O. Straume et al., GlobSed: Updated total sediment thickness in the world's oceans. *Geochem. Geophys. Geosyst.* **20**, 1756–1772 (2019).

3 T. Riehl, A.-C. Wöfl, N. Agustin, C. W. Devey, A. Brandt, Discovery of widely available abyssal rock patches reveals overlooked habitat type and prompts rethinking deep-sea biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 15450–15459 (2020).

4 J. Murray, A. F. Renard, *Report on Deep-Sea Deposits Based on the Specimens Collected During the Voyage of H.M.S. Challenger in the Years 1872 to 1876* (Challenger Reports, London, 1891).

5 A. Dutkiewicz, A. Judge, R. D. Müller, Environmental predictors of deep-sea polymetallic nodule occurrence in the global ocean. *Geology* **48**, 293–297 (2020).

6 L. M. Wedding et al., From principles to practice: A spatial approach to systematic conservation planning in the deep sea. *Proc. Biol. Sci.* **280**, 20131684 (2013).

7 D. J. Amon et al., Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. *Sci. Rep.* **6**, 30492 (2016).

- 8 T. J. Pitcher et al., Eds., *Seamounts: Ecology, Fisheries, and Conservation* (Blackwell, Oxford, UK, 2007).
- 9 B. C. Heezen, C. D. Hollister, *The Face of the Deep* (Oxford University Press, New York, 1971).
- 10 V. Tilot, R. Ormond, J. Moreno Navas, T. S. Catalá, The benthic megafaunal assemblages of the CCZ (Eastern Pacific) and an approach to their management in the face of threatened anthropogenic impacts. *Front. Mar. Sci.* **5**, 10.3389/fmars.2018.00007 (2018).
- 11 E. Simon-Lledó et al., Preliminary observations of the abyssal megafauna of Kiribati. *Front. Mar. Sci.* **6**, 10.3389/fmars.2019.00605 (2019).
- 12 C. R. Smith, F. C. De Leo, A. F. Bernardino, A. K. Sweetman, P. M. Arbizu, Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol. (Amst.)* **23**, 518–528 (2008).
- 13 K. S. Meyer et al., Rocky islands in a sea of mud: Biotic and abiotic factors structuring deep-sea dropstone communities. *Mar. Ecol. Prog. Ser.* **556**, 45–57 (2016).
- 14 A. Vanreusel, A. Hilario, P. A. Ribeiro, L. Menot, P. M. Arbizu, Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna. *Sci. Rep.* **6**, 26808. (2016).
- 15 J. D. Gage, P. A. Tyler, *Deep-Sea Biology* (Cambridge University Press, Cambridge, UK, 1991).
- 16 A. F. Ziegler, C. R. Smith, K. F. Edwards, M. Vernet, Glacial dropstones: Islands enhancing seafloor species richness in West Antarctic peninsula fjords. *Mar. Ecol. Prog. Ser.* **583**, 1–14 (2017).
- 17 D. J. Amon et al., Deep-sea debris in the central and western Pacific Ocean. *Front. Mar. Sci.* **7**, 10.3389/fmars.2020.00369 (2020).
- 18 E. Simon-Lledó et al., Ecology of a polymetallic nodule occurrence gradient: Implications for deep-sea mining. *Limnol. Oceanogr.* **64**, 1883–1894 (2019).
- 19 P. Bonifácio, P. Martínez Arbizu, L. Menot, Alpha and beta diversity patterns of polychaete assemblages across the nodule province of the eastern Clarion-Clipperton Fracture Zone (equatorial Pacific). *Biogeosciences* **17**, 865–886 (2020).
- 20 L. A. Levin et al., Environmental influences on regional deep-sea species diversity. *Annu. Rev. Ecol. Syst.* **32**, 51–93 (2001).