nature ecology & evolution

PERSPECTIVE
https://doi.org/10.1038/s41559-019-1091-z

Ecological variables for developing a global deep-ocean monitoring and conservation strategy

Roberto Danovaro[1,2]*, Emanuela Fanelli[1], Jacopo Aguzzi[3], David Billett[4], Laura Carugati[1], Cinzia Corinaldesi[5], Antonio Dell'Anno[1], Kristina Gjerde[6], Alan J. Jamieson[7], Salit Kark[8], Craig McClain[9], Lisa Levin[10], Noam Levin[11], Eva Ramirez-Llodra[12], Henry Ruhl[4,13], Craig R. Smith[14], Paul V. R. Snelgrove[15], Laurenz Thomsen[16], Cindy L. Van Dover[17] and Moriaki Yasuhara[18]

The deep sea (>200 m depth) encompasses >95% of the world's ocean volume and represents the largest and least explored biome on Earth (<0.0001% of ocean surface), yet is increasingly under threat from multiple direct and indirect anthropogenic pressures. Our ability to preserve both benthic and pelagic deep-sea ecosystems depends upon effective ecosystem-based management strategies and monitoring based on widely agreed deep-sea ecological variables. Here, we identify a set of deep-sea essential ecological variables among five scientific areas of the deep ocean: (1) biodiversity; (2) ecosystem functions; (3) impacts and risk assessment; (4) climate change, adaptation and evolution; and (5) ecosystem conservation. Conducting an expert elicitation (1,155 deep-sea scientists consulted and 112 respondents), our analysis indicates a wide consensus amongst deep-sea experts that monitoring should prioritize large organisms (that is, macro- and megafauna) living in deep waters and in benthic habitats, whereas monitoring of ecosystem functioning should focus on trophic structure and biomass production. Habitat degradation and recovery rates are identified as crucial features for monitoring deep-sea ecosystem health, while global climate change will likely shift bathymetric distributions and cause local extinction in deep-sea species. Finally, deep-sea conservation efforts should focus primarily on vulnerable marine ecosystems and habitat-forming species. Deep-sea observation efforts that prioritize these variables will help to support the implementation of effective management strategies on a global scale.

Industrial activities spanning from fisheries to oil and gas extraction are accelerating anthropogenic pressures on the deep sea[1–3], leading to the degradation of benthic and pelagic environments, where biological diversity remains largely unknown (Box 1). However, global impacts have not spared deep-sea ecosystems[4–7] and species loss and habitat destruction severely alter an increasing portion of deep-sea ecosystems[2,8,9]. Cumulative anthropogenic impacts act synergistically with climate-induced changes on properties and processes of the deep ocean, thus degrading environmental quality[10–12].

Deep-sea biodiversity plays a central role in provisioning services (for example, food, biochemical compounds for human health and wellbeing), and species loss can greatly reduce ecosystem functions that support these services[8]. Furthermore, high biodiversity levels increase ecosystem resilience to perturbations[13], elevating the importance of maintaining biodiversity as a key management objective in the pursuit of sustainable use of resources[14].

Sustaining healthy and productive deep oceans requires knowledge of baseline conditions and rates of change in marine ecosystems. The environmental status and resources of the coastal zones link to deep-sea ecosystems[6,15] through bi-directional exchanges of materials, nutrients, contaminants and organisms[16–18]; changes in one system may therefore impact others. Several ongoing initiatives consider the need for monitoring baseline conditions in marine shallow and deep-sea ecosystems and their changes (Box 2).

The Group on Earth Observations Biodiversity Observation Network (GEO BON) has proposed some Essential Biodiversity Variables (EBVs), to set up future monitoring programs[19]. These variables are organized into six classes and are general enough to be applied to terrestrial, freshwater and marine realms[20].

The Global Ocean Observing System (GOOS) has started the identification of the Essential Ocean Variables (EOVs[21]) and has promoted the Deep Ocean Observation Strategy (DOOS), which enhances the need for identification of EOVs relevant to the deep-sea environment[22]. However, GOOS EOVs do not include the analysis of stressors (for example, habitat integrity, pollutants, plastics and so on), which are clearly needed to assess deep-sea ecosystem health. Moreover, the monitoring of deep-sea ecosystems for biodiversity conservation requires specific variables and technological

[1]Department of Life and Environmental Sciences, Polytechnic University of Marche, Ancona, Italy. [2]Stazione Zoologica Anton Dohrn, Naples, Italy. [3]Instituto de Ciencias del Mar (ICM-CSIC), Paseo Marítimo de la Barceloneta, Barcelona, Spain. [4]National Oceanography Centre, Southampton, UK. [5]Department of Sciences and Engineering of Materials, Environment and Urban Planning (SIMAU), Polytechnic University of Marche, Ancona, Italy. [6]IUCN Global Marine and Polar Programme, Gland, Switzerland. [7]School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK. [8]The Biodiversity Research Group, The School of Biological Sciences, Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, Queensland, Australia. [9]Louisiana Universities Marine Consortium, Chauvin, LA, USA. [10]Center for Marine Biodiversity and Conservation and Integrative Oceanography Division, Scripps Institution of Oceanography, University of California, La Jolla, CA, USA. [11]Department of Geography, The Hebrew University of Jerusalem, Jerusalem, Israel. [12]Norwegian Institute for Water Research, Oslo, Norway. [13]Monterey Bay Aquarium Research Institute, Moss Landing, CA, USA. [14]Department of Oceanography, University of Hawaii at Mano'a, Honolulu, HI, USA. [15]Departments of Ocean Sciences and Biology, Memorial University of Newfoundland. St, John's, Newfoundland, Canada. [16]Jacobs University, Bremen, Germany. [17]Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, Durham, NC, USA. [18]School of Biological Sciences and Swire Institute of Marine Science, The University of Hong Kong, Hong Kong SAR, China. *e-mail: r.danovaro@univpm.it

Box 1 | Main threats for deep-sea ecosystems

The deep oceans are increasingly impacted by human activities[1,2]. Here the four major threats for deep-sea species/habitats/ecosystems are presented, and although they are treated individually, their effects can be cumulative and multiple threats can be interactive.

Climate change: ocean warming is expected to reduce surface ocean production[78] and hence the particulate organic carbon (POC) flux (that is, food supply) to the deep-sea life, altering structural and functional variables of deep-sea assemblages[79–81]. Temperature changes in the deep sea influence biodiversity and key life-history traits (that is, reproductive effort, larval development[55,82], longevity, and metabolic rates, and body size of deep-sea organisms[83]). Higher temperatures increase deep-sea respiration, thus exacerbating the effects of food limitation[84]. Such changes are expected to select the species pre-adapted to new conditions, thus increasing beta diversity over time[85]. Moreover, climate change will presumably cause oxygen decline and expand OMZs[86], accelerate organic matter biogeochemical cycling, miniaturize organism size and increase mortality of deep-sea biota, potentially resulting in extinctions in species with limited dispersal capabilities, or where suitable habitats become unavailable. Also, ocean acidification reduces the calcification capacity of corals and crustaceans, alters their metabolism, and dissolves the non-living components of coral reefs[87].

Hydrocarbon extraction and mining: the substantial development of exploration for—and in the future exploitation of—seabed minerals and fossil fuels is exacerbating conservation concerns despite the absence of baseline ecological knowledge in many cases[24]. The impact of proposed large-scale deep-sea mining activities can potentially transform deep-sea ecosystem structure and functions irreversibly[88], removing most life locally, possibly leading to 'desertification' of the ocean[44]. Such environmental degradation associated with exploitation has well-known parallels on land, where poor environmental practices have promoted land degradation and eventual desertification in many terrestrial ecosystems[77,89,90]. The potential consequences of this degradation can add tensions between the pressure to develop industrial exploitation rapidly and the desire to establish robust and quantitative baseline knowledge on the status of deep-sea ecosystem goods and services[3,24].

Deep-sea fisheries: historically established deep-sea fisheries have a proven capacity to remove slow-growing, long-lived species[91] and many habitat-forming organisms from the seafloor[92] (Box 1 figure), greatly altering habitat properties (for example, re-shaping seafloor topography and resuspension of bottom sediment[93]). Further, many deep-sea commercial species congregate in large numbers around seamounts to feed and spawn, making them extremely vulnerable to overfishing (for example, the case of the Patagonian toothfish and orange roughy fished to commercial extinction in just a few years). Presently, most deep-water species are likely to be over-exploited, as approximately 40% of the world's fishing grounds are now in waters deeper than 200 m (ref. [46]).

Continued

Box 1 | Main threats for deep-sea ecosystems (Continued)

Contaminants and litter: the growing human population has led to increased inputs of pollutants and marine litter, including plastic, into the ocean, where they are transferred through passive sinking or trophic transfer into the deep sea. Both macroplastic and organic contaminants are common in sediments and organisms all the way to the deepest waters in the Mariana Trench[45,94]. Microplastics are pervasive in deep-sea sediments where they make their way into the food web[95]. Deep-water oil spills, cargo spillage, intentional waste disposal, pharmaceuticals and other organic contaminants threaten the integrity of deep-sea populations, but the sources, pathways, fates and ultimate consequences are poorly known[1].

Box 1 Figure: Examples of species that inhabit deep-sea ecosystems. From left to right, from the top to the bottom: *Grimpoteuthis robson* (Dumbo octopus), *Uroptychus* sp. (purple squat lobster), *Chaunacops coloratus* (sea toad), *Isidella tentaculum*, *Abyssocladia polycephalus*, *Euprymna scolopes* (bobtail squid), *Bathynomus giganteus*, *Ophidion holbrookii* (cusk eel), *Harriotta raleighana*, *Beryx decadactylus* (alfonsino). Credit: *Grimpoteuthis robson*, NOAA Office of Ocean Exploration and Research, Exploration of the Gulf of Mexico 2014; *Uroptychus* sp., NOAA Office of Ocean Exploration and Research, Hohonu, Moana 2016; *Chaunacops coloratus*, NOAA Office of Ocean Exploration and Research, Deepwater Wonders of Wake; *Isidella tentaculum*, NOAA Office of Ocean Exploration, Gulf of Alaska 2004; *Abyssocladia polycephalus*, adapted with permission from ref. [96], Magnolia Press, S. A. Pomponi; *Euprymna scolopes*, NOAA Office of Ocean Exploration and Research, Windows to the Deep 2018; *Bathynomus giganteus*, *Ophidion holbrookii*, *Harriotta raleighana*, NOAA Office of Ocean Exploration and Research, Gulf of Mexico 2017; *Beryx decadactylus*, USGS.

tools[23,24]. The expanding proposals of variables indicates a lack of consensus within the scientific community, which requires expert elicitation on prioritizing essential biological and ecological variables needed for future deep-sea ecosystem investigations.

Here, we identify a complete set of biological and ecological variables, parameters, attributes and indicators (hereafter reported as 'variables') designed to capture the most relevant aspects of the biology and ecology of deep-sea ecosystems, including deep-sea conservation and resilience potential, thus enabling sound evaluation of their status.

Biological and ecological variables are particularly relevant to achieving important societal goals, such as the maintenance of deep-ocean goods and services and, in a broader perspective, Sustainable Development Goal 14 of the United Nations Development Program, which can define strategies for sustainable industrial exploitation of deep-sea ecosystems (Fig. 1).

We define a list of deep-sea essential ecological variables (DEEVs) needed for developing a holistic approach in deep-sea ecosystem management and conservation: (1) biodiversity: water column and seafloor components and measures; (2) ecosystem functions; (3) impacts and risk assessment; (4) global climate change, adaptation and evolution; and (5) ecosystem conservation. The DEEVs represent a development of the GOOS EOVs and GEO BON EBVs, as they do include the biological and ecological variables covering a complete spectrum of variables needed for long-term observations in the deep ocean.

For the expert elicitation of the DEEVs, we first identified a set of variables through an extensive scientific literature analysis (Supplementary Table 1). We then circulated a questionnaire on these variables amongst the authors, discussed, cleared for ambiguities and prioritized the list (through a Qualtrics platform[25]; see Supplementary Information). After that, we distributed the questionnaire to 1,155 international deep-sea scientists, of which 112 provided responses. The responding scientists spanned a wide range of competences and experience, and a global geographic distribution (Supplementary Figs. 1–4). The respondents, who are primarily scientists, although they also hold other roles, were asked to prioritize the variables for each scientific area, based on a unipolar rating scale, from the highest priority variable to the lowest (see Supplementary Information for a detailed description of the methodology used to analyse the responses). Then, the authors of this study discussed the potential use of prioritized variables in future monitoring and conservation strategies, particularly considering available technologies and their ongoing development.

Finally, our global literature analysis identified deep-sea areas with the highest number of deep-sea biodiversity hotspots and pressures (for mapping vulnerable deep-sea ecosystems) in order to identify the priority regions for future transnational deep-sea conservation actions based on the DEEVs here identified.

Measuring deep-sea species and habitat biodiversity

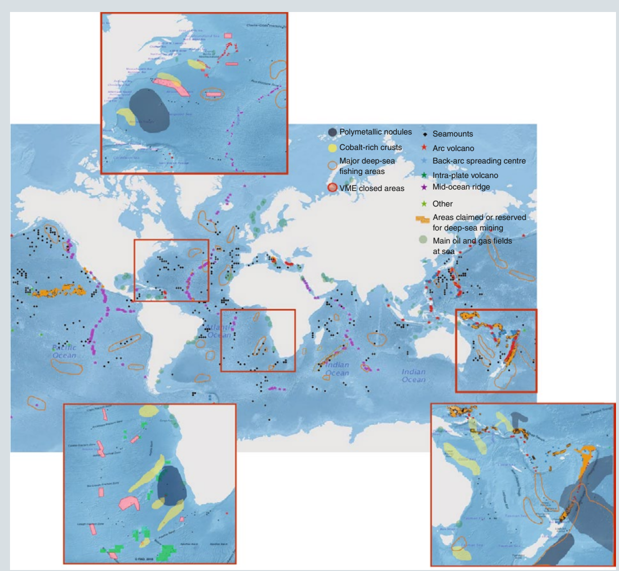
Measuring deep-sea biodiversity has challenged deep-sea scientists since the pioneering expeditions of the nineteenth century[26]. Indeed, although researchers have maintained some ship-based water column time-series for more than 50 years[27,28], most water-column biological data come from shallow waters and coastal areas of European seas and the North Atlantic and Southern oceans, but almost none from the dark portion of the oceans. Deep-sea ecosystems host a multitude of captivating rare species (for example, deep-sea sharks such as *Mitsukurina owstoni*, giant squids such as *Architeuthis* spp., sperm whales such as *Physeter macrocephalus*, several cephalopod species, such as the Dumbo octopus *Opisthoteuthis californiana*, new crustaceans such as *Kiwa hirsuta*, *Psychrolutes marcidus*, giant cnidarians such as *Praya dubia*; see Box 1), and commercially harvested species (for example, red corals, blue and red shrimps, deep-sea lobsters, orange roughy and Alfonsino fish), as well as unique habitats (for example, hydrothermal vents, cold seeps and mud volcanoes) and ecosystem engineers (for example, cold-water corals, sponges, xenophyophore fields and bivalve beds).

The prioritized list of biodiversity variables, determined through the expert elicitation both for the water column and seafloor, is illustrated in Fig. 2 and in Supplementary Fig. 5. This list shows that, among the different deep-sea biological components considered, respondents considered medium to large-sized organisms the most relevant in both water column and sediments. This result is consistent with many marine policies that focus on large organisms (for example, marine mammal protection, fishery management measures, vulnerable marine ecosystems (VMEs)). Of the water column variables, nekton ranked highest in priority reflecting crucial interaction with many benthic and pelagic components[29] and an almost complete dearth of information below depths of 1,500–2,000 m. Mega- and meso-zooplankton were followed by macro-zooplankton and micro-nekton, which play a central role as mid-trophic level prey for species of economic and conservation concern, and in transporting carbon to depth through the biological pump[30]. Within the benthic domain, macrofauna ranked highest in priority, followed by epibenthic megafauna. These components include habitat-forming species and the expert elicitation considered the importance of such ecosystem engineers and their role in structuring benthic habitats and promoting biodiversity hotspots. Mega-, meso- and microzooplankton in deep waters and meiofauna in

Box 2 | Current monitoring initiatives

The Deep-Ocean Stewardship Initiative (DOSI), the International Network for Scientific Investigation of Deep-Sea Ecosystems (INDEEP), and the Group on Earth Observation Biodiversity Observing Network (GEO BON) aim at providing scientific advice to support the United Nations Sustainable Development Goal (SDG) 14 (that is, conservation and sustainable use of the ocean and its resources). The Global Ocean Observing System (GOOS), and the Deep Ocean Observation System (DOOS) are attempting to define strategies for identifying Essential Ocean Variables[97], but lack an adequate biological/ecological approach[87,97]. With support from INDEEP a World Register of Deep-Sea Species (WoRDSS) was launched, based on the World Register of Marine Species (WoRMS). The Census of Marine Life (CoML[98]) has contributed to the census of deep-sea species, which however remains far from being complete as 50% of macro–megafaunal species and likely more than 80–90% of meiofaunal species remain undiscovered[99,100]. Existing approaches, protocols and technologies have focused on deep-sea pelagic and benthic ecosystems processes including variables of ecosystem functioning[101] as well as indicators of ecosystem efficiency[8]. The identification of the variables of ecological impacts requires a holistic approach. Environmental risk assessments rely on understanding the intensity and frequency of disturbance created by an activity and the sensitivity of the target ecosystem to those disturbances[1]. Current monitoring initiatives consider the needs of baseline studies to analyse baseline conditions, thus facilitating routine monitoring of environmental impacts of human activities (and natural events) to gauge ocean health within the context of natural variation. The ideal set of variables should combine a broad spectrum and specific ones, able to provide high sensitivity in detecting a wide range of impacts (that is, degradation or loss of habitat, sediment resuspension, light and noise footprints, and the introduction of toxic materials[102]). The variables of climate change impacts consider shifts in deep-sea species' spatial distribution[103], but also species-specific traits (that is, body size, reproduction mode, feeding behaviour and so on) allow quantification of how species respond to global change including climate change, biological invasions, overexploitation and habitat fragmentation[104]. New ecosystems and habitat types are continuously discovered at depths below 200 m (ref. [105]), and many of these represent hotspots of key processes or endemic species[16,106], which require conservation strategies. Currently, deep-sea conservation initiatives include off-shore MPAs (that is, Special Areas of Conservation) and Other Effective Area-Based Conservation Measures, including Area-Based Fisheries Management, the designation of Vulnerable Marine Ecosystems (VMEs), or Areas of Particular Environmental Interests (APEIs), which are a form of MPA where no seabed mining will be authorized to take place. However, these conservation measures ensure the effective protection of very few specific habitat-types and species assemblages or even unique species, and over very limited spatial scales[70]. Additionally, the Convention on Biological Diversity (CBD) has begun the effort of deep-sea conservation by designating Ecologically and Biologically Significant Areas (EBSAs), based on several criteria: (1) uniqueness or rarity; (2) special importance for life history of species; (3) importance for threatened, endangered or declining species, and/or habitats; (4) vulnerability, fragility, sensitivity and slow recovery; (5) biological productivity; (6) biological diversity; and (7) naturalness. These criteria can be weighted according to the connectivity of the areas, their representativeness and their extension. There is therefore an urgent need to identify priority areas for protection at a global scale, starting from Areas Beyond National Jurisdiction and the High Seas. The scale and spacing of conservation efforts can depend on the need to protect the full range of habitats within an ecoregion, sufficient to sustain populations[62,107]. Some habitats have three-dimensional characters that warrant special consideration, areas with high topographic complexity and habitat heterogeneity, and biodiversity hot-spots with high levels of endemism.

Box 2 Figure: Global map of deep-sea areas that according to international standards we identified as priority targets for protection. VME closed areas, seamounts, arc volcanoes, back-arc spreading centres, intra-plate volcanoes, mid-ocean ridges and other similar features and bottom fishing areas. Map redrawn with permission from ref. [108], FAO; orange areas are areas claimed or reserved for deep-sea mining, redrawn from the International Seabed Authority, Flanders Marine Institute, Nautilus Mineral (public domain); areas in blue and light green are marine mineral deposits (that is, polymetallic nodules (blue) and cobalt-rich ferromanganese crusts (light green)), redrawn with permission from ref. [109], Miller, Thompson, Johnston and Santillo, under a Creative Commons license CC BY 4.0; yellow lines define main deep-sea fishing areas and major fisheries on seamounts and ridges, redrawn with permission from ref. [110], IUCN.



sediments were considered medium priority. We interpreted these results as a reflection of the experts' limited available knowledge of the quantitative importance of some of these biological components and their intermediate position in the deep-sea food webs.

Finally, and somewhat surprisingly, respondents ranked microorganisms (that is, bacteria, archaea and unicellular eukaryotes both in water column and in seabed) from medium to very low priority. We attribute these responses to a bias in specific skillsets that often did not include microbial ecology/microbiology, acknowledging increasing evidence of the potential contribution of microorganisms to overall marine biodiversity. For large-sized organisms, such as deep-water corals and deep-sea sharks, the experts widely recognized that 50 to 90% of these biological components remain undiscovered[31], and therefore prioritized them. The high prioritization of large animals also means that researchers need better complete data of large-size species, but do not discount the importance of smaller organisms[32].

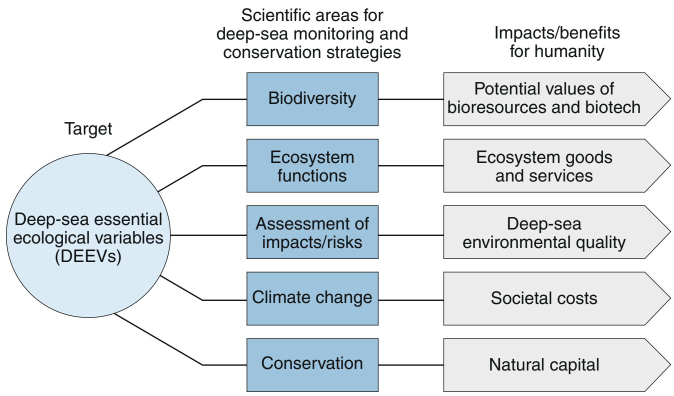


Fig. 1 | Deep-sea monitoring strategy based on DEEVs. This monitoring strategy will facilitate the achievement of important societal and industrial objectives, including the discovery of the largest remaining fraction of unknown biodiversity on Earth, the development of new deep-sea technologies and exploitation of biotechnological potential, the maintenance of deep-ocean goods and services, the achievement of sustainable development goals, and finally the mitigation of global change.

The expert elicitation also provided information regarding standardizing/expressing biodiversity variables, and prioritized community composition, species distribution, species richness and habitat structure (see Extended Data Fig. 1). Respondents ranked population size, endemicity and phylogenetic distinctness medium in priority, and ranked expected species richness, species rarity and evenness as low priority.

Measuring ecosystem functions in the deep sea

Terrestrial ecologists quantify ecosystem processes by determining rates of energy and material flow between biotic and abiotic compartments (for example, biomass production, transport, decomposition or loss of organic matter, as well as nutrient regeneration). However, not all terrestrial functional variables transfer to marine ecosystems. Variables that capture deep-sea functions and processes can differ greatly from those used in coastal environments[33]; photosynthetic production that ranks high in coastal ecosystem functions is absent in the deep-sea ecosystems because of the lack of light. Conversely, respondents consider organic carbon (C) input as a key variable for assessing deep-sea functioning because of strong carbon limitation in most deep-sea ecosystems, which depend upon the 'rain' of organic matter from the surface photic layer that decreases exponentially with depth[34]. Similarly, organic matter decomposition, an important functional variable in most deep-sea environments, ranks lower in some carbon-rich deep-sea ecosystems (for example, hydrothermal vents, cold seeps and canyons/fjords, and oxygen minimum zones (OMZs)). Such ecosystems have higher trophic levels that do not fully exploit organic carbon pools that include highly refractory components[35], resulting in a substantial fraction of organic carbon burial[36,37].

The expert elicitation ranked trophic structure, benthic faunal biomass and production as the most important measures of deep-sea ecosystem functions (Fig. 2), followed by functional traits, organic matter decomposition, and organic C inputs from the water column.

This emphasis on trophic structure follows from prioritization on large organisms, megafauna (for example, holothurians and sponges) in the biodiversity section as an important driver in carbon energy transfer; all healthy ecosystems tend to maximize biomass, especially at higher trophic levels. However, smaller organisms in deep-sea ecosystems increasingly dominate with increasing water depth[26]. Meiofaunal biomass and production, for instance, dominate macro- and megafauna at depths of >1,000–2,000 m (ref. [38]), therefore small and large faunal components contribute to deep-benthic functions.

We also agreed on the relevance of functional traits, which the scientific community recognized as a key variable, but are often missing from available studies of ecosystem functioning[8]. Here, the lack of a specific, standardized metric adds a problem with endorsing this variable.

At bathyal and abyssal depths, microbes (primarily bacteria followed by archaea) largely dominate overall biomass and production[39]. These microscopic components, essential for deep-sea ecosystem functions, contribute to carbon cycling, nutrient regeneration and the food webs[40]. In addition, in some deep-sea systems (including hydrothermal vents, cold seeps and OMZs), chemosynthetic production forms the basis of the food web[35]. Therefore, despite the results of the expert elicitation, we stress microbial heterotrophic and chemoautotrophic C production as two essential ecological variables needed for understanding the key processes sustaining the functioning of deep-sea food webs and biogeochemical cycles.

Measuring deep-sea ecosystem health, impacts and risk assessment

The oil, gas and fisheries industries impact the deep water column and seabed (for example, seamounts, hydrothermal vents, cold seeps, bathyal slopes, canyons and abyssal plains)[2,11]. Mineral extraction will potentially impact vast areas of seafloor[1]. Concurrently, overfishing of deep pelagic species, and plastics, microplastics and/or other chemical contaminants already affect deep-water food webs[41]. The European Marine Strategy Framework Directive (MSFD)[42], through the descriptors of Good Environmental Status, provides tools for assessing the health of marine ecosystems, but focuses mainly on coastal environments. However, some MSFD descriptors of ecosystem health alteration (for example, habitat damage, overfishing, sediment and seafood contamination, litter and noise) apply to deep-sea ecosystems. Here, we examined some of the variables utilized for the MSFD.

Our expert elicitation ranked habitat degradation as the most relevant indicator of impact, because many species depend on habitat integrity to complete their life cycle, to reproduce, and find refuge from predation[43] (Fig. 2). In addition, recovery rates (as a proxy of ecosystem resilience) also ranked amongst the most important measures of deep-sea ecosystem health, because this variable describes the ability of an ecosystem to recover after impact cessation. However, recovery rates depend on many variables, and still lack adequate standardization both in measurement or appropriate metric. For instance, a recent study proposed to use the rate of benthic faunal recovery (that is, time) after a disturbance event (for example, mining), as an indicator of resilience[44], but rates of recovery vary considerably with the biological component considered (for example, meiofauna versus deep-water corals). Thus, this indicator requires further consideration before defining a standardized approach. Sediment contamination also ranked highly as a priority variable for assessing ecosystem health, followed by resulting eco-toxicological effects, indicating increasing concern that pollution is expanding to the deep sea[45]. Also, the effects of marine litter and sediment resuspension on deep-sea ecosystems resulted in its ranking next as a potential indicator of impact.

Our assessment of the expert elicitation indicates that some risks in the deep sea may differ from those in shallow water. For instance, notwithstanding the widely recognized loss of top predators—even in the deep sea[46] respondents did not identify this variable as a priority. Similarly, the surprisingly low ranking of marine litter (which is 80% plastics) amongst the sources of deep-sea impact may result from the (incorrect) assumption that large amounts of litter never reach the deep sea. Similar differences exist in appreciating potential impacts of underwater noise. Despite recognition of increased noise levels, even at bathyal–abyssal depth[47], deep-sea scientists responding to the survey indicated no strong evidence of serious

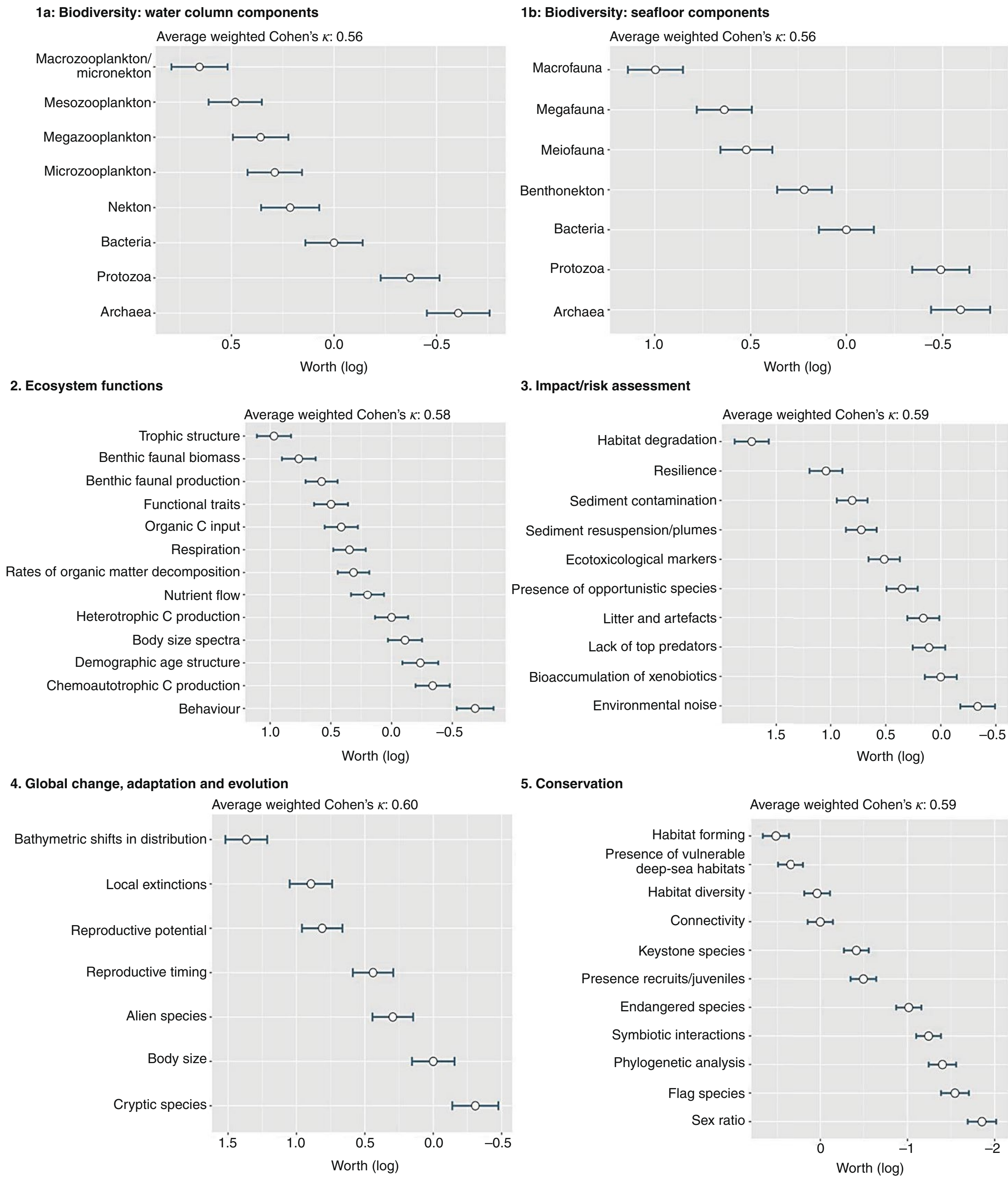


Fig. 2 | Expert elicitation results. Results of the expert elicitation were obtained using the Plackett–Luce model for the analysis of the responses and the priority of the DEEVs (*y* axis), according to the different scientific areas (biodiversity; ecosystem functions; impacts and risk assessment; global climate change, adaptation and evolution of the deep-sea life, and deep-sea ecosystem conservation). The worth of each variable is reported on log scale (*x* axis). Error bars represent standard errors of coefficients, corresponding to variation in estimated variable importance. Average weighted Cohen's κ values are also reported on the upper part of each graph.

harm. Overall, however, the authors and survey respondents unanimously agreed on prioritizing monitoring habitat damage, given the high levels of concern regarding the impact of bottom-contact fisheries and deep-sea mining (among other sources of habitat impact) for the sustainable future of the deep oceans.

Measuring global climate change impacts, adaptation and evolution of deep-sea life

The constancy of temperature over time represents perhaps the best-known attribute of all deep-sea ecosystems (excluding hydrothermal vents), along with the effects of temperature changes across

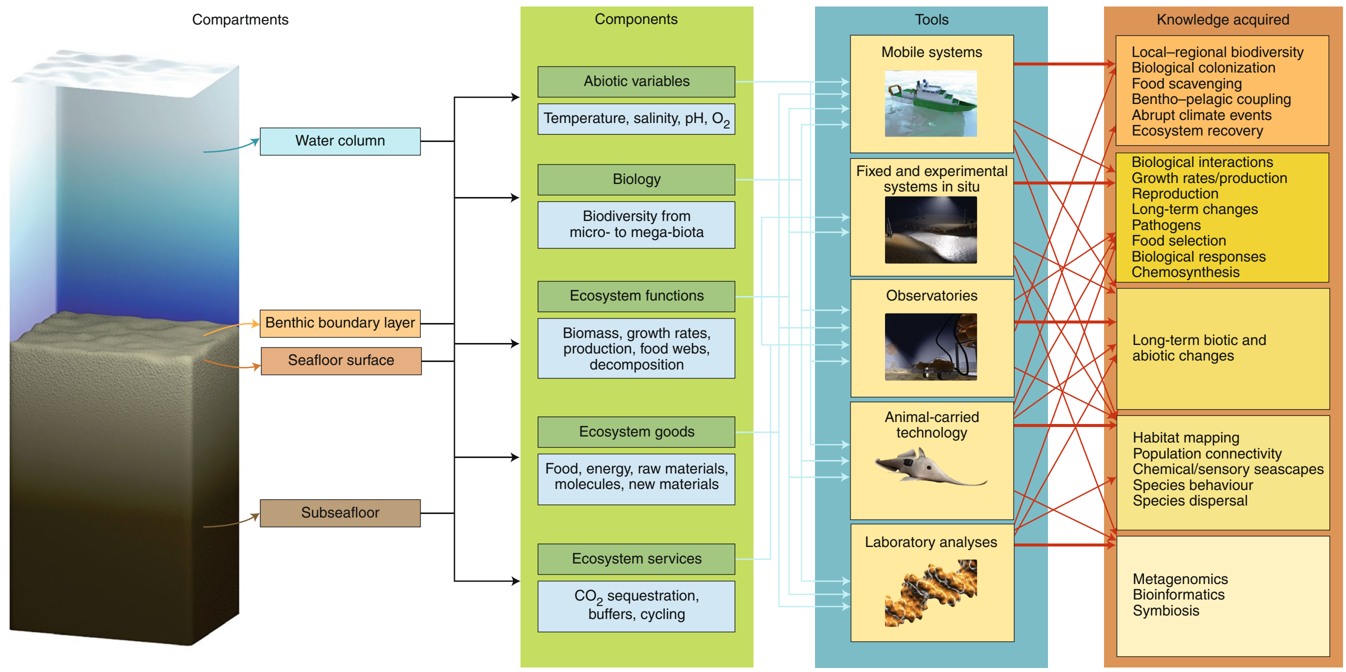


Fig. 3 | Tools for investigating the deep ocean. The conceptual diagram illustrates the potential technological development planned to acquire knowledge for sustainable use/management of the deep ocean. The illustration includes: the deep-sea compartments of interest (left column), the abiotic and biotic components (central-left column), potential tools and intelligent technologies needed to investigate the deep ocean (central-right column), and the potential knowledge acquired (right column). Conceptualized and drawn by R.D., E.F., J.A. and M. Tangherlini.

geographic gradients on marine biota[48]. However, increases in deep-sea temperatures have accelerated in recent decades, resulting in relevant shifts in biodiversity, even in response to temperature variation on the order of 0.1–0.4 °C (ref. [4]). Oxygen levels can also reflect global change, and this represents another important variable[11,12] to measure. At low oxygen concentrations, faunal biodiversity and biomass decrease, whereas microbes play an increasingly important role[49]. However, rates of expansion of OMZs in the deep sea may outpace the ability of species to adapt. The same temporal issues apply to the growing impact of ocean acidification on deep-sea biogeochemical cycles and biota. The greatest documented and projected impacts of acidification are on aragonitic calcifying organisms such as habitat-forming cold-water and red corals[50,51], with further impacts on other deep-sea taxa with calcareous skeletal elements, such as mollusks, sponges and calcareous foraminifera. The rapid rates of ongoing change in the deep sea[50,52] require that organisms adapt locally to changing conditions or migrate (if even possible) to more suitable environments[51].

In evaluating climate change impacts, the expert elicitation (Supplementary Table 2, Fig. 2) ranked documenting bathymetric shifts in species distribution and local extinction of deep-sea species as high priority because they represent simple and effective measures of the response of deep-sea biota to global change. A generalized deepening of middle-slope communities (950–1,250 m), especially decapods, reported in the Mediterranean[53] in relation to deep-water warming, indicates the high sensitivity of deep-sea species to changing temperatures[12,54,55], potentially leading to local extinctions[56]. Local extinctions, as well as reproduction potential and timing were also prioritized for understanding the impact of global change. The selection of these variables appears well justified, given the primary concern regarding local extinctions related to habitat loss, especially for the large number of endemic species associated with specific deep-sea habitats. Moreover, reproduction potential and timing relate strongly to shifts in timing of food inputs from the photic zone, as well as their amount and composition[57], thus reflecting changes occurring in the photic zone. Shifts in body size and presence of alien and cryptic species were ranked low in priority in the survey. We think that this outcome again reflects a discrepancy in the perception of threats because shallow-water experts rank changes in body size and presence of alien and cryptic species amongst the top three concerns for biodiversity conservation[58]. In fact, evidence suggests that deep-water warming could favour the invasion of alien species pre-adapted to such thermal conditions[59], and recent studies report the presence of alien species in the deep sea[60]. We therefore believe that even scientists underestimate the presence and impact of alien species in deep-sea ecosystems, which will likely increase in the future.

Measuring essential variables needed for deep-sea ecosystems conservation

The sustainable future of the Earth ultimately depends on the functioning of the deep-sea biosphere, which regulates key biogeochemical processes, sustains biomass production and mitigates climate change stressors. Most of these processes link intimately to deep-sea biodiversity[61]. The protection of deep-sea ecosystems can be thus considered the most challenging goal of global nature conservation and, at the same time, the least standardized. Limited knowledge of deep-sea ecosystems (<0.0001% of their surface area explored in detail) and the almost complete lack of data on interactions amongst deep-sea ecosystems over large spatial scales have long constrained all efforts to develop robust criteria for deep-sea ecosystem conservation[62].

Our initial review of deep-sea ecosystem conservation (that is, definition of the variables to include in the survey) prioritized the maintenance of biodiversity and connectivity among different deep-sea eco-regions and between shallow and deep-sea habitats. Other priority variables included species rarity or endemism, and indicators to quantify the capacity of a deep ecosystem to serve as a source area for biodiversity in surrounding (even remote) shallow and deep-sea ecosystems through connectivity (spill-over effects). However, the expert elicitation identified the presence of habitat-forming species and vulnerable habitats (that is, groups of species or habitats that may be vulnerable to anthropogenic impacts[62]; Fig. 2) as the most important ecological variables for deep-sea ecosystem conservation. The expert elicitation also identified habitat diversity (that is, the presence of unique and/or rare habitats, or the concentration of different habitat types in close proximity) as a key variable for prioritizing deep-sea areas for protection. Given the intrinsic links between habitat and species diversity[63], identification of priority areas must include the mapping of deep-sea biodiversity 'hotspots'[64]. Connectivity of deep-sea species/ecosystems ranks next in priority and provides crucially important information for deep-sea conservation. Indeed, connectivity plays a key role in the resilience of deep-sea species, populations, communities and ecosystems following a disturbance[65]. Connectivity analysis is particularly important for sessile and habitat-forming species, such as deep-water corals, for species that inhabit patchy habitats (for example, hydrothermal vents, cold seeps, seamounts and canyons among others), and for species with long life spans. Assessing population connectivity of deep-sea species and understanding the drivers of dispersal are some of the great challenges of current deep-sea research, because of the microscopic nature of larvae being transported in the largest biome on Earth. However, new molecular methods and biophysical modelling approaches provide tools to improve our understanding of gene flow and population connectivity among ecosystems traditionally challenging to sample and study[66].

Despite increasing information on nursery areas of deep-sea commercial species, and the existence of some fishery management measures[67], the experts did not prioritize the presence of recruits/juveniles, presumably because vulnerable habitats and habitat-forming species already represent nurseries for many species, and offer refugia for many juveniles. We also predict that ongoing and new discoveries, such as the use of vents and seeps as nursery habitats for cephalopods and elasmobranchs[68], may increase their priority in the future.

Observing and monitoring managed and protected deep-sea areas at a global scale

Current theoretical approaches to deep-sea conservation generally consider impacts individually (for example, trawling or mining) rather than cumulatively, resulting in substantive differences in the identification of essential ecological variables among proponents (Supplementary Table 3). The presence of multiple stressors and cumulative impacts makes spatial integration of all quantitative and qualitative data difficult. Here, we attempted to combine available knowledge and DEEVs in order to identify deep-sea conservation priorities. These priorities consider: (1) ocean regions expected to experience direct human impacts (for example, resource extraction or waste disposal); (2) seas and ocean regions indirectly affected by human impact, given their increased vulnerability to climate change (including acidification and deoxygenation); (3) biodiversity hotspots and ecosystems providing important goods and services; and finally, (4) areas of interest because of previous catastrophic events (for example, the Gulf of Mexico region impacted by the *Deepwater Horizon* accident). As a result, we produced a global map of deep-sea ecosystems and priority areas to begin the discussion, with expectation of subsequent refinement (see Box 2).

Identifying deep-sea areas to prioritize for protection (in addition to those already included in exclusive economic zones (EEZs) and large marine protected areas (MPAs), for example, around some Pacific islands), offers a first step, but will prove insufficient without appropriate management plans. Along with the establishment of deep-sea MPAs, restrictions on fishing gear, quotas, bycatch and maximum fishing depth can reduce both the removal of organisms and physical disturbance[69,70]. Periodic restriction in fishing and/or rotation of exploited areas, as well as regulations for dumping, waste disposal, emissions, turbidity and toxin release (for example, Toxic Maximum Daily Loads for the open ocean), also merit action[71,72]. The DEEVs proposed in our study also offer a global and standardized tool for monitoring the efficacy of the protection measures.

Technologies enabling measurement of deep-sea ecological indicators

An array of sensors and platforms (for example, floats, moorings and ships) presently support ocean monitoring, predominantly measuring physical and biogeochemical properties of the water column[22]. Biologists have begun to address essential ocean variables in the context of the Global Ocean Observing System[73]. A few biological and ecosystem variables relevant to the deep ocean have been identified[22], but these still lack consensus. Moving towards an ecosystem-based approach for monitoring, the deep sea presents a double challenge. From one side, it requires a clear innovation in the current cultural build on lessons from the development of physical–chemical variable specifications. From another side, developing technologies able to capture the biological and ecological variables adds a considerable challenge. Current monitoring efforts in shallow-water habitats[74] cannot transfer directly to the deep ocean.

Our study combined the availability of validated technological tools for deep-sea monitoring with the list of the DEEVs (Extended Data Fig. 2). Tools to assess 'biodiversity', with proven or advanced technologies, are already available for both the water-column and benthic domains (for example, high-definition (HD) and acoustic imaging, technology readiness level (TRL) 9), while only laboratory-validated technologies are available for the microbial component (for example, as DNA in situ sequencers, TRL 2). HD video (that is, HD colour, stereo 3D, as well as acoustic cameras[75]) can improve understanding of organism-level biology and ecology for macro- and megafauna living above or on the seabed. Deep-sea monitoring becomes more difficult as organism body size decreases, requiring integration of high-resolution observations with direct collection of samples. Technology to trace the presence of species is now in development through the analysis of environmental DNA (eDNA), but species traceability needs improvement through taxonomic verification and image cross-checking[76]. An integrated approach, indeed, would also enable the monitoring of small-sized organisms (for example, meiofauna and infauna), which imaging technologies cannot adequately assess. Technological tools for monitoring 'ecosystem functions' are generally less advanced (TLR from 4 to 5) than those for biodiversity monitoring, except for those relating to geochemical measurements such as respiration. Optoacoustic imaging tools can provide direct information on life-history traits as well as intra- and inter-specific interactions and trophic niches, but these technologies require further validation. For 'health, impacts and risk assessment', field-validated technologies support measurements of the variable habitat degradation, whereas only laboratory-validated tools exist for analysis of recovery rates (that is, ecosystem resilience). Laboratory-validated technologies exist for most of the variables ranked as lower priority by the expert elicitation (TLR 3–5). Overall, technologies related to the quantification of (macro) marine litter and artefacts offer the best options through highly developed optoacoustic imaging tools. The essential variables prioritized for deep-sea ecosystem conservation are largely laboratory validated and, in some cases, close to a proven technology (TLR 8–9 for censusing vulnerable habitats and habitat diversity). Much more work is needed to prove the technologies (most are barely laboratory validated) necessary to support monitoring of

Table 1 | Summary of actions required for deep-sea monitoring of the most important DEEVs

Scientific areas		Essential ecological variables	Monitoring approach	Technology readiness level (TRL)
Biodiversity	Water-column components	Macro- and meso-zooplankton	Classifying and quantifying species by HD video and active acoustic imaging (that is, multi-beam cameras) and photomultipliers (for bioluminescence)	TRL 9 (HD and acoustic imaging, photomultipliers), TRL8 (bioacoustic sonars)
	Sediments components	Macro- and megafauna	Classifying and quantifying species by HD video and active acoustic imaging (that is, multi-beam cameras)	TRL 9 (HD and acoustic imaging)
	Measures	Community composition	Computing species distribution and assemblage structure per sampling zone and summing up the data for the whole area	TRL 9 (HD and acoustic imaging), TRL 2 (DNA in situ sequencers; eDNA)
		Species distribution		TRL 9 (HD and acoustic imaging)
Ecosystem functions		Trophic structure	Classifying and quantifying feeding-oriented interactions (that is, listing food items for trophic niche characterization), combining the use of direct ethological observations as well as statistical proxies (that is, via recurrent species spatiotemporal co-presence). The food web architecture could be then inferred by joining together trophic niche data for all species	TRL 8 (bio-acoustic sonars), TRL 3 (in-sediments HD imaging), TRL 2 (geosonars)
		Benthic faunal biomass	Biovolume estimates (for example, class size frequencies from individuals' body lengths)	TRL 8 (bio-acoustic sonars), TRL 2 (geosonars)
Impact/risk assessment		Habitat damage	The analysis of seascapes changes based on habitat mapping approaches and georeferenced photomosaic compositions	TRL 9 (high-resolution multi-beam bathymetry), TRL 7 (laser scanning)
		Recovery rate (as a proxy of resilience)	Multivariate analysis time-series counts for species depicting fluctuations according to concomitant oscillations of key environmental drivers (for example, temperature and oxygen maxima and minima)	TRL 9 (HD and acoustic imaging), TRL 8 (bioacoustic sonars), TRL 3 (in-sediments HD imaging), TRL 2 (geosonars)
Global change, adaptation and evolution		Shifts in bathymetric distribution	Assessing changes in the geographic, bathymetric and endemic detection of individuals (both juveniles and adults)	TRL 8 (bioacoustic sonars)
		Local extinctions	Richness data comparison over consecutive years and identification of abundance decreasing trends. Changes in richness due to disappearing or not previously detected species	TRL 9 (HD and acoustic imaging), TRL 3 (in-sediments HD imaging)
Conservation		Habitat-forming species	Quantifying density and distribution patterns of dominant (that is, abundant) sessile species as 'facies' (for example, sea pens, cold-water corals, sponges, tube worms and bivalves) per each sampling area	TRL 9 (high-resolution multi-beam bathymetry), TRL 9 (HD and acoustic imaging), TRL 7 (laser scanning)
		Vulnerable deep-sea habitats	Quantifying density and distribution patterns of dominant (that is, abundant) sessile species as 'facies' (for example, sea pens, cold-water corals, sponges, tube worms and bivalves) per each sampling area	TRL 9 (high-resolution multi-beam bathymetry), TRL 9 (HD and acoustic imaging)

The most important DEEVs are those ranked as 'very high' in the expert elicitation for the five scientific areas. Developed monitoring actions utilize high-resolution technologies (see types and current level of technological development in Supplementary Table 4).

global change impacts and consequent biological adaptations and evolutionary implications. For instance, the technologies for monitoring reproductive features and local extinctions require laboratory validation.

One main challenge remains: the need to develop robust and ready-to-use technologies that enable equally advanced monitoring of the DEEVs both in the water column and in benthic environments. Integration of different navigating and seabed moving technologies can support the simultaneous monitoring of different portions of deep-sea ecosystems, including: (1) pelagic; (2) epi-benthic; and (3) endo-benthic compartments. Such integrated systems might combine cabled observatories with high-frequency time-lapse imaging, associated with benthic landers, autonomous underwater vehicles (AUVs), gliders, rovers and crawlers (Fig. 3) in order to expand this observation capability across even wider spatial scales (several km^2) and in three dimensions[77].

Conclusions and future perspectives

The current scenarios of blue growth anticipate increased exploitation of deep-ocean resources, with associated unknown impacts on deep-sea ecosystems. Increasing interest in deep-sea exploitation creates an urgent need to expand biological and ecological knowledge at appropriate spatial and temporal scales. Future deep-sea monitoring requires agreed standardized protocols. Deep-sea ecosystem management and conservation success can be defined by sustaining biodiversity and ecosystem functions on short-to-mid-term temporal scales to preserve ecosystem services but also considering the rapid rates of global change that exert evolutionary pressure for adaptation that could have implications for timing of evolution of deep-sea species.

We define a list of DEEVs (see Table 1), needed in future protocols for deep-sea studies (including the water column) that could be utilized in territorial waters within the EEZs or in Areas Beyond

National Jurisdictions (ABNJ). The use of the variables proposed here will also increase our ability to identify vulnerable and representative deep-sea ecosystems and prioritize areas deserving protection. The variables proposed here also allow comparisons with existing data sets, data sharing, as well as contributions to open-access data portals.

The specific features of deep-sea ecosystems make technologies a key aspect for implementing deep-sea monitoring and represent one of the key issues for the United Nations Decade of Ocean Science for Sustainable Development (2021–2030). Future technological development should address the cost-effective monitoring of essential variables. At the same time, identifying appropriate spatial and temporal (including historical) scales remains a challenge, which merits additional transnational efforts.

The endorsement and adoption of these DEEVs by industry, governmental organizations and environmental non-governmental organizations could provide momentum towards a common scientific framework at the global scale that will allow scientists and policy makers and managers to implement deep-sea monitoring, conservation, and enhance the sustainable management of the highly valuable and understudied deep-sea ecosystems.

Data availability

The dataset generated and analysed during the current study is available from the corresponding author on reasonable request.

Received: 7 December 2018; Accepted: 19 December 2019;
Published online: 3 February 2020

References

1. Ramirez-Llodra, E. et al. Man and the last great wilderness: human impact on the deep sea. *PLoS ONE* **6**, e22588 (2011).
2. Mengerink, K. J. et al. A call for deep-ocean stewardship. *Science* **344**, 696–698 (2014).
3. Cordes, E. E. et al. Environmental impacts of the deep-water oil and gas industry: a review to guide management strategies. *Front. Env. Sci.* **4**, 58 (2016).
4. Danovaro, R., Dell'Anno, A. & Pusceddu, A. Biodiversity response to climate change in a warm deep sea. *Ecol. Lett.* **7**, 821–828 (2004).
5. Halpern, B. S., Selkoe, K. A., Micheli, F. & Kappel, C. V. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conserv. Biol.* **21**, 1301–1315 (2007).
6. Armstrong, C. W., Foley, N. S., Tinch, R. & van den Hove, S. Services from the deep: steps towards valuation of deep-sea goods and services. *Ecosyst. Serv.* **2**, 2–13 (2012).
7. Thurber, A. R. et al. Ecosystem function and services provided by the deep sea. *Biogeosciences* **11**, 3941–3963 (2014).
8. Danovaro, R. et al. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Curr. Biol.* **18**, 1–8 (2008).
9. Pusceddu, A. et al. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proc. Natl Acad. Sci. USA* **111**, 8861–8866 (2014).
10. Mora, C. et al. Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st century. *PLoS Biol.* **11**, e1001682 (2013).
11. Levin, L. & Le Bris, N. The deep ocean under climate change. *Science* **350**, 766–768 (2015).
12. Sweetman, A. K. et al. Major impacts of climate change on deep-sea benthic ecosystems. *Elem. Sci. Anth.* **5**, 4 (2017).
13. Hughes, T. P., Bellwood, D. R., Folke, C. S., McCook, L. J. & Pandolfi, J. M. No-take areas, herbivory and coral reef resilience. *Trends Ecol. Evol.* **22**, 1–3 (2007).
14. Kachelriess, D., Wegmann, M., Gollock, M. & Pettorelli, N. The application of remote sensing for marine protected area management. *Ecol. Indic.* **36**, 169–177 (2014).
15. Levin, L. A. & Dayton, P. K. Ecological theory and continental margins: where shallow meets deep. *Trends Ecol. Evol.* **24**, 606–617 (2009).
16. Canals, M. et al. Flushing submarine canyons. *Nature* **444**, 354–357 (2006).
17. Rogers, A. D. Environmental change in the deep ocean. *Annu. Rev. Environ. Resour.* **40**, 1–38 (2015).
18. Thomsen, L. et al. The oceanic biological pump: rapid carbon transfer to depth at continental margins during winter. *Sci. Rep.* **7**, 10763 (2017).
19. Scholes, R. J. et al. Building a global observing system for biodiversity. *Curr. Opin. Environ. Sustain.* **4**, 139 (2012).
20. Pereira, H. M. et al. Essential biodiversity variables. *Science* **339**, 277–278 (2013).
21. Lindstrom, E. J., Gunn, A., Fischer, A. & McCurdy, L. K. *A Framework for Ocean Observing. By the Task Team for an Integrated Framework for Sustained Ocean Observing* (UNESCO, 2012).
22. Levin, L. A. et al. Global observing needs in the deep ocean. *Front. Mar. Sci.* **6**, 241 (2019).
23. Woodall, L. C. et al. A multidisciplinary approach for generating globally consistent data on mesophotic, deep-pelagic, and bathyal biological communities. *Oceanography* **31**, 76–89 (2018).
24. Danovaro, R. et al. An ecosystem-based deep-ocean strategy. *Science* **355**, 452–454 (2017).
25. *Qualtrics, I.* (Qualtrics, 2013).
26. Danovaro, R., Snelgrove, P. V. & Tyler, P. Challenging the paradigms of deep-sea ecology. *Trends Ecol. Evol.* **29**, 465–475 (2014).
27. Karl, D. M. & Lukas, R. The Hawaii Ocean Time-series (HOT) program: background, rationale and field implementation. *Deep-Sea Res. II* **43**, 129–156 (1996).
28. Hurtt, G. C. & Armstrong, R. A. A pelagic ecosystem model calibrated with BATS data. *Deep-Sea Res. II* **43**, 653–683 (1996).
29. Aguzzi, J. & Company, J. B. Chronobiology of deep-water decapod crustaceans on continental margins. *Adv. Mar. Biol.* **58**, 155–225 (2010).
30. Herná, S. et al. Carbon sequestration and zooplankton lunar cycles: could we be missing a major component of the biological pump? *Limnol. Oceanogr.* **55**, 2503–2512 (2010).
31. Appeltans, W. et al. The magnitude of global marine species diversity. *Curr. Biol.* **22**, 2189–2202 (2012).
32. Gotelli, N. J. & Colwell, R. K. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391 (2001).
33. Yool, A. et al. Big in the benthos: future change of seafloor community biomass in a global, body size-resolved model. *Glob. Change Biol.* **23**, 3554–3566 (2017).
34. Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K. & Arbizu, P. M. Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol.* **23**, 518–528 (2008).
35. Pusceddu, A., Dell'Anno, A., Fabiano, M. & Danovaro, R. Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Mar. Ecol. Prog. Ser.* **375**, 41–52 (2009).
36. Van Dover, C. L. Hydrothermal vent ecosystems and conservation. *Oceanography* **25**, 313–316 (2012).
37. Levin, L. A. et al. Hydrothermal vents and methane seeps: rethinking the sphere of influence. *Front. Mar. Sci.* **3**, 72 (2016).
38. Rex, M. A. et al. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Mar. Ecol. Prog. Ser.* **317**, 1–8 (2006).
39. Danovaro, R., Corinaldesi, C., Rastelli, E. & Dell'Anno, A. Towards a better quantitative assessment of the relevance of deep-sea viruses, Bacteria and Archaea in the functioning of the ocean seafloor. *Aquat. Microb. Ecol.* **75**, 81–90 (2015).
40. Gambi, C., Pusceddu, A., Benedetti-Cecchi, L. & Danovaro, R. Species richness, species turnover and functional diversity in nematodes of the deep Mediterranean Sea: searching for drivers at different spatial scales. *Glob. Ecol. Biogeogr.* **23**, 24–39 (2014).
41. Robison, B. H. Conservation of deep pelagic biodiversity. *Conserv. Biol.* **23**, 847–858 (2009).
42. *Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a Framework for Community Action in the field of Marine Environmental Policy* (Marine Strategy Framework Directive, 2008).
43. Van Dover, C. L. et al. Ecological restoration in the deep sea: Desiderata. *Mar. Policy* **44**, 98–106 (2014).
44. Gollner, S. et al. Resilience of benthic deep-sea fauna to mining activities. *Mar. Environ. Res.* **129**, 76–101 (2017).
45. Jamieson, A. J., Malkocs, T., Piertney, S. B., Fujii, T. & Zhang, Z. Bioaccumulation of persistent organic pollutants in the deepest ocean fauna. *Nat. Ecol. Evol.* **1**, 0051 (2017).
46. Morato, T., Watson, R., Pitcher, T. J. & Pauly, D. Fishing down the deep. *Fish Fish.* **7**, 24–34 (2006).
47. André, M. et al. Listening to the deep: live monitoring of ocean noise and cetacean acoustic signals. *Mar. Pollut. Bull.* **63**, 18–26 (2011).
48. Costello, M. J. & Chaudhary, C. Marine biodiversity, biogeography, deep-sea gradients, and conservation. *Curr. Biol.* **27**, R511–R527 (2017).
49. Meier, D. V. et al. Niche partitioning of diverse sulfur-oxidizing bacteria at hydrothermal vents. *ISME J.* **11**, 1545–1558 (2017).
50. Foster, L. C., Schmidt, D. N., Thomas, E., Arndt, S. & Ridgwell, A. Surviving rapid climate change in the deep sea during the Paleogene hyperthermals. *Proc. Natl Acad. Sci. USA* **110**, 9273–9276 (2013).
51. Fabry, V. J., Seibel, B. A., Feely, R. A. & Orr, J. C. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* **65**, 414–432 (2008).

52. Roberts, J. M. & Cairns, S. D. Cold-water corals in a changing ocean. *Curr. Opin. Environ. Sustain.* **7**, 118–126 (2014).
53. Cartes, J. E., Maynou, F., Fanelli, E., López-Pérez, C. & Papiol, V. Changes in deep-sea fish and crustacean communities at 1000–2200 m in the Western Mediterranean after 25 years: relation to hydro-climatic conditions. *J. Mar. Syst.* **143**, 138–153 (2015).
54. Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915 (2005).
55. Smith, K. E. & Thatje, S. The secret to successful deep-sea invasion: does low temperature hold the key? *PLoS ONE* **7**, e51219 (2012).
56. Yasuhara, M., Cronin, T. M., Okahashi, H. & Linsley, B. K. Abrupt climate change and collapse of deep-sea ecosystems. *Proc. Natl Acad. Sci. USA* **105**, 1556–1560 (2008).
57. Adams, D. K. et al. Surface-generated mesoscale eddies transport deep-sea products from hydrothermal vents. *Science* **332**, 580–583 (2011).
58. Costello, M. J. et al. A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE* **5**, e12110 (2010).
59. Van der Grient, J. M. & Rogers, A. D. Body size versus depth: regional and taxonomical variation in deep-sea meio-and macrofaunal organisms. *Adv. Mar. Biol.* **71**, 71–108 (2015).
60. Galil, B. S., Danovaro, R., Rothman, S. B. S., Gevili, R. & Goren, M. Invasive biota in the deep-sea Mediterranean: an emerging issue in marine conservation and management. *Biol. Invas.* **20**, 281–288 (2019).
61. Roberts, C. M. et al. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl Acad. Sci. USA* **114**, 6167–6175 (2017).
62. Wedding, L. M. et al. From principles to practice: a spatial approach to systematic conservation planning in the deep sea. *Proc. R. Soc. Lond. B* **280**, 20131684 (2013).
63. Badgley, C. et al. Biodiversity and topographic complexity: modern and geohistorical perspectives. *Trends Ecol. Evol.* **32**, 211–226 (2017).
64. Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
65. Brooks, T. M. et al. Global biodiversity conservation priorities. *Science* **313**, 58–61 (2006).
66. Baco, A. R. et al. A synthesis of genetic connectivity in deep-sea fauna and implications for marine reserve design. *Mol. Ecol.* **25**, 3276–3298 (2016).
67. Pikitch, E. K. et al. Ecosystem-based fishery management. *Science* **305**, 346–347 (2004).
68. Salinas-de-León, P. et al. Deep-sea hydrothermal vents as natural egg-case incubators at the Galapagos Rift. *Sci. Rep.* **8**, 1788 (2018).
69. Roberts, C. M. Deep impact: the rising toll of fishing in the deep sea. *Trends Ecol. Evol.* **17**, 242–245 (2002).
70. Clark, M. R. & Dunn, M. R. Spatial management of deep-sea seamount fisheries: balancing sustainable exploitation and habitat conservation. *Environ. Conserv.* **39**, 204–214 (2012).
71. Pellerin, B. A. et al. Emerging tools for continuous nutrient monitoring networks: sensors advancing science and water resources protection. *J. Am. Water Resour. Assoc.* **52**, 993–1008 (2016).
72. Rochman, C. M., Cook, A. M. & Koelmans, A. A. Plastic debris and policy: using current scientific understanding to invoke positive change. *Environ. Toxicol. Chem.* **35**, 1617–1626 (2016).
73. Miloslavich, P. et al. Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. *Glob. Change Biol.* **24**, 2416–2433 (2018).
74. Bojinski, S. et al. The concept of essential climate variables in support of climate research, applications, and policy. *Bull. Am. Meteor. Soc.* **95**, 1431–1443 (2014).
75. Aguzzi, J. et al. Faunal activity rhythms influencing early community succession of an implanted whale carcass offshore in Sagami Bay, Japan. *Sci. Rep.* **8**, 11163 (2018).
76. Aguzzi, J. et al. New high-tech flexible networks for the monitoring of deep-sea ecosystems. *Environ. Sci. Tech.* **53**, 6616–6631 (2019).
77. Brandt, A. et al. Cutting the umbilical: new technological perspectives in benthic deep-sea research. *J. Mar. Sci. Eng.* **4**, 36 (2016).
78. Steinacher, M. et al. Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* **7**, 979–1005 (2010).
79. Billett, D. S. M. et al. Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Prog. Oceanogr.* **50**, 325–348 (2001).
80. Ruhl, H. A. & Smith, K. L. Jr Shifts in deep-sea community structure linked to climate and food supply. *Science* **305**, 513–515 (2004).
81. Smith, K. L., Ruhl, H. A., Kahru, M., Huffard, C. L. & Sherman, A. D. Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific Ocean. *Proc. Natl Acad. Sci. USA* **110**, 19838–19841 (2013).
82. Ramirez-Llodra, E. Fecundity and life-history strategies in marine invertebrates. *Adv. Mar. Biol.* **43**, 88–170 (2002).
83. McClain, C. R., Allen, A. P., Tittensor, D. P. & Rex, M. A. Energetics of life on the deep seafloor. *Proc. Natl Acad. Sci. USA* **109**, 15366–15371 (2012).
84. Yasuhara, M. & Danovaro, R. Temperature impacts on deep-sea biodiversity. *Biol. Rev.* **1**, 275–287 (2016).
85. McClain, C. R. & Barry, J. P. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* **91**, 964–976 (2010).
86. Breitburg, D. et al. Declining oxygen in the global ocean and coastal waters. *Science* **359**, eaam7240 (2018).
87. Hoegh-Guldberg, O. & Bruno, J. F. The impact of climate change on the world's marine ecosystems. *Science* **328**, 1523–1528 (2010).
88. Jones, D. O. B. et al. Biological responses to disturbance from simulated deep-sea polymetallic nodule mining. *PLoS ONE* **12**, e0171750 (2017).
89. Millennium Ecosystem Assessment *Ecosystems and Human Well-being: Desertification Synthesis* (World Resources Institute, 2005).
90. Hein, L. & De Ridder, N. Desertification in the Sahel: a reinterpretation. *Glob. Change Biol.* **12**, 751–758 (2006).
91. Norse, E. A. et al. Sustainability of deep-sea fisheries. *Mar. Policy* **36**, 307–320 (2012).
92. Pham, C. K. et al. Deep-water longline fishing has reduced impact on Vulnerable Marine Ecosystems. *Sci. Rep.* **4**, 4837 (2014).
93. Puig, P. et al. Ploughing the deep seafloor. *Nature* **489**, 286–289 (2012).
94. Chiba, S. et al. Human footprint in the abyss: 30 year records of deep-sea plastic debris. *Mar. Policy* **96**, 204–212 (2018).
95. Courtene-Jones, W., Quinn, B., Gary, S. F., Mogg, A. O. M. & Narayanaswamy, B. E. Microplastic pollution identified in deep-sea water and ingested by benthic invertebrates in the Rockall Trough, North Atlantic Ocean. *Environ. Pollut.* **231**, 271–280 (2017).
96. Hestetun, J. T., Pomponi, S. A. & Rapp, H. T. The cladorhizid fauna (Porifera, Poecilosclerida) of the Caribbean and adjacent waters. *Zootaxa* **4175**, 521–538 (2016).
97. Constable, A. J. et al. Developing priority variables ("ecosystem Essential Ocean Variables"—eEOVs) for observing dynamics and change in Southern Ocean ecosystems. *J. Mar. Syst.* **161**, 26–41 (2016).
98. McIntyre, A. (ed.) *Life in the World's Oceans: Diversity, Distribution, and Abundance* (John Wiley & Sons, 2010).
99. Danovaro, R. et al. Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. *PLoS ONE* **5**, e11832 (2010).
100. Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. & Worm, B. How many species are there on Earth and in the ocean? *PLoS Biol.* **9**, e1001127 (2011).
101. Gambi, C. et al. Functional response to food limitation can reduce the impact of global change in the deep-sea benthos. *Glob. Ecol. Biogeogr.* **26**, 1008–1021 (2017).
102. Holt, E. A. & Miller, S. W. Bioindicators: using organisms to measure environmental impacts. *Nat. Educ.* **3**, 8 (2010).
103. Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L. & Levin, S. A. Marine taxa track local climate velocities. *Science* **341**, 1239–1242 (2013).
104. Sunday, J. M. et al. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* **18**, 944–953 (2015).
105. Levin, L. A. & Sibuet, M. Understanding continental margin biodiversity: a new imperative. *Ann. Rev. Mar. Sci.* **4**, 79–112 (2012).
106. Fanelli, E., Bianchelli, S. & Danovaro, R. Deep-sea mobile megafauna of Mediterranean submarine canyons and open slopes: analysis of spatial and bathymetric gradients. *Progr. Oceanogr.* **168**, 23–34 (2018).
107. Dunn, D. C. et al. A strategy for the conservation of biodiversity on mid-ocean ridges from deep-sea mining. *Sci. Adv.* **4**, eaar4313 (2018).
108. *FAO Vulnerable Marine Ecosystems Database* (FAO, March 2019); https://go.nature.com/2uBsfOC
109. Miller, K. A., Thompson, K. F., Johnston, P. & Santillo, D. An overview of seabed mining including the current state of development, environmental impacts, and knowledge gaps. *Front. Mar. Sci.* **4**, 418 (2018).
110. Rogers, A. D., Clark, M. R., Hall-Spencer, J. M. & Gjerde, K. M. *The Science Behind the Guidelines: A Scientific Guide to the FAO Draft International Guidelines (December 2007) for the Management of Deep-Sea Fisheries in the High Seas and Examples of how the Guidelines may be Practically Implemented* (IUCN, 2008).

Acknowledgements

We deeply thank M. Rex (University of Massachusetts) for valuable discussion and suggestions on an early draft of the manuscript. We are very grateful to M. Baker for supporting the authors in the distribution of the Qualtrics survey to the INDEEP and DOSI communities and to the deep-sea scientists that participated to the survey and J. Cerri for the analysis of Qualtrics results. This work was supported by the H2020 project MERCES (GA N. 689518) and IDEM (GA N. 11.0661/2017/750680/SUB/EN V.C2.). E.R.-L. was supported by the Norwegian project MarMine (247626), the Norwegian Institute for Water Research and the H2020 project MERCES (GA N. 689518). P.V.R.S. was supported by the NSERC Canadian Healthy Oceans Network and CFREF Ocean Frontier Institute. L.T. is supported by JPI Oceans2 and ONC. J.A. is supported by ARIM (Autonomous Robotic sea-floor Infrastructure for bentho-pelagic Monitoring; MartTERA ERA-Net Cofound). L.L. acknowledges NSF grant OCE 1634172 and the Deep-Ocean Observing Strategy subcontract from the Consortium for Ocean

Leadership. H.R. was supported by the EMSO-Link project of the European Commission (Grant agreement ID: 731036).

Author contributions

R.D., E.F., J.A., D.B., L.C., C.C., A.D., K.G., A.J.J., S.K., C.M., L.L., N.L., E.R.-L., H.R., C.R.S., P.V.R.S., L.T., C.L.V.D. and M.Y. contributed equally to the work, discussion of the data and manuscript writing. All authors critically revised the drafts and the amended version and gave final approval for publication.

Competing interests

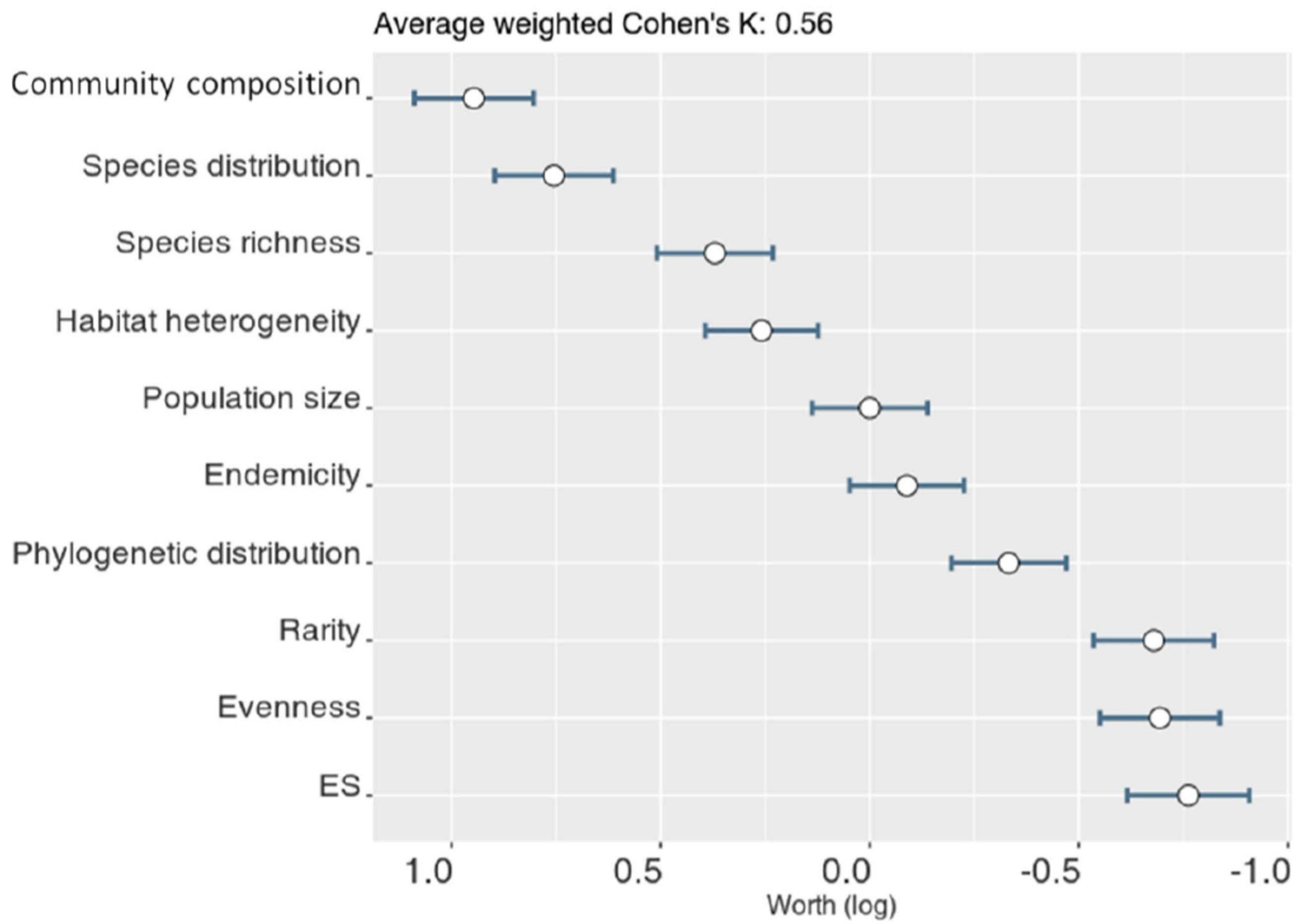
The authors declare no competing interests.

Additional information

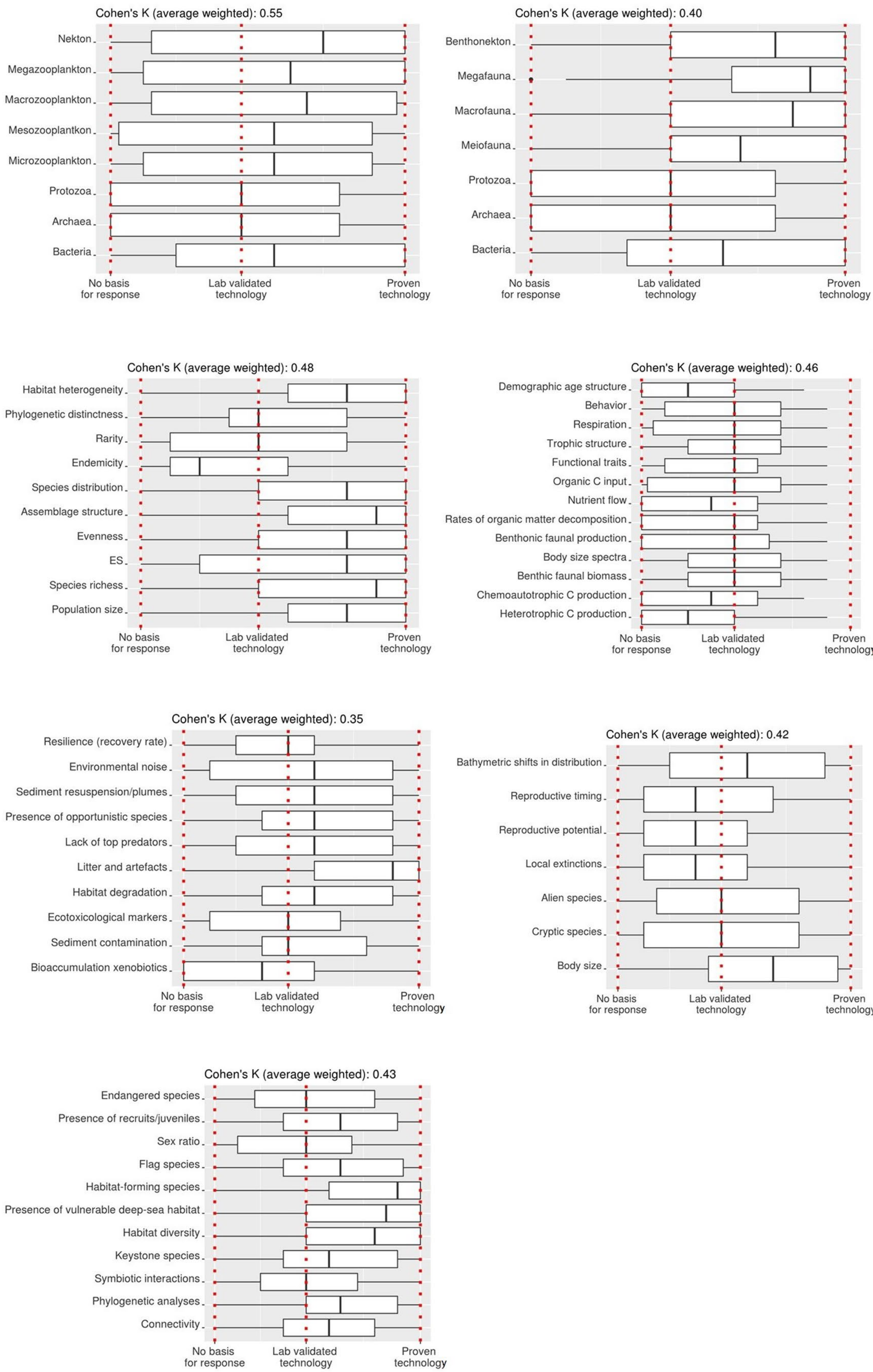
Extended data is available for this paper at https://doi.org/10.1038/s41559-019-1091-z.

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-1091-z.

Correspondence should be addressed to R.D.



Extended Data Fig. 1. | Ranking of the essential variables for biodiversity measures. Results of the Expert Elicitation obtained by using the Plackett–Luce model for the analysis about the prioritization of essential variables for biodiversity measures (*y* axis). The worth of each variable is reported on log scale (*x* axis). Average weighted Cohen's κ is also reported on the upper part of the graph. ES, expected species number.



Extended Data Fig. 2. | Ranking of the readiness of the available technologies for deep-sea ecological monitoring. Results of the Plackett-Luce model for the analysis of responses about the readiness of technology for deep-sea monitoring according to the essential variables identified for each scientific area. The Cohen's κ value is reported on the upper part of each graph.