Discovery of widely available abyssal rock patches reveals overlooked habitat type and prompts rethinking deep-sea biodiversity

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Habitat heterogeneity and species diversity are often linked. On the deep seafloor, sediment variability and hard-substrate availability influence geographic patterns of species richness and turnover. The assumption of a generally homogeneous, sedimented abyssal seafloor is at odds with the fact that the faunal diversity in some abyssal regions exceeds that of shallow-water environments. Here we show, using a ground-truthed analysis of multibeam sonar data, that the seafloor may be much rockier than previously assumed. A combination of bathymetry data, ruggedness, and backscatter from a trans-Atlantic corridor along the Vema Fracture Zone, covering crustal ages from 0 to 100 Ma, show rock exposures occurring at all crustal ages. Extrapolating to the whole Atlantic, over 260,000 km² of rock habitats potentially occur along Atlantic fracture zones alone, significantly increasing our knowledge about abyssal habitat heterogeneity. This implies that sampling campaigns need to be considerably more sophisticated than at present to capture the full deep-sea habitat heterogeneity and biodiversity.

Significance

Ground-truthed analyses of multibeam sonar data along a fracture zone of the northern Mid-Atlantic Ridge reveal an abyssal seafloor much rockier than previously assumed. Our data show rock exposures occurring at all crustal ages from 0–100 Ma along the Vema Fracture Zone and that approximately 260,000 km² of rock habitats can be expected to occur along Atlantic fracture zones alone. This higher than expected geodiversity implies that future sampling campaigns should be considerably more sophisticated than at present to capture the full deep-sea habitat heterogeneity. We provide a baseline to unravel the processes responsible for the evolution and persistence of biodiversity on the deep seafloor as well as to determine the significant scales of these processes in the benthoscape.

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The authors declare no competing interest.

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sampling (17, 30–32). Data from the lower bathyal at the northern Mid-Atlantic Ridge show a relationship between slope angle and sediment coverage where moderate slopes are characterized by occasional rock outcrops while steep slopes are dominated by bare rock surfaces (30, 33). In such studies, hard substrates have been identified as promoters of habitat heterogeneity and diversity (34), and they highlight that hard substrates are required for sessile deep-sea fauna such as many Bryozoa, Porifera, or Cnidaria (30). Nevertheless, the distribution of exposed rock in the abyss and its effects on habitat heterogeneity has not yet been studied.

The Atlantic abyssal region is cross-cut by many “fracture zones”—intratrasal traces of active plate-boundary faults at the spreading axis. We have previously presented geological data from several biological sampling sites within one such zone, the Vema Fracture Zone (VFZ), producing high-resolution habitat maps for the interpretation of species distribution data in several regions of interest (31). These maps of distinct sites showed exposed rock and an overall higher than expected heterogeneity comprising varying slope angles at various sizes and spatial coverage. Here we expand this analysis to the whole fracture zone (crustal ages covered roughly 0–100 Ma), characterizing the seafloor and quantifying habitat types based on the combination of two sonar-related indices and ground-truthed with seafloor sampling. The VFZ data are then extrapolated over the totality of the many Atlantic fracture zones. This allows us to estimate the amount of sediment-free seafloor which may be present in the Atlantic. Our finding suggest that “hard rock” should be added to the list of currently 17–25 (depending on author) habitat types recognized in the abyss (1, 35) and that previous explanations for biodiversity patterns in the abyss may need to be rethought. This approach is an initial step toward using hydroacoustic remote sensing as a mapping tool for habitat and biodiversity assessments in the framework of effective conservation strategies and sustainable exploitation in the abyss.

**Results**

**Seafloor Characterization in the VFZ.** Almost 95,000 km² of seafloor in the VFZ (Fig. 1 and SI Appendix, Fig. S1) was surveyed using a ship-mounted multibeam echosounder, providing information on both seafloor relief and acoustic backscatter (Table 1). In total, 8,289 km² (9%) of the seafloor was characterized as having high hard-rock exposure potential. The VFZ data for the mid-Atlantic Ridge comprised a large proportion of high hard-rock exposure potential (Fig. 2). Regions showing a moderate hard-rock exposure potential comprised 31,194 km² (33%). The moderate backscatter values combined with medium and high ruggedness index (RI) values in these regions indicate a patchy distribution of hard seafloor within sedimented areas.

Geologically, such areas of medium hard-rock exposure potential are characterized by volcanic ridges and steep valley flanks (Fig. 2 and SI Appendix, Fig. S2). In addition, areas with low relief but where polymetallic nodules have been sampled (Figs. 3 and 4 and SI Appendix, Table S1) also fall in this category due to the higher backscatter (BS) response of the seafloor. The remaining low-RI–low-BS regions, which have a low hard-rock exposure potential, account for the largest proportion of seafloor within the survey area covering 54,925 km² (58%).

Interpretation of the acoustic data was confirmed by seafloor sampling and photography (37) using dredges, grabs, gravity corers, a camera-equipped epibenthic sled (C-EBS (38)), and an autonomous underwater vehicle (AUV; Figs. 3 and 4 and SI Appendix, Table S1).

**Surface-Area Estimation of Exposed Hard Rock in Atlantic Fracture Zones.** The abyssal fracture zones of the Atlantic Ocean (Fig. 5) are estimated to cover 92,709 km² of young crust (0–5 Ma), 1,583,55 km² of medium old (5–50 Ma) crust, and 1,237,175 km² of old (50–100 Ma) crust (Table 2). Our own survey did not cover areas much older than 100 Ma and hence, older crust was not considered in this paper.

In the young VFZ (0–5 Ma), 30% of the seafloor had a high hard-rock exposure potential. Based thereupon our estimation of total available hard rock in Atlantic fracture zones is 27,813 km². Taking into account also the two additional age classes medium (11%: 171,191 km²) and old (5%: 61,859 km²), a total area of 263,863 km² is estimated for this habitat type across Atlantic fracture zones (Table 2).

**Discussion**

Our study provides a crude estimation for the availability of hard-rock surfaces at abyssal depths in Atlantic fracture zones. Using multibeam echosounder data, submarine features along the VFZ were revealed in detail. High-resolution bathymetry, BS data, and terrain analyses provided a detailed impression of seafloor characteristics and allowed hard-substrate discovery and quantification. It showed that, depending on the study region, up to 30% of the mapped seafloor comprises exposed hard rock representing habitats for benthos dependent on hard substrate. This has profound implications on the variability and fragmentation of abyssal habitats—important factors for the formation and persistence of biodiversity on the deep seafloor.

Less than 10% of the seafloor has ever been surveyed by multibeam sonar (39)—the only information about its possible shape over the remaining 90% was derived from modeling of satellite gravimetric data. Nevertheless, such data have been used to generate habitat maps of the whole seafloor (5). The data we present here originated from areas classified as “abyssal hill” and “abyssal mountains” in such maps (5). We find that both flat soft-sediment plains and slopes with exposed hard rock occur in both categories, highlighting that low-resolution gravimetric data are insufficient for habitat differentiation. Direct observations from ship-based echosounder data and ground-truthing with seafloor sampling is essential for differentiation between habitat types.

In our analysis, a high potential to encounter hard seafloor was mainly found at and proximal to the Mid-Atlantic Ridge (Fig. 2 and Table 2). This is unsurprising as the young oceanic lithosphere (0–5 Ma) there has little sediment covering. The proportion of hard-rock exposure potential decreases with crustal age and therefore increasing distance to the ridge axis. Far from the ridge, the distribution was spatially widely scattered and patchy. However, at medium crustal ages (5–50 Ma) a significant proportion of area with high hard-rock exposure potential was detected. On very old crust (50–100 Ma) the potential for exposed hard rock was lowest, but with local and regional variation which can be explained by differences in the underlying seafloor topography (Fig. 2 and Table 2).

Seafloor sampling particularly at the station #9–2 shows that the categories A2 (medium BS, low RI) and A3 (high BS, low RI), but also B1–B2 (medium RI, low–medium BS) already indicate hard substrate. The classification at this successful sampling site (Fig. 3) resulted in a complex patchwork of seafloor types including the categories A1–A3, B1, and B2. This habitat diversity is reflected in the seafloor images taken at this site (Fig. 4 E, G, and H) and sampling (SI Appendix, Table S1) featuring sediment plains, nodule fields, and manganese- and manganese-encrusted rock. Thus principally our interpretation of the hydroacoustic data could be confirmed although due to the sampling methods available during that cruise an exact validation of each habitat type has not been possible.

The inferential consequence is that the values provided from RI on the one hand, and BS on the other, cannot be seen as reciprocally interchangeable or necessarily supporting each other but rather as complementary. Accordingly, the combination of the provided values rather than the separate indices converges to a realistic picture of available hard substrate in the abyss.
Implications for Explaining Abyssal Biodiversity. Habitat heterogeneity has been hypothesized to trigger multiple and cascading diversity effects through ecological assemblages (40). While turnover in major habitat types may promote genetic isolation leading to speciation on regional scales, microscale variation in factors such as sediment type and topography may contribute to local coexistence of species (40). On this background it can be assumed that biodiversity regulation through rock surfaces occurs in various ways: primarily through offering attachment sites for sessile organisms, caves, and crevices; secondarily by providing a range of exposures to currents transporting food particles and larvae; thirdly, seafloor topography prompts shear and hence variations in near-seafloor currents, leading to sediment sorting and variation in particle size and food availability (30); finally, rocky outcrop contributes to environmental patchiness, creating barriers to connectivity for some organisms between (semi) isolated abyssal sediment habitats promoting diversification (24, 25). Wherever a variation of slope angle occurs, temporal variability of sediment accumulation and redistribution through slumping may furthermore increase habitat diversity.

Where hard substrate is available in the abyss, the taxonomic composition of the benthic fauna has been found to significantly differ from adjacent sediments. In manganese nodule fields, for instance, sessile suspension-feeding sponges, cnidarians, and Foraminifera were among the dominant taxa which is uncommon for other abyssal habitats (34, 41). The availability of manganese nodules as hard substrate has been shown to drive megafaunal diversity (17, 42). This may also apply to other types of hard substrates in the abyss. Our analysis suggests that species dependent on hard substrates may have much more habitat available than previously assumed. If our observations from the VFZ can be generalized and our estimations for the Atlantic (Fig. 5) hold true, hard substrate may be widely distributed throughout the abyssal depth zone. Data from, for example, the search for flight MH-370 in the Indian Ocean abyss (43), appear to confirm our assumptions. This would help to explain how connectivity between disjunct large seafloor features, such as seamounts and ridges that have so far appeared to be insular and isolated by lack of suitable intermediate habitat, can be maintained.

To further improve our understanding of the biodiversity at the deep seafloor as well as its significant scales—a key goal of marine ecology (44)—abyssal hard rock requires consideration in future research. In the VFZ itself, the populations of endobenthic isopods revealed genetic structure already occurring between stations on either side of the Mid-Atlantic Ridge only a few kilometers apart suggesting population separation at this scale where the topography of the ridge, combined with hydrography, are likely to be the main contributors to the structure (45, 46). The complex landscapes shown by our high-resolution bathymetric maps help to explain these observed genetic patterns. They may play an important role in allopatric

Table 1. Surface area quantification in the VFZ (North Atlantic) by seafloor category and habitat type

| Habitat type | Category | Area, km² | Area, % | Sum (area [%]/habitat type) |
|--------------|----------|-----------|--------|---------------------------|
| Sediment     | A1       | 54,925    | 58.2   | 58                        |
|              | A2       | 3,783     | 4.0    | 33                        |
|              | B1       | 23,120    | 24.5   |                           |
|              | B2       | 4,291     | 4.0    |                           |
| Transitional | A3       | 659       | 0.7    | 9                         |
|              | B3       | 1,824     | 1.9    |                           |
|              | C1       | 3,190     | 3.4    |                           |
|              | C2       | 1,432     | 1.5    |                           |
|              | C3       | 1,193     | 1.3    |                           |

The total area classified (94,408 km²) is illustrated in the overview map (Fig. 1). The habitat types are sediment (= low hard-rock exposure potential), transitional (= medium hard-rock exposure potential), and hard rock (= high hard-rock exposure potential).
speciation, especially in organisms with poor dispersal potential (45). Thorough population-genetic studies in abyssal benthic organisms are still very few (47), yet application of such methods would greatly improve our insight into connectivity and differentiation at the deep seafloor.

Why Only Now? Given the relevance of habitat heterogeneity to explain abyssal biodiversity, it seems difficult to explain why both the rocky habitats themselves as well as their fauna remained principally undetected since the beginning of systematic deep-sea surveys in the 1950s. This is mostly due to undersampling and a

Fig. 2. VFZ (North Atlantic) seafloor at crustal ages of 0 and 55 Ma. (A) Bathymetric grid with 60-m resolution. (B) Bivariate choropleth map showing the combination of BS and RI. (C) Distribution of the RI classes. (D) Distribution of BS classes.
paucity of mapping compared to regions on and close to mid-ocean ridges (31, 48), where recent research programs, such as the ECO-MAR (Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone) project (30, 33), have greatly advanced this field. Moreover, this is due to a systematic sampling bias. Although some sampling gear has been
Fig. 4. Seafloor images of the VFZ taken by C-EBS. Approximated habitat classification categories (cat.) are indicated for every image. Scale bar not available due to variation in camera settings and angles. In the following, station numbers of cruise SO237 are indicated in abbreviated fashion. (A) Sedimented seafloor with lebensspuren, signs of bioturbation, and Sargassum debris, cat. A1, stat. #4–8. (B) Sedimented seafloor with lebensspuren, cat. A1, stat. #4–9. (C) Sedimented seafloor with lebensspuren, signs of cropping and other bioturbation, burrows and hills, and Sargassum debris, cat. A1, stat. #6–8. (D) Relatively undisturbed sediment with few life traces and burrows, cat. A2, stat. #8–4. (E) Sediment with Sargassum debris, traces, and burrows, cat. A1–A2, stat. #9–2. (F) Sediment ripples with burrows in the top left, cat. A1–A2, stat. #9–2. (G) Manganese crusts, likely cat. A3–B1, stat. #9–2. (H) Manganese nodules, cat. A2, stat. #9–2. (I) Sediment bumps, cat. A2, stat. #9–8. (J) Sediment bumps, tubes, and foraminifera, cat. A1, stat. #11–4. Seafloor images credit: Nils Brenke (photographer).
specifically designed sufficiently robust to withstand bedrock encounters (e.g., ref. 49), biological seafloor sampling within the abyss is usually restricted to relatively flat sediments for which most biological deep-sea collection devices—namely trawls, grabs, and corers—have been primarily developed (see, e.g., ref. 50). They are preferably not deployed in regions where uneven topography is expected—a decision usually based on The General Bathymetric Chart of the Oceans maps or preparatory hydroacoustic surveys. Nevertheless, if these types of sampling gear encounter hard seafloor, they return empty or damaged. Trawls which may survive encounters with rocky seafloor tend to integrate sampling over a long track, so the contribution to the total sample from hard-substrate fauna may go unrecognized. If a trawl does not survive the encounter with an obstacle it is generally considered a failed station and not reported. To our knowledge, no study has ever specifically targeted abyssal hard-rock fauna aside from manganese nodules, seamounts, and ridges (e.g., refs. 17, 30, 32–34, 42).

**Outlook.** The presented results show that a substantial amount of previously overlooked hard substrate can be expected in the Atlantic Ocean. The introduced methodology serves the purpose of identifying sites for biological and geological sampling. Future sampling programs should prioritize ensuring an integrated geological–biological program and are thus enabled to specifically study the effects of bedrock patches on the abyssal benthos. Key research questions that should be addressed are what impact a heterogeneous abyssal seafloor has on the distribution and connectivity in the benthos populations; if/how environmental gradients associated with hard substrate correlate with species turnover; if abyssal hard-rock patches facilitate connectivity between populations inhabiting supposedly isolated habitats (e.g., seamounts) by acting as dispersal stepping stones; and over what time- and spatial scales, seafloor geological processes impact biological diversity. To achieve this, remotely operated vehicles (ROV) are the gear of choice, enabling sampling at geological settings too risky for the above-mentioned sampling devices. Furthermore, ROV are modular systems that allow integrating a multitude of other aspects of ecosystem studies (various sampler types, photo and video surveys, platform for sensors) (see, e.g., ref. 51). Currently, however, the feasibility of ROV operations is limited by the high associated costs. AUVs may represent suitable alternatives for photographic or hydroacoustic habitat mapping and ground-truthing but their practical applicability is limited by problems with close-to-seafloor navigation in areas with topological relief.

This study is a baseline for the development of multibeam-based habitat assessments at abyssal depths. It highlights the

| Crustal age, Ma | Hard rock area proportion | Total area, km² | High-potential area, km² |
|----------------|--------------------------|----------------|-------------------------|
| 0–5            | 30%                      | 92,709         | 27,813                  |
| 5–50           | 11%                      | 1,583,556      | 174,191                 |
| 50–100         | 5%                       | 1,237,175      | 61,859                  |
| Total          |                          | 2,913,440      | 263,863                 |

Estimated proportion and absolute quantity of hard-rock exposure potential available in fracture zones of the Atlantic Ocean, divided by three crustal-age categories.
advantages of taking an integrated and collaborative geological–biological approach to benthic surveys. A better understanding of how abyssal hard-rock patches influence benthic biodiversity will be valuable for species distribution assessment and modeling and may be critical to identify vulnerable marine ecosystems (52), the designation of marine protected areas, and impact assessments connected to deep-sea mining (53).

Materials and Methods

Study Region and Data Acquisition. The Vema Transform Fault forms a large left-lateral offset on the Mid-Atlantic Ridge (MAR) at about 11°N (Fig. 1). Until recently, only the transform region of the VFZ had been mapped and sampled geologically (54–57) and these works indicated that extensive outcrop is exposed at the seafloor in the transform region. The off-axis fracture zones to the east and the west of the MAR are presently almost exclusively known from satellite-measured gravity data (58). Their strong signature on these maps suggested that they are associated with significant seafloor relief exceeding 1,000 m across the VFZ.

For the present work, multibeam bathymetry and BS data collected during the Vema-TRANSIT campaign [German research vessel Sonne cruise SO237 (37, 59, 60)] is evaluated and interpreted (Fig. 1 and SI Appendix, Fig. S1) building upon and significantly expanding the scope of a previous publication by Devey et al. (31). Multibeam mapping was performed with the onboard Kongsberg EM 122 multibeam echosounder (Kongsberg Maritime). Data were acquired using SAS acquisition software with equiangular spacing. Sound-velocity profiles were extracted from CTD (instrument measuring conductivity, temperature, and pressure in seawater) data of an AUV and/or on the onboard CTD and were updated every 4–6° of longitude along the transects. Survey line continuous measures the surface sound velocity and gave no errors during the surveys. This, together with 1) the excellent agreement between our data and data from other vessels in regions where they overlap and 2) the fact that the sedimented fracture zone valley is surveyed as being extremely flat (depth variation <5 m over a 4-km-wide section of the swath—sound-velocity correction problems should lead to concave or convex apparent surfaces) all suggest that the data presented here represent the true seafloor shape. The surveys were conducted with a symmetrical beam spacing of 60° to both sides, a survey speed of 10 kn (18.5 km/h), and a line spacing of 7 NM (13.0 km), giving a typical seafloor swath width of around 9 NM (16.7 km). The interpretation of the acoustic data was confirmed by seafloor sampling and photography (37) using dredges, grabs, gravity cores, a C-EBF, and an AUV (Figs. 3 and 4 and SI Appendix, Table S1).

Data Analyses. The QPS Fledermaus Pro software suite (containing the modules DMagic, Fledermaus, and FMGT) was used to postprocess the multibeam data from the VFZ. Besides creating the bathymetric grid, two seafloor parameters were extracted from the multibeam data: ruggedness and BS. BS data represent the acoustic energy that is scattered back to the echosounder after the transmitted sound wave interacted with the seafloor. FMGT was used for the creation of a magnetic corrections to the BS values (in decibel) and to normalize them to grayscale values between 0 (black) and 255 (white). The BS mosaic was created with a resolution of 50 m. These relative intensities allow conclusions about the seafloor acoustic reflectivity, a variable related to surface hardness and roughness. Rocky seafloor with little or no sediment cover (e.g., young lava flows, bare basement outcrop) reflects more energy compared to flat, sediment-covered seafloor (61).

Multibeam data were cleaned manually to remove erroneous values and outliers and a bathymetric model at a resolution of 60 m was created. To quantify the ruggedness, the RI was calculated. It is a measure of terrain heterogeneity and represents the mean difference between the measured value of one grid cell (here: water depth in meters) and its surrounding cells (62). The RI was calculated based on the bathymetric model using the software Quantum GIS (QGIS version 2.18.12). No distance weighting and mean of an eight-cell neighborhood of surrounding cells was chosen as input parameters.

Habitat Classification. The defined habitat types “soft sediment” (low hard-rock exposure potential), “transitional/intermediate” (medium hard-rock exposure potential), and hard rock (high hard-rock exposure potential) were differentiated based on the principal assumption that BS intensity and RI are positively correlated with the occurrence of hard seafloor. Locally, sediments accumulate first in depressions and pockets between morphologic highs. The steeper slopes of mounds and ridges act as catchment zones to sediment slumping, in that way allowing the occurrence of bare base-exposure potential. Because an accumulation of sediments is rather unlikely where terrain is highly rugged with steep slopes. In such areas the reflection coefficient on the acoustic signal is decreased with increasing ruggedness (Fig. 2).

Disagreements between the signals of the two indices can be expected where terrain is highly rugged with steep slopes. In such areas the reflection coefficient on the acoustic signal is decreased with increasing ruggedness (Fig. 2).
proximal Chain Fracture Zone has a width of 20 km over a long distance, but at certain locations narrows down to 5 km and even closes off completely in some places (69). The Sovanco Fracture Zone in the North Pacific Ocean is 15 km wide (70). Fracture zone width can only be a vague estimation until direct observations provide more details on fracture zone morphology. Therefore for this study a conservative minimum-width estimate of 5 km was made. This preliminary assumption of 5-km minimum width is likely rendering this estimation an underestimate.

The extent of the Atlantic Ocean was derived from Marine Gazetteer Point Details on marineregions.org (71). Using the 6-min-resolution crustal age grid of Müller et al. (36), the Atlantic seafloor was divided into three age classes (0–5 Ma, 5–50 Ma, 50–100 Ma, Fig. 5). Based on the availability of the distinct habitat types with low, medium, and high hard-rock exposure potential among these age classes in the VFZ, the coverage of these habitat types was estimated for the entire Atlantic fracture zones up to a crustal age of 100 Ma.

Data Availability. The bathymetric dataset has been made available on PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.893352) (72).

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1. E. Ramirez-Lloreda et al., Deep, diverse and definitely different: Unique attributes of the world’s largest ecosystem. Biogeosciences 7, 2851–2889 (2010).
2. L. Watling, J. Guinotte, M. R. Clark, C. R. Smith, A proposed biogeography of the deep ocean floor. Prog. Oceanogr. 111, 91–112 (2013).
3. C. R. Smith, F. De Leo, A. K. Sweetman, P. M. Arbizu, Abyssal food limitation, ecosystem structure and climate change. Trends Ecol. Evol. 23, 518–528 (2008).
4. D. Thistle, “The deep-sea floor: An overview” in Ecosystems of the Deep Ocean, Ecosystems of the World, P. A. Tyler, Ed. (Elsevier Science, Amsterdam, 2003), pp. 7–27.
5. P. T. Harris, M. Macmillan-Lawler, J. Rupp, E. K. Baker, Geomorphology of the oceans. Mar. Geol. 352, 4–24 (2014).
6. D. Voeller, “Abyssal Plains” in Encyclopedia of Marine Geosciences, J. Harff, M. Meschede, S. Petersen, J. Thiende, Eds. (Springer Reference, 2016), pp. 1–5.
7. J. D. Gage, P. A. Tyler, Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor, (Cambridge University Press, 1991).
8. J. M. Whittaker, A. Goncharov, S. E. Williams, R. D. Müller, G. Leitchenkov, Global species richness across taxa, biomes and spatial scales. Trends Ecol. Evol. 31, 119–125 (2016).
9. S. N. C. Woolley, D. Watling, J. Guinotte, M. R. Clark, C. R. Smith, A proposed biogeography of the deep ocean floor. Prog. Oceanogr. 111, 91–112 (2013).
10. I. G. Priede et al., Does presence of a mid-ocean ridge enhance biomass and biodiversity? PloS One 8, e61550 (2013).
11. C. W. Devey et al., Habitat characterization of the Vema fracture zone and Puerto Rico trench. Deep Sea Res. Part II Top. Stud. Oceanogr. 148, 7–20 (2018).
12. A. Purser et al., Association of deep-sea incise otopods with manganese crusts and nodule fields in the Pacific Ocean. Curr. Biol. 26, R1268–R1269 (2016).
13. T. Niedzielski, A. Hein, M. A. Shields, T. D. Linley, I. G. Priede, A multi-scale in-vestigation into seafloor topography of the northern Mid-Atlantic Ridge based on geographic information system analysis. Deep Sea Res. Part II Top. Stud. Oceanogr. 98, 231–243 (2013).
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. P. A. Tyler, M. Baker, E. Ramirez Lloreda, “Deep-sea benthic habitats” in Biological Sampling in the Deep Sea, M. R. Clark, M. Consalvey, A. A. Rowden, Eds. (Wiley-Blackwell, 2016), pp. 1–15.
16. R. D. Müller, M. Sádolias, C. Gaina, W. R. Roest, Age, spreading rates, and spreading asymmetry of the world’s ocean crust. Geophys. Geochim. Geosyst. 90, 4006 (2008).
17. C. W. Devey, RV SONNE Fahrbericht/Cruise Report SO237 Vema-TRANSIT. Geomar Rep. 23, 110 (2015).
18. A. Brandt et al., Epifauna of the Sea as collected via a new epibenthic sled equipped with camera and environmental sensor systems. Deep Sea Res. Part II Top. Stud. Oceanogr. 86–87, 63–55 (2013).
19. L. Mayer et al., The Nippon Foundation—GEBCO seafloor 2030 project: The quest to see the world’s oceans completely mapped by 2030. Geosciences 8, 63 (2018).
20. C. R. McClain, J. P. Barry, Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. Ecology 91, 964–976 (2010).
21. C. R. Smith, A. W. Demopoulos, “Ecology of the deep Pacific Ocean floor” in Ecosys-tems of the Deep Ocean, Ecosystems of the World, P. A. Tyler, Ed. (Elsevier, 2003), pp. 179–218.
22. 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).
23. Geoscience Australia, MH370—Phase One Data Release (2017). http://www.ga.gov.au/about/projects/mai/370-data-release. Accessed 1 June 2020.
24. D. Zeppilli, A. Pusceddu, F. Trincardi, R. Danovaro, Seafloor heterogeneity influences the biodiversity-ecosystem functioning relationships in the deep sea. Sci. Rep. 6, 26352 (2016).
25. S. Bober, S. Brixi, T. Riehl, M. Schwentner, A. Brandt, Does the Mid-Atlantic Ridge affect the distribution of abyssal benthic crustaceans across the Atlantic Ocean? Deep Sea Res. Part I Top. Stud. Oceanogr. 148, 91–104 (2018).
26. T. Riehl, L. Lins, A. Brandt, The effects of depth, distance, and the Mid-Atlantic Ridge on genetic differentiation of abyssal and hadal isopods (Macrostylidae). Deep Sea Res. Part II Top. Stud. Oceanogr. 148, 74–90 (2018).
27. M. L. Taylor, C. N. Roterman, Invertebrate population genetics across Earth’s largest habitat: The Deep-Sea Floor. Mol. Ecol. 26, 4872–4896 (2017).
28. A. Brandt et al., Challenges of deep-sea biodiversity assessments in the Southern Ocean. Adv. Polar Sci. 25, 204–212 (2014).
29. N. Brenke, An epibenthic sled for investigations on marine soft bottom and-bedrock. Mar. Technol. Soc. J. 39, 10–21 (2005).
30. M. R. Clark, M. Consalvey, A. A. Rowden, Eds., Biological Sampling in the Deep Sea, (Wiley-Blackwell, 2016).
31. I. G. Priede et al., The ECO-MAR (ecosystem of the Mid-Atlantic Ridge at the sub-polar front and Charlie Gibbs fracture zone) project: Description of the benthic sampling programme 2007–2010. Mar. Biol. Res. 9, 624–628 (2013).
32. A. M. Rengstorf, C. Mohn, C. Brown, M. S. Wiss, A. J. Grehan, Predicting the distribu-tion of deep-sea vulnerable marine ecosystems using high-resolution data: Considerations and novel approaches. Deep Sea Res. Part II Top. Stud. Oceanogr. Res. Pap. 93, 72–82 (2014).

Riehl et al. PNAS Latest Articles | 9 of 10
53. 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, 1–25, 10.3389/fmars.2018.00007 (2018).

54. M. Cannat et al., A geological cross-section of the Vema fracture zone transverse ridge, Atlantic ocean. J. Geodyn. 13, 97–117 (1991).

55. M. Cannat, M. Seyler, Transform tectonics, metamorphic plagioclase and amphibolitization in ultramafic rocks of the Vema transform fault (Atlantic Ocean). Earth Planet. Sci. Lett. 133, 283–298 (1995).

56. A. Cipriani, E. Bonatti, D. Brunelli, M. Ligi, 26 million years of mantle upwelling below a segment of the Mid Atlantic Ridge: The Vema lithospheric section revisited. Earth Planet. Sci. Lett. 285, 87–95 (2009).

57. Y. Lagabrielle et al., Vema Fracture Zone (central Atlantic): Tectonic and magmatic evolution of the median ridge and the eastern ridge-Transform intersection domain. J. Geophys. Res. Solid Earth 100, 19–991 (1995).

58. I. G. Priede et al., The ecosystem of the Mid-Atlantic Ridge at the sub-polar front and Charlie–Gibbs Fracture Zone; ECO-MAR project strategy and description of the sampling programme 2007–2010. Deep Sea Res. Part II Top. Stud. Oceanogr. 98, 220–230 (2013).

59. G. Brandes, Geotechnical characteristics of deep-sea sediments from the North Atlantic and North Pacific oceans. Ocean Eng. 38, 835–848 (2011).

60. H. Mercier, K. G. Speer, J. Honnorez, Flow pathways of bottom water through the Romanche and Chain fracture zones. Deep Sea Res. Part II Top. Stud. Oceanogr. 41, 1457–1477 (1994).

61. D. S. Cowan, M. Botros, H. P. Johnson, Bookshelf tectonics: Rotated crustal blocks within the Sovanco fracture zone. Geophys. Res. Lett. 13, 995–998 (1986).

62. J. W. Kirchner, W. E. Dietrich, F. Iseya, H. Ikeda, The variability of critical shear stress, friction angle, and grain protrusion in water-worked sediments. Sedimentology 37, 647–672 (1990).

63. M. Urlaub, P. J. Talling, A. Zervos, D. Masson, What causes large submarine landslides on low gradient (< 2°) continental slopes with slow (0.15 m/kyr) sediment accumulation? J. Geophys. Res. Solid Earth 120, 6722–6739 (2015).

64. H. G. Brandes, Geotechnical characteristics of deep-sea sediments from the North Atlantic and North Pacific oceans. Ocean Eng. 38, 835–848 (2011).

65. N. C. Mitchell, Diffusion transport model for pelagic sediments. J. Geophys. Res. 100, 19–991 (1995).

66. I. G. Priede et al., The ecosystem of the Mid-Atlantic Ridge at the sub-polar front and Charlie–Gibbs Fracture Zone; ECO-MAR project strategy and description of the sampling programme 2007–2010. Deep Sea Res. Part II Top. Stud. Oceanogr. 98, 220–230 (2013).

67. H. G. Brandes, Geotechnical characteristics of deep-sea sediments from the North Atlantic and North Pacific oceans. Ocean Eng. 38, 835–848 (2011).

68. K. J. Matthews, R. D. Müller, P. Wessel, J. M. Whittaker, The tectonic fabric of the ocean basins. J. Geophys. Res. Solid Earth 116, B12109 (2011).

69. H. Mercier, K. G. Speer, J. Honnorez, Flow pathways of bottom water through the Romanche and Chain fracture zones. Deep Sea Res. Part II Top. Stud. Oceanogr. 41, 1457–1477 (1994).

70. D. S. Cowan, M. Botros, H. P. Johnson, Bookshelf tectonics: Rotated crustal blocks within the Sovanco fracture zone. Geophys. Res. Lett. 13, 995–998 (1986).

71. International Hydrographic Organization, Limits of Oceans and Seas, 3rd Ed. (International Hydrographic Organization Special Publication No. 23, 1953).

72. C. W. Devey, N. Augustin, I. A. Yeo, Raw multibeam EM122 data and data products: SONNE cruise SO237 (North Atlantic). PANGEA. https://doi.org/10.1594/PANGAEA.893352. Accessed 1 June 2020.