A strategy for the conservation of biodiversity on mid-ocean ridges from deep-sea mining

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Abstract

Mineral exploitation has spread rapidly from land to shallow coastal waters and is now being planned for the offshore, deep seabed. Large seafloor areas are being approved for exploration for seafloor mineral deposits, creating an urgent need for regional environmental management plans. Networks of areas where mining and mining impacts are prohibited are expected to be key elements of such plans. Here we adapt marine reserve design principles to the distinctive biophysical environment of mid-ocean ridges, offer a framework for the design and evaluation of such networks to support conservation of benthic ecosystems on mid-ocean ridges, and introduce projected climate-induced changes in the deep-sea to the evaluation of reserve design. We enumerate a suite of metrics to measure network performance against conservation targets and network design criteria promulgated by the Convention on Biological Diversity. We apply these metrics to network scenarios on the northern and equatorial Mid-Atlantic Ridge, where contractors are exploring for Seafloor Massive Sulfide (SMS) deposits. A latitudinally distributed network of areas (extending ≥ 200 km along the ridge axis and 500 km to either side of the ridge axis) performs well at i) capturing ecologically important areas and 30% to 50% of the spreading ridge areas, ii) replicating representative areas, iii) maintaining along-ridge population connectivity, and iv) protecting areas potentially less impacted by climate-related changes. Critically, the network design is adaptive, allowing for refinement based on new knowledge and the location of mining sites, provided design principles and conservation targets are maintained. This framework can be applied along the global mid-ocean-ridge system as a precautionary measure to protect regional biodiversity and ecosystem function from impacts of SMS mining.
Mid-ocean ridges are located at divergent oceanic plate boundaries, where volcanism associated with seafloor spreading creates new oceanic crust. In these regions, seawater percolates through seafloor cracks and fissures to depths where it reacts with host rock at high temperature and pressure, stripping the rock of metals such as copper and zinc. The heated, chemically modified, fluid is thermally buoyant and rises to exit the seafloor as hydrothermal vents, where metal sulfides precipitate and can accumulate as Seafloor Massive Sulfides (SMS; also referred to as polymetallic sulfides). Where uplifted and exposed as ophiolite complexes on land, SMS deposits have long been exploited for their ores (1). They are now targeted for mining at the seabed (2). At slow seafloor spreading rates (< 4 cm yr\(^{-1}\)), SMS deposits may accumulate over thousands of years and can be of sufficient size and ore quality to be of commercial interest (2, 3). Some large SMS deposits on the seabed are located at ‘active’ hydrothermal vents, operationally defined as vents that emit diffuse and/or focused hydrothermal fluid and support symbiont-hosting invertebrate taxa that rely on uptake of inorganic compounds in the hydrothermal fluid to support microbial chemosynthesis (4). Large, inactive or ‘extinct’ SMS accumulations on mid-ocean ridges are less well-studied than active vent systems. They generally lack biomass-rich assemblages of vent-endemic taxa, but likely support highly diverse and complex benthic communities (5, 6). SMS deposits at inactive vents may be the preferred target for commercial mining, based on environmental considerations (7), estimated size of the ore bodies (8–10), and the practicalities of avoiding equipment exposure to the high-temperature, acidic conditions at active vents (11).

The United Nations Convention on the Law of the Sea (UNCLOS) sets out the legal framework for seabed mining beyond the limits of national jurisdiction (referred to as ‘the Area’). The Convention, along with the 1994 Implementing Agreement, established the International Seabed Authority (ISA) as the regulatory agency for deep-sea mining in the Area. The ISA is also charged with, among other things, ensuring effective protection of the marine environment from harmful effects arising from mining-related activities on the seabed (UNCLOS Art. 145). These responsibilities include the need to adopt and periodically review environmental rules, regulations, and procedures for the prevention, reduction and control of pollution and other hazards to the marine environment, the protection and conservation of the natural resources of the Area, and the prevention of damage to the flora and fauna of the marine environment (UNCLOS Art. 145). Current regulatory efforts by the ISA focus on three mineral resources: SMS on mid-ocean ridges, polymetallic nodules on abyssal plains, and ferromanganese crusts on seamounts. Each occurs in different geological and ecological settings, with ecosystem processes that operate on different spatial and temporal scales (12), and with communities with varying degrees of resilience to mining activities (13). Environmental impacts from exploitation of SMS deposits are predicted to include loss of biological diversity resulting from direct habitat destruction and modification of vent fluid geochemistry, as well as degradation of surrounding benthic and pelagic environments through indirect impacts such as toxic and particle-rich sediment plumes, noise, vibration, and light created by the mining activity (4, 12, 14, 15). Any given SMS mine site on a mid-ocean ridge will encompass only a small area, with direct impacts covering up to a few square kilometers, but a series of small mines may be required to provide an overall profitable enterprise within a single mining contract area (3).
Potential cumulative impacts of multiple or long-duration SMS mining events on regional scales are of concern. These impacts will result from direct and indirect effects and include disruption of population connectivity, loss of ecosystem functions and services, as well as the potential for regional and global extinctions (4).

To address potential impacts from deep-sea mining, the ISA is developing regional Environmental Management Plans (EMPs) as a best practice (16). In 2012, the ISA approved its first EMP (17) for abyssal polymetallic nodule fields in the Clarion-Clipperton Zone (CCZ) in the central Pacific Ocean. The goals of the CCZ-EMP include facilitation of exploitation and cooperative research, monitoring of the environment, area-based management, application of an ecosystem-based approach to management, and broad stakeholder participation. Area-based planning to support management of the Area through EMPs should include, but not be limited to, the design of networks of no-mining areas, consideration of vulnerable habitats at risk of serious harm outside of such conservation areas, and the identification of Preservation and Impact Reference Zones (PRZs & IRZs) (Jones & Weaver, in review).

Operationally, the CCZ-EMP uses a network of no-mining areas (referred to by the ISA, and herein, as ‘Areas of Particular Environmental Interest’ or APEIs) for preservation of unique and representative ecosystems, and for protection of biodiversity and ecosystem structure and function (17). APEI networks contribute to a precautionary approach to environmental management of deep-sea mining by ensuring representative benthic habitats and associated ecosystems are protected from serious harm on regional scales, particularly given uncertainties regarding the severity, frequency, and spatial extent of mining impacts (16). Establishment of such conservation areas does not preclude the need for additional regional environmental management actions that consider both benthic and pelagic ecosystems including, inter alia, environmental impact assessments, site-based conservation, transparent monitoring, and mitigation measures (Jones & Weaver, in review).

The CCZ-EMP adopts principles for area-based conservation used elsewhere (19) as elaborated in Wedding et al. (2013, 2015). These include “the principle that 30 to 50% of the total management area should be protected, that the network of protected areas should capture the full range of habitats and communities, and that each [APEI] should be large enough to maintain minimum viable population sizes for species potentially restricted to a sub-region” (21). The APEI network design process for the CCZ polymetallic nodule beds employed a regional benthic classification system where, in the absence of detailed data on the composition and distribution of benthic communities, surrogate measures and drivers of alpha and beta diversity, such as nodule abundance, Particulate Organic Carbon (POC) flux to the seafloor, seamount distributions, bathymetry, and macrobenthic abundance were assessed in the context of existing mining exploration claims. Biophysical surrogates of biodiversity have also been used to aid design of conservation networks (e.g., in the Northeast Atlantic; Howell 2010), and have been tested at least once and proven to be effective (23). Through this surrogate approach, the CCZ was divided into nine representative sub-regions, each with a ‘no-mining’ APEI of sufficient area (400 km x 400 km comprising a 200 km x 200 km core area surrounded by a 100-km wide buffer zone) to support self-sustaining populations in each APEI core (24). To avoid overlap with existing exploration claim areas, the ISA positioned two of the APEIs from subregions within the core of the CCZ to the CCZ periphery (24);
Together, the 9 APEIs represent ~24% of the total CCZ management area. At the 22nd Session of the ISA in 2016, consideration was given to creation of two additional APEIs in the CCZ region, which would yield a total APEI coverage of ~29% of the CCZ management area.

The United Nations General Assembly (UNGA), in its resolution 68/70 adopted in 2013, encouraged the ISA to develop and approve environmental management plans for other seabed regions with potential to support deep-sea mining, in particular regions where exploration contracts had been granted. The UNGA reiterated this recommendation in subsequent annual resolutions on oceans and law of the sea (UNGA 69/245 & UNGA 70/235). The ISA followed with a call for EMPs “in particular where there are currently exploration contracts” (Council Decisions ISBA/20/C/1 §9; ISBA/21/C/20 §10; ISBA/22/C/28 §11). The ISA has yet to consider a regional EMP for any SMS deposits, but has encouraged the scientific community to support the development of such EMPs. In response, an international initiative was begun in 2015 to advance a framework for the development of networks of APEIs on mid-ocean ridges, using a portion of the Mid-Atlantic Ridge (MAR) as a case study. This region includes three SMS exploration contracts, covering a total area of 30,000 km², granted by the ISA to France, the Russian Federation, and Poland (Figure 1). This scientific initiative adopted an inclusive, expert-driven consultative process like that used for the CCZ APEI network design (24, 25). Two large international workshops were convened in June 2015 and November 2016 with deep sea biologists, geospatial ecologists, lawyers, and mining contractors to discuss network designs. Supporting activities also fed into the workshops, including a comprehensive data report, a smaller working group that drafted design principles and assessed multiple network options, and outreach activities to obtain input from a larger scientific community. Through this process, a framework was developed for the design and assessment of various APEI network scenarios for the MAR. As reported below, this framework includes a conservation goal, specific conservation objectives and targets, and performance metrics.

The CCZ-EMP served as a starting point for area-based planning for networks of no-mining areas on mid-ocean ridges. However, key features of ridge systems—including their quasi-linear nature, their along- and cross-axis bathymetric complexity, their complex and turbulent flow environments, and the patchy occurrence of hydrothermal vents and SMS on ridges—differ substantially from those of the abyssal plains of the CCZ and required de novo considerations for network design (26). A list of habitat indicators and biodiversity drivers on and around mid-ocean ridges was refined (Table S1), and metrics for climate-change stressors based on model projections were introduced. In addition to the Wedding et al. (2013) biodiversity variables of bathymetry and seamount distribution, this MAR case study included other variables for performance metrics, including biogeographic region, latitude, POC flux to the seafloor (replacing particulate organic nitrogen flux used by Wedding et al. 2013), slope, other habitat types (transform faults, hydrothermal vents), and future in situ environmental conditions (pH, T, dissolved O2 concentrations, POC flux to the seafloor) derived from climate-change projections for the year 2100 (Table 1). Consideration was given to applying a more quantitative approach, including use of optimization tools such as MARXAN (27, 28), but given the limited available data on species distributions and alpha and beta diversity, a MARXAN or related approach would have conveyed a greater level of certainty with respect to the optimal
placement of APEIs than is warranted. Further, such an approach would indicate preferred placement of APEIs which is counter to our intent to develop a framework, not to presuppose a specific solution before the ISA develops one.

The development of the network of APEIs in the CCZ was based on scientific (ecological and biogeographic) principles, and included both legal and socioeconomic considerations related to existing exploration contracts and commitments (24). Here, the linear nature of the mid-ocean ridge and the distribution of existing exploration contracts (Figure 1) precluded design of a network of adequately sized and scientifically justifiable APEIs that avoided existing contracts. We thus use a solely science-based, ecological approach to adapt marine reserve design principles to the distinctive ridge setting. In doing so, we consider the APEI network design to be fungible, recognizing that mineral exploration will inform placement of networked APEIs that can meet conservation and exploitation objectives.

Article 4 of the CBD states that the convention applies to ABNJ “in the case of processes and activities, regardless of where their effects occur, carried out under its jurisdiction or control”. The CBD is also charged with “provision of scientific and, as appropriate, technical information and advice related to marine biological diversity” (29). In designing APEI network scenarios, we apply five network criteria identified by the Convention on Biological Diversity (30): important areas, representativity, connectivity, replication, and adequacy & viability. For each of these criteria, we propose conservation objectives for APEI networks (Box 1) that are used in an assessment of network performance. Our approach closely resembles that suggested in Annex III of the above CBD decision (albeit in a different order), and involved (1) delineation of a study area based on biogeographical considerations; (2) identification of known ecologically or biologically important areas (cf. Ecologically or Biologically Significant Areas (EBSAs); 30); (3) iterative site selection; and (4) consideration of ecological coherence (e.g., ecological connectivity and viability), including viability under climate change. We then developed three network scenarios and assessed the performance of the scenarios. This approach allowed the
development of scenarios that meet current understanding of what an ecologically robust
network of APEIs on a mid-ocean ridge could look like.

Although we focus our study on the northern and equatorial Mid-Atlantic Ridge, the general
principles, design criteria, and evaluation approach should be applicable to mid-ocean ridge
systems (and potentially other deep-sea settings) worldwide. Our intent was to develop a
framework for the design and assessment of networks of no-mining areas based on

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**Box 1. Network criteria and conservation objectives for APEIs on a mid-ocean ridge based on CBD MPA network criteria. Viability under climate change is newly integrated into the Adequacy/Viability criterion.**

1. Important Areas
   a) Placement of APEIs within the network should capture areas considered to be ecologically and/or evolutionarily important based on best available science. APEIs should conserve 100% of identified Important Areas.

2. Representativity
   a) APEI should conserve 30% - 50% of each habitat type (e.g., the spreading ridge, seamounts, transform faults) within each management unit.
   b) APEIs should be representative of the biophysical seascape (e.g., depth, slope, POC flux to the seafloor) within each management unit.

3. Connectivity
   a) The APEI network should minimize the average and maximum distances between core areas to the greatest extent possible to conserve all dispersal scales and to ensure exchange across the entire network.

4. Replication
   a) APEIs should be replicated within biogeographic provinces (where the size of the management unit permits) to capture along-axis variation in faunal composition and protect against localized catastrophes.

5. Adequacy/Viability
   a) The APEI network should protect 30 to 50% of the total management unit.
   b) Each APEI unit within the network should include a core area of sufficient length and width to maintain viable populations and ecosystem function.
   c) Each APEI unit within the network should include an appropriately sized buffer zone to protect core areas from indirect mining effects.
   d) Viability under climate change
      i) Projected biophysical conditions (T, pH, dissolved O₂ concentrations, POC flux to the seafloor) in APEIs should include the range of current conditions across the study area.
      ii) APEIs should include at least 30% of the area projected to be least impacted by reasonable climate change scenarios (based on predicted changes in T, pH, dissolved O₂ concentrations, POC flux to the seafloor).
internationally agreed conservation network criteria to inform the sustainable use of SMS mineral resources. While we consider networks of APEIs to be necessary elements of sustainable use of such resources, we emphasize that they are not sufficient on their own; additional environmental management tools will be needed to protect and preserve the marine environment. For mid-ocean ridges and exploitation of SMS deposits, one such additional tool may be site-based closures to protect all active hydrothermal vent ecosystems, which have been identified as vulnerable and at risk of serious harm (7, 12). Vulnerable marine ecosystems, including cold-water corals and sponges outside of APEIs will also need protection. Non-area-based tools might include, for example, management of the frequency and timing of mining activities in a region, or monitoring of environmental thresholds for turbidity and toxicity.

Conservation Goal

Building on the conservation goal reported in Wedding et al. (2013) for the CCZ, the conservation goal for the design of an APEI network on the Mid-Atlantic Ridge is to contribute to "the protection of the natural diversity, ecosystem structure, function, connectivity, and resilience of deep-sea communities in the context of seabed mining in the region."

Results

Study area and biogeographic approach

To inform governance of deep-sea mining on the seafloor in the Area, and the UNGA and ISA calls for regional Environmental Management Plans in areas that contain exploration contracts, we focus on areas beyond national jurisdiction on the northern Mid-Atlantic Ridge with existing or pending exploration contracts and an extension to the south that illustrates how regional management units may be defined by biogeography. The study area is centered on the axis of the Mid-Atlantic Ridge and extends latitudinally from the southern boundary of the Portuguese ECS claim at 32.84°N to the northern boundary of the United Kingdom ECS claim for Ascension Island at 02.43°S, exclusive of the Brazilian EEZ (Figure 1). The study area extends 500 km on either side of the axis of the Mid-Atlantic Ridge (unless restricted by national jurisdictions) to include the range of representative benthic habitats that might be impacted by deep-sea mining of SMS or other seabed resources and provide a zone of sufficient size for population connectivity through larval dispersal.

To ground the study in ecological principles underpinning ecosystem-based management (32, 33), we apply a biogeographic approach using the most recent classification scheme for ocean floor biogeography (Watling et al. 2013). The primary management feature is the spreading axis of the Mid-Atlantic Ridge, which for most of its length in the study area is encompassed by the lower bathyal (800-3500 m) and abyssal (3501-6500 m) North Atlantic biogeographic provinces of Watling et al. (2013). There is an isolated hadal (> 6500 m) biogeographic unit (HD9 of Watling et al. 2013) and a bathyal (North Atlantic/South Atlantic) biogeographic transition zone at the southern margin of the study area. The study area was thus partitioned into two subunits: (1) the northern Mid-Atlantic Ridge (nMAR) subunit, north of the Brazilian EEZ, and (2) the Romanche Transform Fault (RTF) subunit, south of the Brazilian EEZ (Figure 1).

Identification of Important Areas
APEI network design should incorporate features of ecological importance. For the MAR, these features include (i) major transform faults that serve as conduits for deep-water circulation between west and east basins of the Atlantic (35, 36) and support a diverse set of habitats and fauna (37), (ii) transition zones between biogeographic units (so-called ‘biogeographic crossroads’ or ‘suture zones’), where there is high species richness, beta diversity (38), and hybridization that may foster evolution (39), and (iii) recognized genetic hybrid zones (e.g., Won et al. 2003). As noted above, all active hydrothermal vent ecosystems on the mid-ocean ridge are vulnerable and at risk of serious harm, and so deserve protection (7, 12); some of these ecosystems will fall within APEI units, the others will need to be protected through other area-based conservation measures.

Placement of APEIs in the MAR region was designed to capture the following important ecological features (Figure 2A):

**nMAR Subunit:**
- The Vema Transform Fault, a major water-mass transport pathway between the deep western and eastern Atlantic Basins (35) and an area with presumed reducing habitats as suggested by the record of the indicator species *Abyssogena southwardae* (Krylova et al. 2010).
- The hybrid zone at Broken Spur (40, 41); while multiple mussel hybrids are known along the MAR (the symbiont-bearing mussels *Bathymodiolus azoricus* and *B. puteoserpensis*), Broken Spur has the greatest proportion of hybrid individuals in a stabilized population with indications of local adaptation (42, 43); this region also corresponds to a biogeographic sub-boundary between northern ‘bathyal’ and southern ‘abyssal’ vent faunas (44).

**RTF Subunit:**
- The bathyal biogeographic transition zone between the North Atlantic and South Atlantic units (Watling et al. 2013).
- The Romanche Transform Fault, which includes a hadal biogeographic unit (Watling et al. 2013. The Romanche is a major transport pathway between the western and eastern Atlantic basins for dense water masses originating in polar regions (35, 36, 45). The proposed Romanche Transform Fault (RTF) subunit also overlaps substantively with the EBSA known as the “Atlantic Equatorial Fracture Zone and High Productivity System” (46).

**Iterative site selection: orientation, size, and spacing of APEI units**

The cross-axis bathymetric profile of the Mid-Atlantic Ridge includes a central axial valley with ridge flanks, canyons, seamounts, flat sedimented areas and abyssal hills extending laterally from the axis. To capture cross-axis habitat heterogeneity, APEIs are recommended as rectangular bands with their length following the strike of the ridge axis and their width oriented perpendicular to the ridge axis. The cross-axis orientation of a banded-APEI approach also captures the special characteristics of transform faults, which represent extremes in depth and other environmental variables, including hydrographic regimes, that support diverse deep-sea habitats and thus merit protection.
Latitudinal variation in POC flux to the seafloor \((47, 48)\), a primary determinant of biodiversity and ecosystem structure and function in the deep sea \((22, 49–52)\), indicates that a network of APEIs should be distributed along the entire length of the ridge axis in the study area to capture this and other latitudinal variations in biophysical characteristics. Such a network of APEIs provides replication that protects against catastrophic loss of habitat in any one locality and increases demographic stability by promoting inter-APEI connectivity.

**Core length along the ridge axis.** APEIs consist of core and buffer areas, where mining should not occur. Each core should be large enough to maintain a minimum viable population size for a large percentage of deep-sea invertebrates through self-replenishment \((\text{Wedding et al. 2013})\). The 75th-percentile median dispersal distance for deep-sea benthic invertebrates is used to define the distance from the core-area center point required to capture ecological dispersal within the APEI. This distance is calculated from both genetic, reflecting evolutionary time scales \((53)\), and larval dispersal models, reflecting contemporary time scales \((\text{Hilario et al. 2015, Ross et al. 2016, Breusing et al. 2016})\). These calculated distances were 103 km for vent invertebrates and 74 km for non-vent deep-sea invertebrates \((\text{Baco et al. 2016})\). A nominal 100-km dispersal distance thus captures estimated dispersal distances for vent and non-vent deep-sea invertebrate datasets, within the 75th percentile allowance. This 100-km dispersal distance matches the dispersal distance used in the APEI network design for the CCZ \((\text{Wedding et al. 2013})\), but was derived using a new synthesis of dispersal distances for deep-sea (rather than shallow-water) organisms \((53)\). As in the case of the CCZ-EMP, the length (and width) of the core conservation area is at least two times the median faunal dispersal distance \((\text{Gaines et al. 2010, Wedding et al. 2013})\). This indicates the minimum APEI core length along the ridge axis should be 200 km. Large-scale genetic connectivity over evolutionary time \((57)\) can be the result of temporally discontinuous short-distance (e.g., <26 km) dispersal mediated by stepping stone habitats \((58)\). Such short dispersal distances that occur discontinuously at contemporary time scales should also be well contained within the minimum core length of 200 km.

**Core width across the ridge axis.** The mid-ocean ridge has complex, cross-axis physical characteristics (including depth gradients and hydrographic regimes) that drive ecosystem processes and there is evidence for differentiation in the faunal composition of the eastern and western flanks of the Mid-Atlantic Ridge \((59, 60)\). Near-bed currents on the flanks of the ridge axis can be channeled in canyons and faults, resulting in a topographically forced flow toward the ridge crest \((61, 62)\). Because large, buried SMS deposits are expected on the flanks of the ridge crest \((3, 63–66)\) flow toward the ridge crest enhances the potential for mining plumes from flank SMS deposits to impact habitats closer to the crest. Where species’ distributions extend across ridge flanks, protecting cross-ridge swaths will be important for internal connectivity within an APEI. To capture representative habitats that vary with depth (from upper bathyal to abyssal) and other biophysical characteristics along the flanks \((34)\), we extend the width of the core area to 500 km on either side of the ridge axis. Such an approach protects the bathyal-abyssal biogeographic transition areas on the ridge flanks and the ridge axis, helps to meet the conservation target of 30 to 50% of each habitat type in the management unit, and accommodates future exploitation of buried SMS deposits and of other minerals on ridge flanks.
**Buffer zones.** SMS mining is expected to produce plumes of particulates at the seabed during mining activities as well as plumes at some height above the seabed during discharge of water and fine particles from the shipboard dewatering plant (12). While details of SMS mining plume structure and dispersion are not well constrained at present, SMS plumes are expected to impact a smaller region than those created by polymetallic nodule mining, where dispersion distances may extend to 100 km (67). Test mining of deep-sea sulfides was undertaken in 2017 off Japan, but the results of the associated environmental monitoring program have not yet been made publicly available. Given that passive particles suspended in the water at 1000 m on the MAR travel on average more than 2 km per day (based on ARGO float data and models; 68 and pers. comm.), we assume that plume dispersal may be on the order of tens of kilometers. Until more data are available on plume dispersal and toxicity, we use a buffer zone of 50 km on the northern and southern borders of the APEI cores. We assume an absence of exploitable mineral resources beyond 500 km on the western and eastern flanks of the ridge axis and thus do not indicate buffer zones on these borders of the core area.

**Spacing.** All conservation networks involve trade-offs between (i) promoting larval connectivity between closed areas (improved by smaller spacing between closures), (ii) providing spillover of larvae (or emigrants) from closed areas to unprotected areas, thus enhancing productivity/recovery outside protected zones (improved by creating many small closures), and (iii) maintenance of self-sustaining populations within APEI cores (improved by increasing the size of individual closures). We adopt a common design guideline for conservation networks, namely to minimize the difference between the maximum dispersal distance protected by the core area and the distance between core areas (69). Using this approach, species with larval dispersal distances greater than the length of the core areas should be able to disperse to adjacent APEIs, while those with dispersal distances less than the core length are likely to maintain populations (including metapopulations) within a single APEI core. Consideration also needs to be given to the maximum distance between adjacent core areas. Large gaps between core areas can result in core areas effectively acting as separate units, rather than as a network. To address this issue, we minimize the maximum distance between adjacent core areas to ensure network functionality. Spacing between APEIs is also necessarily affected by the overall percentage of the management unit to be protected (in this case, 30-50%).

**nMAR Management Subunit APEI network design.** Based on the size and spacing requirements outlined above, network scenarios of APEIs with 100 km, 200 km, and 300 km core lengths along the ridge axis (oriented ∼north-south), 1000 km wide (centered on the ridge axis), and spaced at distances as near as possible to the length of the APEI core were placed in the nMAR subunit (Figure 2B, C, D). These APEI network scenarios were “anchored” by two Important Areas identified in the nMAR: the Broken Spur hybrid zone and the Vema Transform Fault. While our premise is that the 200-km core length scenario is a minimum core length, the 100-km and 300-km core length scenarios allow us to understand what ecological performance might be lost (or gained) by changing the core length of an APEI.

**RTF Management Subunit.** Assuming APEI core lengths should be 200 km or more and the identification of the Romanche Transform Fault as an Important Area, the areal extent of the RTF subunit does not allow for a replicated network of APEIs. A single APEI centered on the
Romancé Transform Fault is proposed. The width of the RTF APEI is extended to protect the full extent of the transform offset and the hadal biogeographic unit between the ridge axes. In addition, the APEI extends 500 km to either side of the adjacent northern and southern ridge axes, as for the nMAR APEIs.

APEI Network Performance Assessment: nMAR Management Subunit

The guidelines for size and spacing of APEIs described above are based on scientific theory but do not guarantee that such a network would meet the network criteria set out by the CBD; i.e., that the network would be ecologically coherent (70, 71). Ecological coherence of APEI network scenarios with core lengths of 100, 200, and 300 km was assessed by evaluating performance against conservation targets for 17 metrics developed to quantify the five CBD network criteria (Figure 3, bottom panel). The representativity criterion is subdivided into metrics for discrete habitats and for continuous biological or physical oceanographic variables that describe the regional seascape. Summary scores for each scenario are also reported for each network criterion (Figure 3, Top Panel).

All scenarios met the Important Areas target in this management subunit and did well at representing the current biophysical seascape conditions (Representativity: Continuous). Each scenario also outperformed the other scenarios in at least one criterion (Figure 3, Top Panel). The 100-km scenario performed better in the Connectivity and Replication criteria. The 200-km core scenario out-performed in representing key discrete habitat types and replication. The 300-km scenario did slightly better in achieving targets for representing the regional biophysical seascape and in mitigating effects from projected changes in climatic conditions (Figure 3). While the 200-km scenario performed well across all criteria, the 100-km scenario underperformed in Adequacy and Viability and the 300-km scenario underperformed in Connectivity. As noted in the introduction, the 100-km scenario also does not meet our critical design requirement for a ≥ 200 km core length.

APEI Network Performance Assessment: RTF Management Subunit

For the RTF Management Subunit, all scenarios protect the hadal biogeographic province. Two of the Important Areas identified by experts are in the RTF Management Subunit, namely the RTF itself and the biogeographic transition zone between the North Atlantic and South Atlantic bathyal biogeographic provinces. Only the 300-km scenario completely protected both the Romanche Transform Fault and the biogeographic transition zone within a single APEI. The 200-km scenario performed well, protecting the RTF and greater than 70% of the biogeographic transition zone, but the 100-km scenario was unable to adequately conserve either the RTF or the biogeographic transition zone. Other network criteria were not evaluated, as there was only one APEI and thus consideration of metrics for network criteria was inappropriate.

Discussion

From the assessment above, it is evident that there are trade-offs in scenario performance across network criteria. While all scenarios performed well in certain criteria, each criterion must be met to support an ecologically coherent network. The poor performance of the 100-km...
scenario in the Viability & Adequacy criterion and the 300-km scenario in the Connectivity criterion raise questions about the ecological coherence of those network scenarios. Further, the 100-km scenario failed to meet the basic target to conserve the 75th-percentile median dispersal distance for deep-sea benthic invertebrates within core areas and was unable to fully conserve the Important Areas in the RTF management unit. Given the need to place buffers around core areas, smaller APEIs are a less efficient mechanism with which to meet conservation targets. Therefore, we recommend the use of a 200-km core length for APEIs, but recognize that the size of an APEI is contingent on the characteristics of the management unit (e.g., the need to use an APEI with a 300-km core length to fully conserve Important Areas in the RTF subunit).

The nMAR network scenarios described here do not take into account locations of existing exploration contracts. Exploration contracts influenced decisions by the ISA regarding placement of APEIs in the CCZ, leading to a network of APEIs that are not necessarily representative of the local and regional biodiversity (Wedding et al. 2013, 2015). Exploration contracts on the Mid-Atlantic Ridge continue to be granted, with the most recent contract awarded in 2017. Before applying for exploitation contracts, contractors will have to relinquish 75% of the area under the exploration contract. Future exploration and exploitation contracts may also need to consider what other management measures with overlapping objectives have been introduced by other intergovernmental organizations with mandates to regulate human activities (e.g., fisheries). Thus, the legal and geographic landscape in which networks of APEIs are being developed continues to (and is designed to) change. Given this situation, the size and spacing of core areas is flexible and the network development process can be adaptive to accommodate mineral extraction (16), so long as the overall regional conservation goal and design targets are not compromised. Critically, lengths of APEIs along the ridge axis can be varied to fit between existing exploration or exploitation contracts, provided these conditions are met.

More important than the precise dimensions of each APEI is the distribution of those APEIs along the ridge axis; size and spacing of APEIs along the ridge must deliver a network of areas that maintain population connectivity. Connectivity is not merely a function of the mean and maximum distance between APEIs, but also of the size of individual APEIs and the percent of habitat protected (69). Thus, any network design should ensure that: (1) habitat conservation targets are met, (2) the average length of a core area is at least 200 km, (3) the distance between APEIs is as close as possible to the core lengths of adjacent APEIs, and (4) the maximum distance between adjacent APEIs is minimized. Maintaining average core lengths of 200 km should promote self-sustaining populations within APEIs. Limiting what we refer to as the “gap ratio” (the ratio of the APEI core length to the distance to adjacent APEIs), will help ensure connectivity between APEIs. Given the highly linear nature of Mid-Ocean Ridge systems, the maximum distance between APEIs is a critical factor in determining whether the design will act as a network, or whether it will simply be multiple isolated conservation areas with concomitant losses in resilience. This becomes more critical as the average size of APEIs decreases, resulting in more larval export from the no mining area.

The conservation targets, network criteria, and performance assessment framework applied here can provide the scientific basis for design of banded APEIs on mid-ocean ridges across the
globe, facilitating broad applications of a precautionary approach for the protection of biodiversity and ecosystem function in the context of SMS mining. This process can be readily adapted for design of APEI networks on the other mid-ocean ridges where there are, or may be, mining interests. These include the spreading ridges in the Indian Ocean, where the ISA has already awarded SMS exploration leases to India, Germany, Korea, and China, and the southern and more northern extensions of the Mid-Atlantic Ridge.

Our APEI design process also considered, for the first time in the deep sea, mitigation of projected climate-induced changes. Projected climate-driven changes in pH, temperature (T), dissolved O2 concentrations, and POC flux to the seafloor will occur throughout the water column and at the sea floor (72). Such environmental shifts could alter connectivity regimes (73), induce species range shifts, change latitudinal or depth distributions of species, alter food webs, weaken carbonate skeletons, and ultimately alter biodiversity and ecosystem functions (74). In the context of area-based planning in the deep sea, conservation areas should incorporate existing syntheses and future projections of warming, deoxygenation, acidification, and POC flux to the seafloor into evaluation of habitat vulnerability and resilience (75). We used projected changes in these variables to capture current biogeochemical habitat conditions (and their associated biota) within APEI networks in the future (specifically in the year 2100). Climate induced changes in ecosystem structure and function are critical to include in the design of APEI networks to ensure that the goals of the protected-area networks are sustainable as deep-sea ecosystems are altered by climate change.

Although change in seafloor conditions appears inevitable, it is unknown exactly how much change might be physiologically stressful. POC flux is a proxy for food supply, with effects on species diversity, trophic interactions, and other ecosystem attributes (52), and POC flux to the seabed is projected to decrease in some parts of the management area by as much as 10 to 25%. Projected increases in temperature (0.1 – 0.2 °C) and reductions in oxygen seem modest (Sperling et al., 2016) but could raise metabolic energy demands of resident species and, when combined with decreased POC flux to the seafloor, even small increases might be detrimental (76). Impacts of climate change are not restricted to metazoan life. Microbial and microbial-metazoan systems in the deep sea are also expected to be influenced by climate-induced changes in temperature, oxygen concentration, POC flux, and pH, with the potential for consequences that modify or disrupt ecosystem structure and function (77). Climate-induced stressors will not act alone; changes in environmental conditions will co-occur (78) and may interact in unpredictable ways (79), highlighting the need for a precautionary approach.

Uncertainty in climate projections and their ecological impacts should not preclude considering climate issues in ongoing spatial planning for APEIs. The analysis undertaken here represents a first attempt to assess how APEI scenarios will reflect or resist change in key environmental variables under future climate change and demonstrated the relatively poor performance of the 100-km core length APEI network scenario in these metrics (Figure 3, bottom panel). We strongly encourage future studies to expand on the climate change related metrics developed here and test their ecological relevance (e.g., Sperling et al. 2016).

Our current knowledge of deep-sea ecosystems is sparse and spatially biased (81). The development of validated models of potential habitat suitability (82) and other methods to
predict the distribution of deep-sea habitats in unsurveyed areas (83) can be an important next step in refining network design. Higher resolution and more comprehensive data sets of habitat and species’ distributions, important ecological drivers, population genetic structure, connectivity at ecological and evolutionary time scales, oceanographic currents, and higher resolution of earth system models to describe future change and ecological response are needed. In the near term, it is critical important to validate plume dispersal models to inform adaptive management of the size of buffer zones around APEIs, to better understand impacts on the deep pelagic, and interlinkages between benthic and pelagic systems in the deep sea (84). The designation and valuation of ecosystem services for high seas and deep-sea ecosystems is just beginning (85–88) and will also be important for refining APEI network design in the future. With sufficient data, it should be possible to map the supply and demand of ecosystem services to guide area-based planning (89–91). Network criterion 1 (Box 1) should then be revised so that those areas providing multiple or highly valued ecosystem services would receive priority for protection from activities that may deteriorate these services. Due to the prohibitive costs of sampling in deep and distant locations under extreme environmental conditions, meeting the data needs for these management approaches will require engagement with mining contractors, who must collect high-quality baseline environmental data as part of their exploration contract, as well as the scientific research community.

The ultimate design and timing of implementation of regional APEI networks on mid-ocean ridges remains to be resolved. Regional Environmental Management Plans, including area-based tools, are within the aegis of the International Seabed Authority. Placement of APEI networks on the ridge axis prior to awarding exploration contracts is, at face value, an optimal precautionary approach for protection of the marine environment. However, given that few commercially viable mine sites are thought to exist even over many thousands of kilometers of ridge axis (3), such a strategy reduces the likelihood of discovering a commercially viable mine along the ridge axis or identifying important biodiversity areas. Further, large extents of ridge axis in the Atlantic and Indian Oceans are already under exploration contracts, potentially compromising the ability to design networks to meet the conservation goal, objectives, and design targets, if these contracted areas must be excluded from APEI network design.

We encourage the ISA and civil society to consider incentives for regional-scale environmental baseline surveys to identify commercially viable mine sites and important biodiversity areas. Our knowledge of deep-sea ecosystems is scant and, without investment in regionally intensive baseline data collection, will likely remain so for decades. Partnerships involving the ISA, contractors, and the scientific community in the environmental planning process, including baseline surveys, are critical if we are to ensure that mining activities can proceed with due regard to the environment. For now, we recommend that the best approach is for regional environmental management plans, including APEI networks based on a representative approach such as the one described here, to be implemented as soon as possible. The ISA recently released a preliminary strategy for the development of such plans especially for areas where there are currently contracts for exploration (92), with supporting activities proposed through 2020.

Materials and Methods
Data

To ensure repeatability, only published data were used. Biogeographic units of interest were the abyssal, bathyal, and hadal regions, extracted from (34). Depth and slope were derived from the General Bathymetric Chart of the Oceans (GEBCO) 2014 Grid (v. 20150318; www.gebco.net). The spreading-ridge feature was extracted from GRID-Arendal’s Global Seafloor Geomorphic Features dataset (93). Locations of known and inferred active and inactive hydrothermal vents sites were taken from the InterRidge Vent Database (94); seamounts were clipped from the Global Seamount Database (95); transform faults were obtained from the Global Seafloor Fabric and Magnetic Lineation Data Base (96). Data for contemporary (2013) pH, temperature, dissolved O\textsubscript{2} concentrations, POC flux to the seafloor were those used in Sweetman et al. (2017), as were the projected (2100) variables generated from Coupled Model Inter-comparison Project Phase 5 (CMIP5; 71, 96, 97).

All geospatial analyses were done in ArcGIS 10.4.1 and all data layers were clipped to the case study area using a custom projection (Mollweide, with the central meridian set to -36.00°) that allowed for the best compromise between exact area calculations and exact distance calculations.

Derived Variables

Distance, total area, and area by habitat coverage

Pairwise distances between APEI core areas in each scenario were calculated by running the “Near” tool using geodesic distances between nearest edges of cores. The area of the management unit conserved in each scenario was calculated by summing the core areas of the APEIs and dividing by the area of the management subunit to describe the percent area conserved. To analyze the degree to which targets for areal coverage of specific habitat types (i.e., area of spreading ridges and biogeographic units; number of active and inactive hydrothermal vents, seamounts; length of transform faults) were achieved, habitats falling within the core areas of each scenario were computed using the “Identify” tool; area of the habitat within the cores was divided by the total area of the management subunit to get the percent conserved by each network scenario.

Geomorphologic, oceanographic, and climate-change variables

Distributions of depth and slope (geomorphological features) within APEI core areas were compared to their distributions within the entire management subunit for each scenario. Core and management subunit areas were converted to 1 km resolution rasters to ensure that the succeeding calculations in ArcMap were not performed at a coarser resolution. Variables were then binned by depth (100-m bins) or slope (1° bins) before extracting values. The “Zonal Histogram” tool was used to generate frequency histograms for each variable within APEI cores and for the management units. The same process was used to calculate histograms for the current (2013) and future (2100) distributions of four oceanographic variables at the seafloor, each binned into 20 equal-interval variables: acidity (pH), temperature (°C), oxygen (ml L\textsuperscript{-1}), POC flux to the seafloor (mg C m\textsuperscript{-2} d\textsuperscript{-1}). Percent change between current and future conditions for pH, T, dissolved O\textsubscript{2} concentrations and POC flux to the seafloor were calculated for each grid cell in the study area.
Eighteen quantifiable metrics were developed to gauge network performance against the conservation targets identified in Box 1 (Table 1). The three APEI scenarios with core lengths of 100 km, 200 km or 300 km were evaluated to assess how size and spacing of APEIs influence the degree to which the conservation targets were met. Each scenario was scored based on how well it achieved specific conservation goals for individual metrics and each criterion. Equations and conservation targets for all metrics are included in Table 1. For ease of interpretation and to allow summarizing within a criterion, all scores were normalized to a range of 0 to 5, with 5 being the best score.

The metrics used in each criterion are linked by their properties and objectives. As such, we opted to include a summary metric for each criterion to improve ease of interpretation of the results. The criteria scores were calculated by taking the average of the scores across the metrics included in that criterion. Due to differences in what the criteria measure, and in accordance with current consensus on multicriteria analytical methods, no effort was made to average across all criteria.

Supplementary Materials

Table S1. Drivers of deep-sea biodiversity. Variables used as surrogates to guide the development of a spatial management plan, and those that might inform future efforts at the development of networks of MPAs on mid-ocean ridges.

Table S2. Network scenario performance (non-climate change metrics). Raw values and comments for performance of the scenarios for each metric.

Table S3. Network scenario climate change performance. Analysis of APEI network scenarios relative to current and future modeled values for pH, temperature, dissolved O₂ concentrations and POC flux to the seafloor.

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Author contributions: C.L.V.D., T.M., A.C., D.D., and P.W. conceived the project; D.D., T.M., and P.H. undertook the GIS mapping; D.D. extracted feature data for performance assessment; R.E., C.S., L.L., D.D. and C.L.V.D. undertook the performance assessment; all authors contributed to iterative discussions, writing, and edits to the manuscript. D.D. & C.L.V.D. led those discussions and the writing and editing.

Competing interests: The authors declare there are no competing interests.

Data and materials availability: All geospatial information used in this analysis is publicly available.
Figure 1. Study area and management context. The case study area is centered on the ridge axis from the southern boundary of the Portuguese Extended Continental Shelf (ECS) claim to the northern boundary of the UK ECS claim at Ascension Island, and extends 500 km to either side of the axis. Two management subunits are proposed here: northern Mid-Atlantic Ridge (nMAR) & the Romanche Transform Fault (RTF). Existing French, Polish and Russian Federation exploration contracts for SMS are from the ISA database (https://www.isa.org.jm).

Figure 2. Biogeographic context, Important Areas and APEI scenarios. APEI scenarios were anchored by Important Areas identified by expert opinion before scenario development began. Important Areas include (A) critical transform faults (i.e., Vema, Romanche), biogeographic transition zones (i.e., the bathyal transition zone in the region of the Romanche Transform Fault), and genetic hybrid zones (i.e., Broken Spur). Three APEI network scenarios were developed for the nMAR subunit, with core lengths along the ridge axis of (B) 100 km, (C) 200 km, and (D) 300 km; each APEI also has a 50 km buffer on the northern and southern sides of the core zone.

Figure 3. APEI Network Performance Assessment (nMAR Management Subunit). Bottom Panel: Scores for 17 metrics derived to capture performance (5 being the best) of scenarios against the five CBD network criteria (see legend for color code; light shading: 100-km scenario, medium shading: 200-km scenario; dark shading: 300-km model). Metrics and metric equations are defined in Table 1; raw values and commentary is provided in Table S2. Dotted line: Conservation targets for each score; CC: Climate Change. Top Panel: Summary scores for each network criterion (calculated by taking the average scenario score of the metrics for a criterion). Scenario core lengths are provided on the x-axis. APEI: Area of Particular Environmental Interest.

Table 1. Network Criteria, Conservation Targets & Metrics. CBD network criteria (bold) including definitions quoted from Convention on Biological Diversity (2008), metrics (italics), conservation targets, and metric equations used in this study, with relevant comments.
<table>
<thead>
<tr>
<th>Network Criteria</th>
<th>Definitions &amp; Metric Equations</th>
<th>Conservation Targets &amp; Comments</th>
</tr>
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<tbody>
<tr>
<td><strong>Important Areas</strong></td>
<td>“[Important Areas are] geographically or oceanographically discrete areas that provide important services to one or more species/populations of an ecosystem or to the ecosystem as a whole, compared to other surrounding areas...”</td>
<td>The objective is to protect 100% of Important Areas. Scores are based on percent area conserved (for transition zones), percent by number of features conserved (for hybrid zones), and by percent of length conserved (for transform faults).</td>
</tr>
<tr>
<td><strong>Major Transform Faults</strong></td>
<td>APEI percent coverage/100% * 5.</td>
<td>The objective is to protect 100% of Important Areas. Scores are based on percent area conserved (for transition zones), percent by number of features conserved (for hybrid zones), and by percent of length conserved (for transform faults).</td>
</tr>
<tr>
<td><strong>Biogeographic Transition Zones</strong></td>
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<td><strong>Genetic Hybrid Zones</strong></td>
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<tr>
<td><strong>Representativity</strong></td>
<td>“Representativity is captured in a network when it consists of areas representing the different biogeographical subdivisions of the global oceans and regional seas that reasonably reflect the full range of ecosystems, including the biotic and habitat diversity of those marine ecosystems.”</td>
<td>The objective is to protect a representative amount (30% - 50%) of key habitat within the study region. Scores are based on percent area conserved (for spreading ridges), percent by number of features conserved (for active and inactive vents, and seamounts), and by percent of length conserved (for transform faults).</td>
</tr>
<tr>
<td><strong>Discrete habitat variables:</strong></td>
<td>APEI percent coverage/50% * 5, where any score greater than 5 was set to 5.</td>
<td>Note: Active hydrothermal vents and other vulnerable marine ecosystems are at risk of serious harm from SMS mining activities. We expect 100% of active hydrothermal vent ecosystems and other habitats at risk of serious harm to be protected through conservation measures, including but not limited to APEIs.</td>
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<tr>
<td><em>Spreading Ridge</em></td>
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<td><em>Active vents</em></td>
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<td><em>Inactive vents</em></td>
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<td><em>Fracture zones</em></td>
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<td><em>Seamounts</em></td>
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<tr>
<td><strong>Continuous variables that describe the regional seascape:</strong></td>
<td>5 - (RMSE * 5)</td>
<td>The objective is to mimic the distribution of variables determined to be key drivers of biodiversity in proportion to their occurrence in the management subunit. Root Mean Squared Error (RMSE) was calculated as the difference between cumulative frequency distributions within the APEI scenario and the study region. All variables were classified into 10-15 bins to remove the effect of the number of bins on RMSE.</td>
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<td><em>Slopes</em></td>
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<td><em>Depth</em></td>
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<tr>
<td><em>Seafloor POC Flux</em></td>
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<tr>
<td><strong>Connectivity</strong></td>
<td>“Connectivity in the design of a network allows for linkages whereby protected sites benefit from larval and/or species exchanges, and functional linkages from other network sites. In a connected network individual sites benefit one another.”</td>
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</tr>
<tr>
<td><strong>Regional connectivity</strong></td>
<td>6 - (max distance between cores/75th percentile median dispersal distance), where any score greater than 5 was set to 5.</td>
<td>The objective is to ensure that there is no major disruption to dispersal across the network of APEIs. The maximum distance between APEIs compared to median faunal dispersal distances is an indicator of the potential for disrupting dispersal within the entire management subunit.</td>
</tr>
</tbody>
</table>

| **Network Population Persistence** | 6 - mean gap ratio (i.e., the mean distance between cores/mean core length), where any score greater than 5 was set to 5. | The objective is to promote the viability of populations by self-seeding within APEIs and/or dispersal between APEIs. By minimizing the difference in length of APEI core areas versus distance between core areas, species that on average disperse beyond the APEI have a good chance of being able to disperse to adjacent APEIs. Minimizing this “gap-ratio” should enhance persistence of species across the network as well as within individual APEIs, and increase resilience across the network to localized disturbances. |

| **Replication** | “Replication of ecological features means that more than one site shall contain examples of a given feature in the given biogeographic area. The term “features” means “species, habitats and ecological processes” that naturally occur in the given biogeographic area.” |  |

| **Replication** | Number of APEIs where any score greater than 5 was set to 5. | The objective is to have 3-5 replicate APEIs within a management unit, to decrease the likelihood of local catastrophes causing systemic biodiversity loss. |

| **Viability & Adequacy** | “Adequate and viable sites indicate that all sites within a network should have size and protection sufficient to ensure the ecological viability and integrity of the feature(s) for which they were selected.” |  |

| **Total Area** | \((\text{APEI percent coverage}/50\%) \times 5\), where any score greater than 5 was set to 5. | The objective is to conserve an adequate portion (30% - 50%) of the management unit to ensure the viability of populations within it. Total area conserved is a proxy for overall adequacy of a network. The total area metric was calculated similarly to the habitat representativity metrics above. |

| **Within APEI Persistence** | \(5 \times (\text{APEI core length}/200 \text{ km})\) where any score greater than 5 was set to 5. | The objective is to ensure APEIs are large enough to maintain minimum viable populations, and metapopulations, within a single APEI. The larger the APEI, the greater the probability self-recruitment within the APEI, and the lower the percentage of larval export from the APEI, which should enhance the persistence of populations, metapopulations and communities within an APEI. 200 km was used as the minimum scale required to encompass two times the median dispersal distance |
of 75% of deep-sea fauna with known dispersal scales (Baco et al. 2016).

| **Climate Change:** Absolute Similarity | 5 - (RMSE * 5) | The objective is to conserve areas where climate impacts would be minimized. The more closely distributions of key climate variables (pH, T, dissolved O₂ concentrations and seafloor POC flux) in the future (i.e., 2100) APEI cores mimic the current (i.e., 2013) distribution in the management unit, the less impact is expected. Root Mean Squared Error (RMSE) was calculated as the difference between cumulative frequency distributions within the APEI scenario and the study region. All variables were classified into 10-15 bins to remove the effect of the number of bins on RMSE. |
| **Climate Change:** Relative Local Change | APEI percent coverage/50% * 5 where any score greater than 5 was set to 5. | The objective is to conserve 30% - 50% of the areas projected to be least impacted by climate change. Least impacted cells were defined as the 10% of cells with the lowest percent change between current (2013) and predicted (2100) values of the four key climate variables (pH, T, dissolved O₂ concentrations and POC flux to the seafloor). The percent of those cells falling in APEI cores for each scenario were calculated following the approach used for representativity metrics (continuously distributed variables). |
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<table>
<thead>
<tr>
<th>Parameter or Data Set</th>
<th>Examples and Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathymetry (Depth)</td>
<td>Fish diversity patterns with depth and physiological adaptations (Brown &amp; Thatje 2014); beta diversity of deep sea echinoderms (Wagstaff et al. 2014) and other organisms (McClain &amp; Rex 2015) along depth gradients; a bathymetric effect on biodiversity is often attributable to energy availability (Stuart et al. 2017) and/or pressure adaptations (Lacey et al. 2016)</td>
</tr>
<tr>
<td>Seamount Distribution</td>
<td>Potential for seamount-scale endemism (Cho &amp; Shank 2010, though see Kvile et al. 2014); role in regional biodiversity (Bongiorni et al. 2013); fish vertical zonation (Menezes et al. 2006)</td>
</tr>
<tr>
<td>Biogeographic Region</td>
<td>Spatially interpreted using global data sets for depth, temperature, POC flux, oxygen concentration (Watling et al. 2013)</td>
</tr>
<tr>
<td>Latitude</td>
<td>Latitudinal gradients in species richness (Rex et al. 2000, McClain &amp; Rex 2015)</td>
</tr>
<tr>
<td>POC Flux</td>
<td>A primary determinant of α and β diversity, biomass, and trophic interactions in bivalves (Brault et al. 2013); ocean biodiversity structured through a species-energy framework (Woolley et al. 2016)</td>
</tr>
<tr>
<td>Transform Faults</td>
<td>Serve as conduits for E-W movement of water masses between basins (Mercier &amp; Speer 1998); transport of larvae and physicochemical properties (van der Heijden et al. 2012); steep slopes, occurrence of hard and soft substrata, high current and deposition regimes support a diverse fauna (Gebruk &amp; Krylova 2013) (Mercier &amp; Speer 1998, Morozov et al. 2010, van der Heijden et al. 2012, Gebruk &amp; Krylova 2013)</td>
</tr>
<tr>
<td>Hydrothermal Vents</td>
<td>Host endemic species of invertebrates and fishes that depend on microbial chemosynthetic primary productivity (VanDover 2000); beta diversity patterns influenced by availability of multiple microhabitats (Sarradin et al. 2015)</td>
</tr>
<tr>
<td>Water mass properties</td>
<td>Water masses influence seamount species richness (Henry et al. 2014); temperature, pH, O2 water mass properties and diversity patterns (McClain &amp; Rex 2015, Yasuhara &amp; Danovaro 2016); critical in predicting biogeographic units (Watling et al. 2013)</td>
</tr>
<tr>
<td>Other key parameters for which there is insufficient data coverage or resolution or that are not relevant within the study area</td>
<td></td>
</tr>
<tr>
<td>Bathymetric Position Index, curvature, rugosity (derived from high-resolution bathymetry)</td>
<td>Proxies for seabed substratum type (Dunn &amp; Halpin 2009), proxies for current flow and predictors of coral habitats (Anderson et al. 2011, Rengstorf et al. 2014); data not available with high enough coverage and resolution for the study area.</td>
</tr>
<tr>
<td>Substratum type</td>
<td>Coral distributions on the Mid-Atlantic Ridge (Morris et al. 2012); seamount assemblages (Anderson et al. 2011); data not available with high enough coverage and resolution for the study area</td>
</tr>
<tr>
<td>Fronts</td>
<td>Atlantic Sub-Polar Front is an asymmetric, taxon-specific biogeographic boundary for deep pelagic fish in the North Atlantic (Priede et al. 2013, Sutton et al. 2013); no known fronts within the study area</td>
</tr>
<tr>
<td>High-resolution hydrodynamic variables (e.g., ROMS, vertical and)</td>
<td>Can predict, for example, coral distributions (Mohn et al. 2014, Rengstorf et al. 2014); data not available with high enough coverage and resolution for the study area</td>
</tr>
<tr>
<td>Characteristic friction velocities and critical sheer stress</td>
<td>Ecologically relevant variables, including measures of seafloor disturbance and scope for growth (Kostylev &amp; Hannah 2007); data not available with high enough coverage and resolution for the study area</td>
</tr>
<tr>
<td>Sediment characteristics</td>
<td>Positive correlation between sediment particle size diversity and species diversity for macrofaunal infauna (Etter &amp; Grassle 1992, Leduc et al. 2012); grain size and meiofauna on seamounts (Zeppilli et al. 2013); particle size and abyssal hills (Durden et al. 2015); data not available with high enough coverage and resolution for the study area</td>
</tr>
<tr>
<td>Other factors</td>
<td>Seabed litter (Woodall et al. 2015), keystone structures (canyons, abyssal hills) (Vetter et al. 2010, Durden et al. 2015); data not available with high enough coverage and resolution for the study area</td>
</tr>
</tbody>
</table>

**Table S1 Bibliography**


Table S2. Raw values and performance metric scores for the assessment of the three APEI network scenarios. Methods for each metric are described in Table 1.

<table>
<thead>
<tr>
<th>nMAR Management Unit</th>
<th>Raw Values (RMSE, % Habitat Coverage &amp; Distance ratios)</th>
<th>Metric Scores</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100 km</td>
<td>200 km</td>
</tr>
<tr>
<td>IMPORTANT AREAS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hybrid zones</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Major transform faults</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
</tr>
<tr>
<td>REPRESENTATIVITY</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spreading Ridge</td>
<td>37.6%</td>
<td>42.9%</td>
</tr>
<tr>
<td>Active vents</td>
<td>45.5%</td>
<td>54.5%</td>
</tr>
<tr>
<td>Inactive vents</td>
<td>42.9%</td>
<td>50.0%</td>
</tr>
<tr>
<td>Fracture zones</td>
<td>27.4%</td>
<td>28.7%</td>
</tr>
<tr>
<td>Seamounts</td>
<td>25.7%</td>
<td>27.2%</td>
</tr>
<tr>
<td>Discrete Habitat Average</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slopes</td>
<td>0.02</td>
<td>0.02</td>
</tr>
<tr>
<td>Depth</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>POC Flux to the Seafloor</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>Continuous Seascape Variable Average</td>
<td>4.8</td>
<td>4.8</td>
</tr>
<tr>
<td>CONNECTIVITY</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional Connectivity</td>
<td>2.7</td>
<td>2.6</td>
</tr>
<tr>
<td>Network Population Persistence</td>
<td>2.4</td>
<td>1.5</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
</tr>
<tr>
<td>REPLICATION</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of APEIs</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
</tr>
<tr>
<td>VIABILITY &amp; ADEQUACY</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent Management Unit Conserved</td>
<td>21.3%</td>
<td>25.6%</td>
</tr>
<tr>
<td>Within APEI Population Viability</td>
<td>100</td>
<td>200</td>
</tr>
<tr>
<td>Climate Change: Absolute Similarity</td>
<td>4.5</td>
<td>4.5</td>
</tr>
<tr>
<td>Climate Change: Relative Local Change</td>
<td>2.1</td>
<td>2.2</td>
</tr>
<tr>
<td>Average</td>
<td>2.8</td>
<td>3.6</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>RTF Management Unit</th>
<th>Raw Values (RMSE, % Habitat Coverage &amp; Distance ratios)</th>
<th>Metric Scores</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100 km</td>
<td>200 km</td>
</tr>
<tr>
<td>Transition Zones (Romanche)</td>
<td>10.3%</td>
<td>70.1%</td>
</tr>
</tbody>
</table>
**Table S3. Climate change metric results.** Analysis of APEI placement scenarios relative to current and projected future oceanographic variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Raw Values (RMSE &amp; % Habitat Coverage)</th>
<th>Metric Scores</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100 km</td>
<td>200 km</td>
</tr>
<tr>
<td>Climate Change: Absolute Similarity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>pH</td>
<td>0.23</td>
<td>0.22</td>
</tr>
<tr>
<td>POC</td>
<td>0.19</td>
<td>0.17</td>
</tr>
<tr>
<td>Oxygen</td>
<td>0.02</td>
<td>0.03</td>
</tr>
<tr>
<td>Metric Average</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Climate Change: Relative Local Change</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>15.8%</td>
<td>26.3%</td>
</tr>
<tr>
<td>pH</td>
<td>14.6%</td>
<td>17.1%</td>
</tr>
<tr>
<td>POC</td>
<td>34.2%</td>
<td>36.8%</td>
</tr>
<tr>
<td>Oxygen</td>
<td>19.6%</td>
<td>8.7%</td>
</tr>
<tr>
<td>Metric average</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>