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

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ABSTRACT

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 its surface). It also provides critical climate regulation and other ecosystem services. New species and ecosystems are continuously being discovered in the deep oceans, but commercial fisheries, deep-sea mining, and off-shore oil and gas extractions, along with pollution and global change effects, threaten this vast under-explored frontier region. The future of both benthic and pelagic deep-sea ecosystems depends upon effective ecosystem-based management strategies enhancing deep-sea conservation, yet we lack consensus on monitoring of the biological and ecological variables that reflect ecosystem status and are needed to support management and environmental decisions at a global scale. Here, we present and discuss the results of an Expert Elicitation of more than 110 deep-sea scientists to prioritize variables and parameters for the future of deep-sea monitoring. We identified five main scientific pillars that need to be further investigated for deep-ocean conservation: i) species and habitat biodiversity, ii) ecosystem function; iii) ecosystem health, impacts, and risk assessment; iv) climate change impacts, the adaptation and evolution of deep-sea life, and v) deep-sea ecosystem conservation. As observing and monitoring can provide the necessary scientific framework for scientists and policy makers to implement effective deep-sea conservation strategies at a global scale, the proposed variables should be further studied in the context of available sensor and other advanced technologies, which are becoming increasingly available.

Key-words: deep sea, monitoring, impacts, biodiversity, conservation, global change, adaptation and evolution.

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 whose biological diversity remains largely unknown (**Box 1**). Global decreases in marine ecosystem services, such as fisheries, that provide direct benefit to humanity have not spared deep-sea ecosystems[4-7]. In particular, species loss and deep-sea habitat destruction produce severe alteration of ecosystem functioning and reduce overall ecosystem goods and services[2,8,9]. In addition, cumulative marine impacts act synergistically with climate-induced changes in deep-ocean properties and processes, degrading environmental quality[10-12].

Deep-sea biodiversity plays a central role in provisioning services (e.g., fisheries, nutrition, bioprospecting), and species loss can greatly reduce ecosystem functions that support these services[8,13]. Furthermore, high biodiversity levels increase ecosystem resilience to perturbations[14,15], elevating the importance of maintaining biodiversity as an important management objective in the pursuit of sustainable use of resources[16,17]. Sustaining healthy and productive deep oceans requires knowledge of baseline conditions and rates of ecosystem change (**Figure 1**). In turn, the environmental status and resources of the coastal zones link with deep-sea ecosystems[6,18]. Bi-directional exchange of materials, nutrients, contaminants, and organisms between shallow and deep-sea ecosystems occurs widely in all oceans[19-23] and thus changes in one system may impact other ecosystems. Several ongoing initiatives are considering monitoring needs of baseline conditions and environmental impacts (**Box 2**).

Here, we focus on the identification of a set of biological and ecological variables and parameters designed to capture the most relevant aspects of the biology and ecology of deep-sea ecosystems, thus enabling sound evaluation of their status. We have selected the proposed parameters and variables to address five pillars of knowledge needed for deep-sea ecosystem management and conservation: i) species and habitat biodiversity (including standardization of measures); ii) ecosystem functions; iii) ecological impacts, drivers, and stressors; iv) climate change effects on adaptive and evolutionary features; and v) deep-sea conservation. An international group of more than 110 deep-sea scientists with a broad range of scientific expertise in deep-sea science identified these variables based on a Qualtrics[24] (see **Supplementary Methods**) survey, prioritized variables and parameters for each ecosystem pillar and discussed their potential use in future monitoring and conservation strategies, particularly in light of available technologies and their ongoing development. Finally, we identified those deep-sea areas globally, based on current knowledge that contain a high number of biodiversity hotspots and vulnerable ecosystems and could represent priority regions for future transnational deep-sea conservation actions.

Measuring deep-sea species and habitat biodiversity

Measuring deep-sea biodiversity has been a major challenge for deep-sea science since the pioneering expeditions of the 19th century (**Box 2**). To identify the essential variables that capture the different components of deep-sea biodiversity and their potential use in habitat management and conservation, we prepared a list of all known major biological variables and ecological parameters. The prioritized list of biodiversity variables, both in the water column and on the seafloor, including sediments, determined by Expert Elicitation is presented in **Table 1**. Among the different biodiversity components, medium to large-sized organisms (i.e. from macrofauna to megafauna) were considered most relevant in both marine compartments. For the water column, bacteria also ranked very high, given recent evidence of their importance in ecosystem functioning. Mega-zooplankton and nekton (including micro-nekton) are also included because of their central role as mid-trophic level prey for species of economic and conservation concern, and for their key roles in the biological pump, which transports carbon to depth. The nekton interacts with many benthic and pelagic systems across depths[25] emphasizing the importance of quantifying nekton abundance and biodiversity, including their role in ocean health. In addition, citizens often appreciate the relevance of this component and prioritize its monitoring, especially when referred to iconic and flagship animals (e.g. deep-sea sharks, giant squids, sperm whales, Dumbo octopus, Yeti crabs, Blob fish, giant cnidarians), or species of commercial interest (e.g. red corals, blue and red shrimps, deep-sea lobsters, orange roughy and Alfonsino fish), as well as critical habitats and ecosystem engineers (e.g. deep-water corals, giant sponges) (**Figure 2**). Indeed, these species play crucial functional roles, sometimes as habitat-forming species, and their visual appeal to a wide audience offers potential for outreach and raising awareness.

Unfortunately, although some ship-based water column time-series have been maintained for more than 50 years[26] most of the water-column monitoring has been performed in shallow waters and coastal areas in the North Atlantic and the Antarctic Ocean, but not in the deep sea. Ecologists recognize that deep-sea ecosystems host a huge microbial (i.e. viral and bacterial[27]), meiofaunal and macrofaunal biodiversity, which contributes to regulate deep-sea ecosystem functioning[28-31]. We therefore highlight these components as a priority in terms of their contribution to the functioning of deep-sea ecosystems. In this study, assemblage structure, species distributions, and habitat heterogeneity resulted as the most fundamental measures of deep-sea biodiversity. Conversely, the quantification of biodiversity in terms of derived indices (i.e. expected species richness and evenness) are ranked with a lower priority, because many different indexes can be utilized, in an interchangeable way.

Measuring ecosystem functions in the deep sea

Terrestrial ecologists quantify ecosystem processes by measuring rates of energy and material flow between biotic and abiotic compartments (e.g. biomass production, transport, decomposition or loss of organic matter, as well as nutrient regeneration). However, not all terrestrial functional variables transfer easily to marine ecosystems, and variables that capture deep-sea functions and processes can differ somewhat from those used in coastal environments[32-34].

At some carbon-rich deep-sea ecosystems (e.g. hydrothermal vents, cold seeps and canyons/fjords, OMZs), the higher trophic levels do not fully use organic carbon pools (due to their highly refractory composition[35]), with consequent substantial organic carbon burial[36-39]. However, most deep-sea ecosystems are strongly carbon-limited because the 'rain' of organic matter from the surface photic layer decreases exponentially with depth[40-42].

The Expert Elicitation ranked trophic structure of deep-sea assemblages as the highest priority variables for ecosystem function, followed by benthic faunal biomass and morpho-functional traits (**Supplementary Table 1**). While megafauna (e.g.

holothurians, sponges) may be important drivers in carbon energy transfer, smaller fauna can contribute significantly to overall benthic biomass in deep-sea ecosystems. For instance, meiofaunal biomass becomes comparable or higher than that of macro- and megafauna at depths greater than 1000 m[43,44]. Morpho-functional traits represent a key indicator for ecosystem functioning[44], although a more specific metric needs to be developed.

Measuring deep-sea ecosystem health, impacts, and risk assessment

The European Marine Strategy Framework Directive[45], through the descriptors of Good Environmental Status and the Essential Biodiversity Variables (EBV[46]), provides tools for assessing the health of marine ecosystems, but focuses mainly on coastal environments. However, some MSFD descriptors also offer utility for deep-sea ecosystems. For instance, the MSFD and its descriptors of good environmental status include criteria defining ecosystem health alterations (e.g. habitat damage, overfishing, sediment and seafood contamination, litter and noise).

In the present study, these variables were used for selecting those enabling the assessment of various kinds of impact on deep-sea ecosystems (**Supplementary Table 2**) and the Expert Elicitation indicated that "habitat damage" was the most relevant indicator of impact, because many species depend on habitat integrity to complete their life cycle, to reproduce, and find refuge from predatio[47,48]. Species distributions also depend on habitat heterogeneity. Resource exploitation/extraction (i.e. fisheries, mining, and oil and gas extractions) determines physical impacts and can destroy habitat with consequent biodiversity loss[49]. The outcome of the Expert Elicitation, therefore, prioritizes these impacts as highest concern.

Ecosystem resilience also ranked amongst the high-priority variables because it represents the ability of an ecosystem to recover after impact cessation. However, this indicator, which depends on many other variables, still lacks adequate standardization either in how it is measured or in its metrics. For instance, one recent study proposed to use the rate of benthic faunal recovery after a disturbance event (e.g. mining), as an indicator of resilience[50], but rates of recovery vary significantly with the biological component considered (e.g. meiofauna vs. deep-water corals). Thus, this indicator requires further consideration before defining a standardized approach.

Contamination of sediments ranked next in importance for assessing ecosystem health, followed by the consequent eco-toxicological effects, indicating an increasing perception that pollution is expanding down to the deep sea[51-53]. Also, marine litter and sediment resuspension might have a significant effect on deep-sea ecosystems and, for this reason, have been ranked next as potential indicators of impact.

The Expert Elicitation demonstrates that shallow-water and deep-sea ecosystems are subjected to different risks/impacts. For instance, the loss of top predators and/or invasion by alien species are considered priority concerns in coastal ecosystems, but not (yet) in the deep sea. Similar differences exist in appreciating potential impacts of noise. Despite the recognition of marine soundscape concerns even at bathyal-abyssal depth[54], no strong evidence of serious harm is perceived by deep-sea scientists contributing to the survey.

Measuring climate change impacts, the 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 geographic gradients[55-57]. However, increases in deep-sea temperatures have accelerated in recent decades, resulting in significant shifts in biodiversity, even for variation on the order of 0.1°C[4].

The rapid rates of ongoing changes in the deep sea[58-59] require that organisms adapt locally to changing conditions or migrate to more suitable environments[60]. In this scenario, the results of the Expert Elicitation (**Supplementary Table 3**) indicate that “bathymetric shifts” in species distribution and “local extinction” of deep-sea species ranked of highest priority as they represent simple and effective indicators of the response of deep-sea biota to deep-water warming. A generalized deepening of middle-slope communities (950–1250 m), especially decapods, reported in the Mediterranean[61] relates to the high sensitivity of deep-sea species to changing temperature and limited thermal tolerance[12,62,63], potentially leading to local extinctions[64]. Deep-water warming could also facilitate penetration of alien species pre-adapted to such conditions[63] and recent studies reported the presence of alien species even in the deep sea[65]. Reproduction potential and timing of reproductive activities are useful variables, because they relate to shifts in timing, amount, and composition of food inputs from the photic zone[66-68]. Body-size miniaturization has been also identified as a potentially sensitive variable due to the expectation that sea-surface warming, by increasing vertical stratification can reduce the food supply to the deep sea.

Oxygen can be another important driver of adaptation[69]. At low oxygen concentrations, eukaryotic biodiversity and biomass decrease, whereas microbes play an increasingly important role[70]. However, rates of expansion of OMZs in the deep may outpace the ability of these species to adapt. The same temporal issues apply to the growing impact of ocean acidification on deep-sea biogeochemical cycles and biota. The greatest impacts of acidification have been documented on aragonitic calcifying organisms such as habitat forming cold-water and red corals[59,71,72], with further impacts implicated on other deep-sea taxa with calcareous skeletal elements such as mollusks, sponges and calcareous foraminifera.

Measuring essential variables needed for deep-sea ecosystems conservation

Oil, gas, and mineral extraction, as well as bottom trawl fisheries will potentially impact large portions of deep seabed areas (e.g. seamounts, hydrothermal vents, cold seeps, canyons and abyssal plains)[11]. These current and impending activities add urgency for action on deep-sea conservation, especially given the paucity of scientific data to identify priority and/or representative areas for protection[73-77].

Ecological indicators for deep-sea ecosystem conservation should consider variables related both to biodiversity (i.e. species richness, abundance) and to the interconnection among deep-sea eco-regions and between shallow and deep-sea habitats. Other variables can be relevant, such as species rarity or endemism, and some indicators should 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).

Current approaches for deep-sea conservation vary widely among proponents, with potential application of many approaches and tools to maintain the integrity of marine ecosystems (**Supplementary Table 4**). Along with the establishment of deep-sea marine protected areas, restrictions with respect to fishing gear, quotas, bycatch, and maximum sampling depth, among others, can reduce both removal of organisms and physical disturbance[78-81]). Temporal tools could also be considered, by defining periodic restriction in fishing and/or extraction, or rotation of exploited areas. At the same time, regulations for dumping, waste disposal, emissions, turbidity, and toxin release (e.g. Toxic Maximum Daily Loads for the open ocean) are also important[82-84].

In the present study, a tentative global map of deep-sea ecosystems and priority areas that merit monitoring efforts based on these criteria is presented in **Box 2**. The protection of the following deep-ocean ecosystems should be prioritized based on Expert Elicitation: i) ocean regions expected to experience direct impact from human disturbance (e.g. resource extraction or waste disposal); ii) seas and ocean areas indirectly impacted by human disturbance, given their increased vulnerability to climate change (including acidification and deoxygenation); iii), biodiversity hotspots and providers of important ecosystem services; and finally, iv) areas of interest because of previous catastrophic events (e.g., the region of the Gulf of Mexico impacted by the Deep-water Horizon accident).

The complexity of the subject and the presence of multiple stressors and cumulative impacts, makes spatial integration of all quantitative and qualitative information difficult, but this map offers a start for discussion, with expectation of subsequent refinement.

In this scenario, expert opinion suggests that the most important ecological indicators for conservation is the presence of vulnerable deep-sea species/habitats (i.e. groups of species or habitats that may be vulnerable to impacts from fishing activities[85]; as well as habitat-forming species (**Supplementary Table 5**). Acknowledging considerable overlap in the geographic areas that support habitat-forming species and vulnerable habitats, we considered the two indicators separately because we anticipate that the extent of vulnerable marine ecosystems may exceed that of habitat-forming species. Scientific justification should form the basis for future designations of MPAs, based on the understanding of the geographic ranges and population connectivity of a wide variety of taxa, in order to design spatial management measures at appropriate scales. The only problem with this view is that characterization of distributions, ranges, and connectivity for most deep-sea species will require considerable time and effort, for both common and rare species. Thus, we must start with the best available proxies derived from genetic analyses upon animal sampling.

Connectivity of deep-sea species represents another priority conservation consideration. Connectivity plays a key role in the resilience of deep-sea species, populations, communities, and ecosystems following a disturbance event[86]. Analysis of connectivity is particularly important for habitat-forming species, such as deep-water corals, for species that inhabit patchy habitats (e.g. hydrothermal vents, methane seeps, seamounts among others), and for species with long life spans. New molecular methods and biophysical modelling approaches now facilitate the synthesis of gene flow and connectivity knowledge from ecosystems traditionally challenging to sample and study[87,88]. Habitat and species diversity are intrinsically linked[89], so that identification of priority areas must include the mapping of deep-sea biodiversity 'hotspots'[90,91]. Experts ranked attention to spawning and nursery areas as important conservation interests, but with lower priority, presumably because of the limited knowledge on recruitment and nursery areas in deep-sea ecosystems. Growing knowledge of new discoveries, for example of elasmobranch use of vents and seeps as nursery habitat[92,93], may elevate the importance of this feature.

Experts suggest that endangered species outrank emblematic/flag species in importance, indicating that the deep-sea scientific community attributes these deep-sea species to social commitment and politicization, often coinciding with iconic examples in shallower-water areas. Although iconic deep-sea species exist (see **Figure 2**), the deep-sea research community struggles to evaluate levels of endangerment for most taxa where sampling and monitoring data remain scant. The scientific community therefore cannot promote the need for conservation using examples of endangered species as icons for social awareness**,** though it can promote awareness of the amazing animals in the deep sea through use of iconic images. Long-term global observing can improve our ability to assess endangerment for larger taxa.

Technologies enabling deep-sea ecological indicators measurement

The specific features of deep-sea ecosystems and the measurement of a complex set of biological variables and ecological indicators require sophisticated monitoring technologies. A large part of the priority variables identified by experts use optoacoustic imaging tools (i.e. HD color, stereo 3D, as well as acoustic cameras[94]). High-definition videos improve understanding of organism-level biology and ecology (for macro- and megafauna), providing direct information on life-history traits as well as intra and interspecific interactions and trophic niches. As organism body size decreases, deep-sea monitoring becomes more difficult given the need to integrate high-resolution observation and collection of small organisms.

Camera fields of view at fixed stations can monitor biological features or ecosystems[95]. Combining mobile platforms of different operating capabilities with sensors at fixed stations could expand the monitoring radius. Combinations of different technologies can support the simultaneous monitoring of different portions of deep-sea ecosystems, including: i) pelagic; ii) epi-benthic; and iii) endo-benthic compartments (**Figure 3**). For example, stationary, high-frequency time-lapse imaging over a period of years from cabled observatories can quantify megafaunal species richness[60], with rovers and crawlers expanding local data acquisition to greater distances (several tens of m^2)[23,94,96]. Benthic landers[97] or AUVs and gliders could expand this observation capability across even wider spatial scales (several km^2)[98]. Collection of environmental data in conjunction with these observations will be important.

In the near future, benthic assets at fixed cabled observatories, their moored profilers, and the mobile tethered platforms (e.g. crawlers) will also support 3-D exploration and monitoring of deep-sea ecosystems. Fixed monitoring networks for animal-born telemetric and data-logging technologies will complement these efforts (e.g. Ocean Tracking Network program[99]).

Presently, no in-sediment imaging technology can assay infaunal diversity. This measure requires sorting and DNA sequencing coupled with morphological studies. In recent years, meta-barcoding and genomic analyses of deep-sea organisms have expanded our overall knowledge of taxonomy beyond laboratory-based approaches (see also the Global Genome Initiative – GGI[98,100]). For example, biodiversity assessments of pelagic (mostly surface) ecosystems, already use metagenomic analyses (i.e. sequencing the genome of all species in a sample) to assess microbial diversity (e.g. Tara, Malaspina, Bermuda Atlantic Time Series, SCOPE program at ALOHA), illustrating the potential for developing similar approaches for deep-sea monitoring. Some deep-sea projects (e.g. ABYSS and Deep CCZ) are applying metabarcoding methods to assess benthic faunal biodiversity at regional to global scales. The use of molecular tools for identifying small-sized organisms is becoming a priority given the high cost, intensive labor, and visual limitations associated with traditional microscopic approaches, but current databases remain poor, and methodologies require important refinement[101,102]. Acknowledging ongoing development of technologies enabling *in situ* analyses (e.g. species traceability with eDNA marker sequencing), these *in situ* technologies are not yet operational. Sophisticated technologies are needed for the measurement of the complex set of biological variables and ecological indicators in the deep sea, along with their present readiness level (see **Supplementary Table 6**).

The ocean observing community now supports an array of sensors and platforms (floats, moorings, ships) that predominantly measure physical and biogeochemical properties. The biologists have begun to address essential ocean variables in the context of the Global Ocean Observing System[103], but the deep ocean is poorly represented by these. A major challenge is to integrate the priority variables/parameters identified here with ongoing observing programs.

Conclusions and future perspectives

All current scenarios of blue growth anticipate increased exploitation of deep-ocean resources, with associated impacts of unknown intensity on deep-sea ecosystems. For instance, manganese nodules are non-renewable and will eventually disappear, possibly for millions of years. Deep-sea ecosystem management and conservation should consider similar evolutionary scales, sustaining biodiversity and ecosystem functions to preserve ecosystem services (including evolutionary potential). The increasing interest in deep-sea exploitation creates an urgent need to expand biological and ecological knowledge at appropriate spatio-temporal scales. Future deep-sea monitoring needs agreed standardized protocols. Given the spatial scale of the deep ocean, the management of its resources requires also a wide international collaboration either to address societal needs including for policy development, or for the need to build capacity for sharing advanced technologies and related costs.

The present study defines a list of Deep-sea Essential Ecological Variables (DEEV; see **Table 2**), needed in future protocols for deep-sea studies (including the enforcement of Early-Warning Response Protocols) that can be utilized in territorial waters, in the Exclusive Economic Zones and in Areas Beyond National Jurisdictions (ABNJ). The use of the variables and indicators proposed here will also increase our ability to identify vulnerable and representative deep-sea ecosystems and priority areas deserving protection. Another advantage of the list of variables proposed here is that they allow a comparison with existing data sets, data sharing as well as the contribution 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 issue for the UN 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. We are confident that the endorsement and adoption of these deep-ocean essential variables by industry, governmental organizations, and Environmental Non-Governmental Organizations could optimize the cost-benefits and return of the future monitoring initiative, providing, for the first time, a common scientific framework at the global scale that will allow scientists and policy makers and authorities to implement deep-sea monitoring, conservation, and the sustainable management of deep-sea ecosystems.

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Author contributions

R.D. conceived the idea. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare that they have no competing interests.

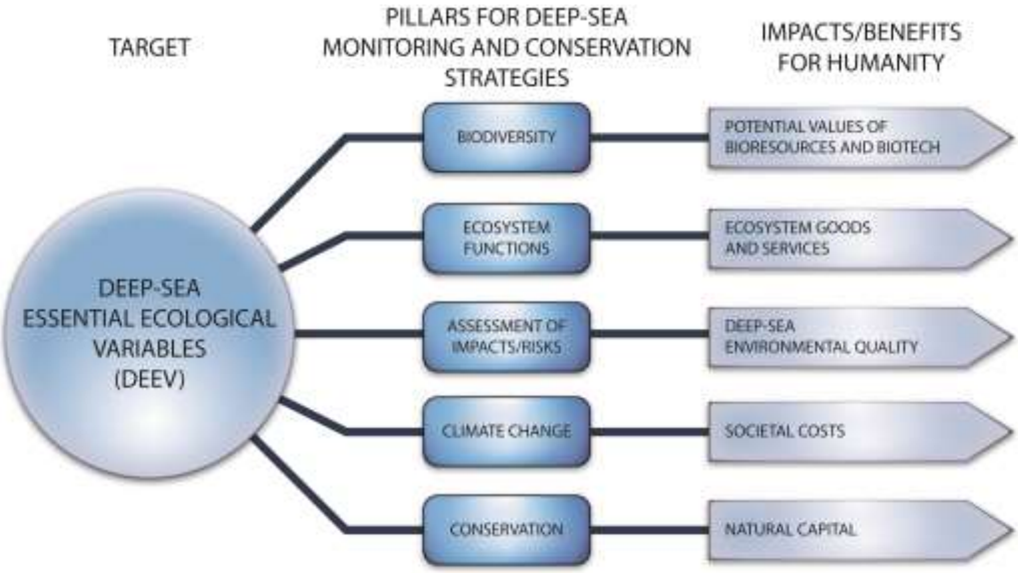

Figure 1. Biology-focused deep-sea monitoring strategy based on internationally standardized variables. This monitoring strategy will facilitate the achievement of important societal and industrial objectives, including the discovery of the largest remaining fraction of unknown biodiversity on Earth, 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.

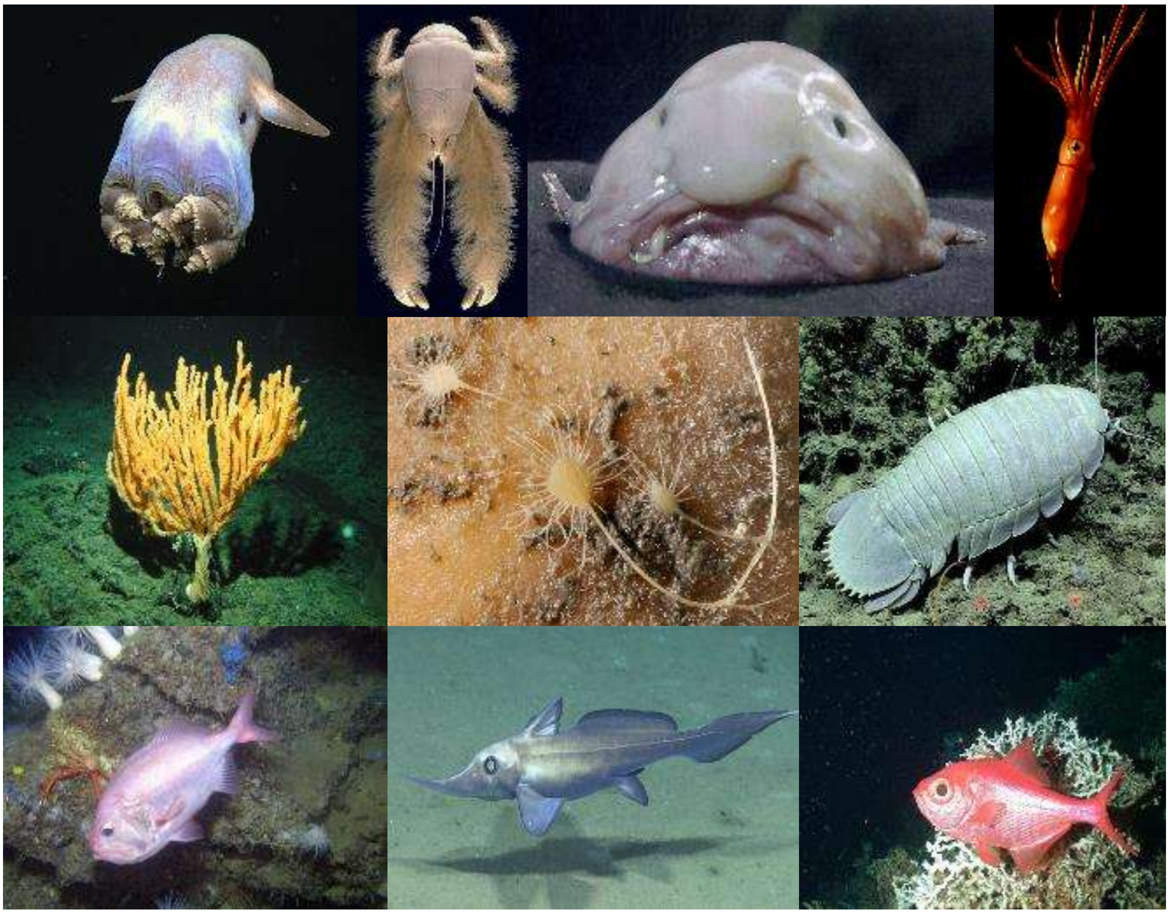

Figure 2. An example of iconic and flag species that inhabit deep-sea ecosystems. From left to right, from the top to the bottom: *Grimpoteuthis robson* (Dumbo octopus), *Kiwa hirsuta* (Yeti crab), *Psychrolutes marcidus* (Blob fish), *Architeuthis sanctipauli* (Giant squid), *Isidella tentaculum, Abyssocladia polycephalus*, *Bathynomus giganteus*, *Hoplostethus atlanticus* (Orange roughy), *Harriotta raleighana*, *Beryx decadactylus*.

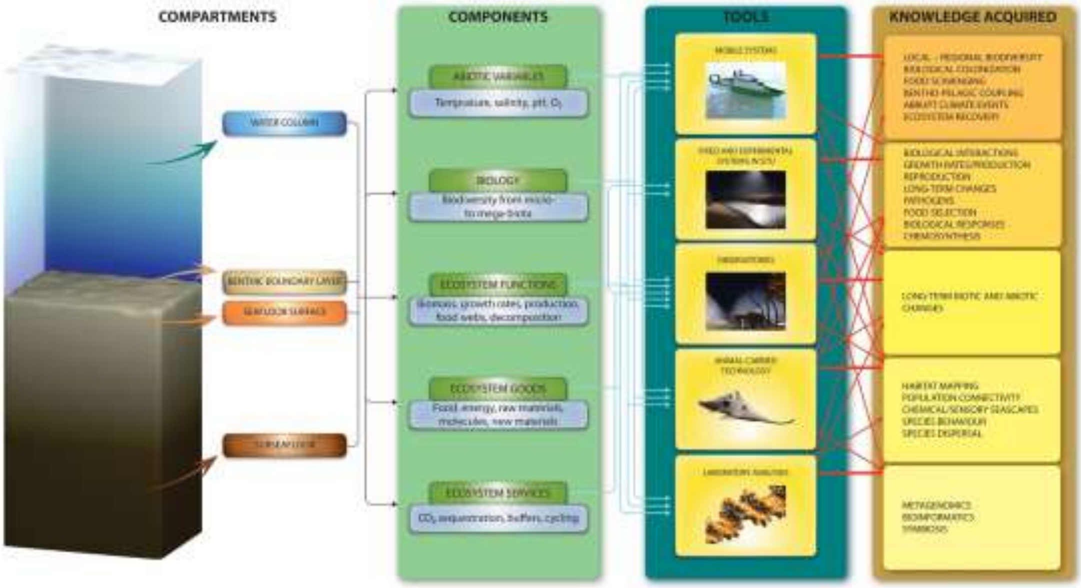

Figure 3. A conceptual diagram illustrating the potential technological development planned to acquire knowledge for sustainable use/management of deep ocean use. The illustration includes: the deep-sea compartments of interest (left column), the abiotic and biotic components (central-left column), potential tools and intelligent technologies needed to investigate the deep ocean (central-right column), and the potential knowledge acquired (right column).

Table 1. Deep-sea essential ecological variables for monitoring biodiversity in the water column and seabed, as well as the associated metrics (Expert Elicitation, n=112).

Biodiversity water column	*Priority*
Nekton	Very high
Bacteria	Very high
Macrozooplankton/Micronekton	High
Megazooplankton	Medium
Mesozooplankton	Medium
Microzooplankton	Medium
Protozoa	Low
Archaea	Very low
Biodiversity in sediments/on the seafloor	
Epibenthic large and sessile megafauna	Very high
Macrofauna	High
Meiofauna	Medium
Nekto-benthos	Medium
Bacteria	Medium
Protozoa	Low
Archaea	Very low
Biodiversity measures	
Assemblage structure	Very high
Species distribution	Very high
Habitat heterogeneity	High
Population size (N)	Medium
Species richness	Medium
ES(100)	Low
Phylogenetic distinctness	Low
Endemicity	Low
Rarity	Very low
Evenness	Very low

Table 2. Summary of actions required for deep-sea monitoring of the most important essential ecological variables (i.e. ranked as "Very high" in the Expert Elicitation) for the five pillars of knowledge (see **Supplementary Tables** from **1** to **3** and **5**). Developed monitoring actions utilize high-resolution technologies (see types and current level of technological development in **Supplementary Table 6**).

Pillar of knowledge	Essential ecological variables	Monitoring approach
Biodiversity	Assemblage Structure Species Distribution	Computing species distribution and assemblage structure per sampling zone and summing up the data for the whole area
Ecosystem functions	Trophic structure	Classifying and quantifying feeding-oriented interactions (i.e. listing food items for trophic niche characterization), combining the use of direct ethological observations as well as statistical proxies (i.e. *via* recurrent species spatiotemporal co-presence). The food web architecture could be then inferred by joining together trophic niche data for all species
	Benthic faunal biomass	Biovolume estimates (e.g. class size frequencies form individuals body length)
	Morpho-functional traits	Classification of species morphological adaptations according to a variable level of dependency upon the substrate (i.e. from endo-benthos as burrowers and buriers to epi-benthos as sheltering taxa, and ending with nekton-benthos freely swimming in the BBL or bentho-pelagos moving into the water column)
Impact/risk assessment	Habitat damage	The analysis of seascapes changes based on habitat mapping approaches and georeferenced photomosaic compositions
	Resilience (recovery rate)	Multivariate analysis time series counts for species depicting fluctuations according to concomitant oscillations of key environmental drivers (e.g. temperature and oxygen maxima and minima)
Adaptation & Evolution	Shifts in bathymetric distribution	Assessing changes in the geographic, bathymetric, and endemic detection of individuals (both juveniles and adults).
	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.
Conservation	Vulnerable deep-sea habitats Habitat forming species	Quantifying density and distribution patterns of dominant (i.e. abundant) sessile species as "Facies" (e.g. sea pens, cold water corals, sponges, tube worms, bivalves) per each sampling area

Box 1. Main threats for deep-sea ecosystems

The deep oceans are increasingly impacted by human activities. Here the four major threats for deep-sea species/habitats/ecosystems are presented, 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[104] and hence the POC flux (i.e., food supply) to the deep-sea life[41], altering structural and functional variables of deep-sea assemblages[105-107]. Temperature changes in the deep-sea influence key life-history traits (i.e. reproductive effort, larval development[63,108,109] longevity, and metabolic rates, and body size of deep-sea organisms[110]). Higher temperatures increase deep-sea respiration, thus exacerbating the effects of food limitation[111]. Such changes are expected to select the species pre-adapted to new condition[55], thus increasing beta diversity over time[112]. Moreover, climate change will presumably cause oxygen decline and expand OMZs[69], 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[113], and dissolves the non-living components of coral reefs[72].

Oil/gas extraction and mining. The substantial development of methane hydrate extraction and deep-sea mining is exacerbating conservation concerns despite the absence of baseline ecological knowledge[37]. The impact of proposed large-scale deep-sea mining and oil and gas drilling offshore activities can potentially transform deep-sea ecosystem structure and functions irreversibly[114,115], removing most life locally, possibly leading to "desertification" of the ocean[9]. 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[98,116-118]. 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[3,119].

Deep-sea fishery. Historically established deep-sea fisheries have a proven capacity to remove slow-growing, long-lived species[120] and many habitat-forming organisms from the seafloor[121], greatly altering habitat properties (e.g. removal and resuspension of bottom sediment[122]). Further, many deep-sea commercial species congregate in large numbers around seamounts to feed and spawn, making them extremely vulnerable to overfishing (the case of 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 ca. 40% of the world's fishing grounds are now in waters deeper than 200 m[123].

Contaminants and Debris. Growing human population has led to increased inputs of pollutants and debris, including plastic, into the ocean, where they are transferred through passive sinking or trophic transfer into the deep sea. Both macro-plastic and organic contaminants are common in sediments and organisms all the way to the deepest waters including the Mariana Trench[53,124]. Microplastics are pervasive in deep-sea sediments where they make their way into the food web[125]. 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 2. Current monitoring initiatives

The Deep-Ocean Stewardship Initiative (DOSI), the International Network for Scientific Investigation of Deep-Sea Ecosystems (INDEEP), 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 (i.e. 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[126], but lack of adequate biological/ecological approach[119,127]. The INDEEP has developed A World Register of Deep-Sea Species (WoRDSS) based on the World Register of Marine Species (WoRMS). The Census of Marine Life (CoML[128]) has contributed to the census of deep-sea species, which however remains far from being complete as 50% of macro-megafaunal and likely more than 80-90% of meiofaunal species remain undiscovered[129,130]. These monitoring initiatives supported the characterization of a set of variables described according to the scientific pillars identified. Existing approaches, protocols and technologies focused on deep-sea pelagic and benthic ecosystems processes include the following indicators of **ecosystem functioning**,: i) microbial heterotrophic production and microbial chemoautotrophic production (i.e., the ability to transfer energy to higher trophic levels); iii) size-specific biomass and production in prokaryotes and eukaryotes (including uni- and multicellular organisms) as a measure of the production of renewable resources by ecosystems; iv) predator-prey relationships, food-web structure, and energy flows; v) rates of organic matter respiration, decomposition, and recycling; and vi) habitat provisioning (numbers and composition of fauna utilizing biological structures such as deep-water corals[131]). Carbon limitation may push deep-sea organisms to increase the efficiency of resources' exploitation[132]. Potential indicators of ecosystem efficiency[8] include: i) the ratio of benthic faunal biomass or production to organic C input; ii) the ratio of prokaryote C production to organic C flux; iii) the ratio of benthic faunal biomass to available food in sediments. The identification of the indicators 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 analyze 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 indicators should combine broad spectrum and specific indicators, able to provide high sensitivity in detecting a wide range of impacts (i.e., degradation or loss of habitat, sediment resuspension, light and noise footprints, the introduction of toxic materials[133,134]). The indicators of **climate change impacts** consider shifts in deep-sea species spatial distribution[135], as a measure of the capacity of organisms to adapt to changing conditions or the preference to migrate to more favorable conditions, and loss of marine biodiversity[136]. Species-specific traits (i.e. body size, reproduction mode, feeding behavior, etc.) allow quantification of how species respond to global change including climate change, biological invasions, overexploitation and habitat fragmentation[137, 138]. New ecosystems and habitat types are continuously discovered at depths below 200 m[49,139], and most of these represent hotspots of key processes or endemic species[19, 140,141], which require conservation strategies. Currently, **deep-sea conservation initiatives** include off-shore MPAs (i.e. Special Areas of Conservation) and Other Effective Area-Based Conservation Measures, including Area-Based Fisheries Management, the designation of Vulnerable Marine Ecosystems (VME), or Areas of Particular Environmental Interests –APEIs- which are a form of MPA where no mining will be authorized to take place[142] (see also **Supplementary Table 5**). 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[143]. 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: i) uniqueness or rarity; ii) special importance for life history of species; iii) importance for threatened, endangered or declining species, and/or habitats; iv) vulnerability, fragility, sensitivity, slow recovery; v) biological productivity; vi) biological diversity; and vii) naturalness. These criteria should 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. Conservation efforts should also consider the need to protect the full range of habitats within an ecoregion, at spatial scales and spacing sufficient to sustain populations[76,77]. Deep-sea conservation should target three-dimensional representative habitats, areas with high topographic complexity and habitat heterogeneity, and biodiversity hot-spots with high levels of endemism.

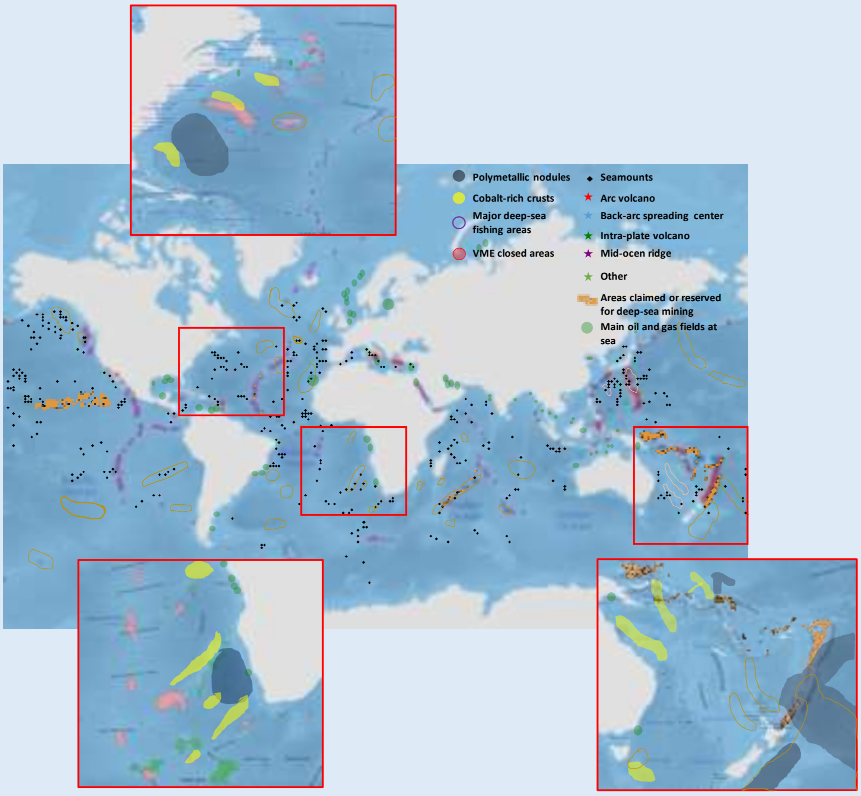

Figure Box 2. Global map of deep-sea areas that according to international standards have been identified as priority target for protection. Source: VME closed areas, seamounts, arc volcanoes, back arc spreading centers, intra-plate volcanoes, mid-ocean ridges and other similar features and bottom fishing areas (green blocks in inset figure off SW Africa, SEAFO area) from the FAO VME database (accessed March 2018); areas claimed or reserved for deep-sea mining from International Seabed Authority, Flanders Marine Institute, Nautilus Mineral (orange areas); marine mineral deposits (i.e. polymetallic nodules (blue) and cobalt-rich ferromanganese crusts (light green)[144]; main deep-sea fishing areas and major fisheries on seamounts and ridges (purple lines)[145].