



The deep sea: The new frontier for ecological restoration

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ABSTRACT

Deep-sea ecosystems are the most extensive on Earth and provide key goods and services for human well-being, such as genetic resources and climate regulation. Maintaining the sustainable functioning of the global biosphere therefore requires protection of deep-sea ecosystems, particularly because these ecosystems face major changes related to human and climate-induced impacts. Although we lack data to evaluate the spatial scale of degraded deep-sea habitats, numerous studies document human impacts on the whole ocean. However, protection alone can be insufficient to reverse habitat degradation in the deep sea. Scientifically, deep-sea restoration actions may be feasible, but whether such actions will achieve sustainability goals when applied at broad spatial scales of impact remain questionable. Successful application of most restoration efforts will first require a deeper understanding of biodiversity and functioning of deep-sea ecosystems, and better knowledge of ecosystem resilience and recovery rates of deep-sea fauna. In addition to limited data availability, expensive technologies (with estimated costs up to millions of dollars ha⁻¹) represent a major obstacle to large-scale deep-sea restoration, but international cooperation (like a stronger collaboration between industry and scientists belonging to the academia) could significantly reduce this operational cost. Future deep-sea ecosystem restoration could offer an important business opportunity for technological development and application and an investment in natural capital for a new and competitive blue-growth sector.

1. Introduction

The deep ocean, Earth's largest ecosystem [1,2], remains largely unexplored [1,3,4], primarily because of the technical challenges and associated high costs of investigation [5,6]. Despite these challenges, it is widely recognized that deep-sea ecosystems host a large portion of Earth's biodiversity that plays a key role in the functioning of our planet [6–10], supporting key ecological processes (including production, consumption and decomposition of organic matter and nutrient regeneration; [1]) and providing essential goods and services for human

well-being [9,11–14]. Marine biodiversity loss can fundamentally alter ocean stability, food and habitat provisioning, water quality, recovery from perturbations and biogeochemical cycles [1,15–20]. Anthropogenic activities and global climate changes threaten life in the global ocean [21–24]. Humans are modifying the environment and ecology of the oceans through top-down (e.g. fisheries overexploitation) and bottom-up impacts (e.g. eutrophication processes induced by excess nutrient release into coastal waters) [18]. Marine ecosystems worldwide are thus subjected to multiple stressors [13,25,26].

The deep sea is not an exception since industries are moving rapidly

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toward exploitation of its resources [22,27], partially in response to the depletion of those provided by terrestrial and coastal habitats. Rising demand for deep-ocean resource exploitation has generated the need for international laws to protect marine Areas Beyond National Jurisdiction (ABNJs, [6]). The United Nations Convention on the Law of the Sea (UNCLOS) works towards Conservation and Sustainable Use of Marine Biological Diversity beyond Areas of National Jurisdiction (BBNJ) and will likely apply in a multi-sectoral and integrated approach towards management, cooperation and coordination [28]. However, the protection of ABNJs is fragmented under different institutions [29] that concern fisheries (Regional Fisheries Management Organizations - RFMOs), mineral resources and mining activities (International Seabed Authority - ISA), and the BBNJ (UNCLOS). Despite this, at time, there is insufficient coordination between these organizations.

Plans for expansion of mineral exploitation and bottom-contact fisheries in the deep sea suggest increasing the potential for degradation of deep-sea ecosystems and call for regulation, protection and eventually funding of possible restoration actions [6,30–32]. Regulation of these activities for sustainable environmental management should follow a mitigation hierarchy [33], which firstly should avoid the impacts that can cause significant loss of biodiversity. The second step should include minimization measures that could reduce biodiversity loss, investing in engineering solutions and technical innovations that can be able to reduce the impacts. As third step, when biodiversity loss occurs, remediation/restoration actions are needed.

There is evidence that protection measures for the deep sea can be effective. As an example, the closure of the zone of the Darwin Mounds from trawling activities was successful, with coral recolonization and re-growth of damaged colonies [34]. The creation of deep-water Marine Protected Areas (MPAs) like that near Okinawa Island provided evidence of the potential success of a right management program. With protection, deep-water snappers can achieve sexual maturity and their reproduction rate could be improved [35]. For what concerns mining activities, ISA has identified some Areas of Particular Environmental Interest (APEIs) in the Clarion-Clipperton Zone located in the Pacific Ocean in which mining is forbidden [36] and the General Fisheries Commission for the Mediterranean and Black Sea established six Fisheries Restricted Areas (FRAs) in the high seas to protect Essential Fish Habitats and Vulnerable Marine Ecosystems (VME). To identify the last ones, new multi-criteria assessment methods are also available [37].

Requirements for remediation are often included in terrestrial projects, but similar approaches in the deep sea will face numerous challenges [38]. Several international conventions and directives, such as the European Marine Strategy Framework Directive or the UN 2030 Agenda for Sustainable Development, emphasize the importance of sustainably managing and protecting marine ecosystems, achieving good environmental status, avoiding significant adverse impacts such as biodiversity loss and loss of ecosystem functions [16], and taking actions for restoration of marine ecosystems. Despite some pilot restoration experiments on cold-water corals provided promising results [39–42], there is still no evidence of successful ecological assisted restoration as a management tool to reverse environmental degradation caused by human activities in the deep sea [38]. However, since protection alone can be insufficient to reverse habitat degradation in the deep sea, restoration actions should be properly defined to remediate and compensate human-induced damages.

The aim of this paper is to review the state of art on ecological restoration in deep-sea ecosystems, highlighting knowledge gaps and the main scientific, technological and economic challenges. We stress that restoration actions in the deep sea will be increasingly required in the future to face the expected progressive habitat degradation and as such they should be included in international conventions as a management tool to support conservation strategies of deep-sea ecosystems.

1.1. Which are the main impacts in the deep sea?

Industrialised states and private companies are expanding exploration of the oceans into deeper waters [43,44] to exploit biotic and abiotic resources [22,43,45–47]. Three major activities (trawling, mining and oil and gas exploitation) can affect deep-sea ecosystems over wide spatial scales (several square kilometres for oil and gas exploitation, thousands of square kilometres for mining and trawling activities) and at different depths. Depending on the type of catch, deep-sea trawling now operates from ca. 200 m down to 1500–2000 m depth [48,49], whereas mining activities are projected to extend to depths from ca 1000–1500 m down to more than 4000 m.

Steep declines in shallow fisheries resources in recent years [50,51] coincide with expansion of fisheries offshore to progressively greater depths [27,46,52–54], threatening ecologically important and sensitive habitats such as canyons and seamounts [52,55,56]. Among all human activities, bottom trawling represents the most serious threat worldwide to cold-water coral reefs and deep-sea sponge grounds, which are both biodiversity hotspots [52,57,58]. These deep-sea habitats are also characterized by species with slow growth rates (e.g., growth rates of the cold-water coral species *Lophelia pertusa* are around 4–25 mm per year and the observed growth rate of the deep-sea sponge *Rossella racovitzae* is around 2.9 mm per year) [59,60]. The use of fishing devices such as otter trawls impacts deep-sea ecosystems in several ways, including stock depletion, alteration of sea-bottom morphology, sediment resuspension, increased bottom-water turbidity, faunal mortality, altered nutrient cycles, and reduced benthic biodiversity [49,55,61–65]. These impacts are increasing worldwide. For example, 90% of the North Sea seabed has been trawled at least once and about 15 million km² of seabed—an area nearly the size of Russia—are trawled every year [66]. Bottom fishing is so far the major threat for seamount ecosystems that cover an estimated area of 21% of the ocean floor (about 76.5 million km²) [56].

Mineral exploitation to support increasing metal demands [67] represents the main future threat for the integrity of large swaths of deep seabed [57,68,69]. Nowadays, there is a strong commercial interest in manganese nodules in abyssal plains [70], cobalt-rich crust on seamounts [45], and seafloor massive sulphides at hydrothermal vents [67,71]. It is known that future mining activities could cause multiple impacts on deep-sea ecosystems, including habitat destruction, smothering of benthic communities by sediments, and increased toxicity associated with the release of heavy metals contained in the mineral ores [43,68,71–76], as well as alteration of a wide range of ecosystem services [77]. Exploration contracts have already been awarded for more than 1,800,000 km² of seabed [78]. Around 1.3 million km² of international seabed have been set aside for mineral exploration in the Pacific and Indian Ocean and along the Mid-Atlantic Ridge. Moreover, about 1,000,000 km² of deep seabed have been licensed and occurred in areas beyond national jurisdiction (ABNJs) [78,79].

Exploitation of oil and gas continues to extend deeper, with increasing risks for drilling-muds dispersal and oil-spills accidents [22,80,81]. More than 500 oil platforms are currently present in waters below 200 m depth in European seas linked to several thousand kilometres of pipelines [82]. These structures often occur near continental slopes, seeps, vents, and coral mounds [22]. Hydrocarbon extraction from the deep seafloor also releases heavy metals, discharges hazardous compounds such as barium in synthetic fluids contained in drilling muds, and leads to loss of habitat and benthic communities [83]. For example, the oil spill from the Deepwater Horizon in 2010 contaminated surrounding ecosystems with polycyclic aromatic hydrocarbons and barium and caused oxygen anomalies together with an alteration of food input to deep-sea benthic communities [84,85]. Laboratory-simulated experiments demonstrated that resuspension of sediments that could be provoked by both oil/gas exploitation and trawling activities causes several damages to deep-sea benthic organisms like corals and sponges [86–88].

Another threat for the deep sea is bioprospecting activity that can lead to genetic exploitation of deep-sea biological resources [89]. Several marine species, including microorganisms, provide a significant source of compounds of interest for biotechnological development [90,91]. For example, pharmaceutical companies are exploring deep-sea microbes for their potential to produce antioxidant, anti-microbial and other bioactive substances [90,92,93]. Enzymes including esterase, lipase, protease, peptidase, polymerase (e.g. Taq-polymerase) from deep-sea microorganisms offer multiple applications because of their capacity to expand the conditions in which biocatalysis can occur [94]. Deep-sea animals, such as the hard coral *Dendrophyllia cornigera*, produce steroids with potential anti-cancer properties [95].

Beyond impacts from resources' exploitation, numerous studies report contamination by multiple chemical compounds (introduced from sewage waters and coastal runoff, marine litter, plastic debris, discharge of industrial or military refuse; [22,96–104]). Scientific activities can alter deep-sea ecosystems using dredges, moorings, and other technical instruments that may affect benthic fauna [22,105].

Due to fossil-fuels use, land deforestation and degradation of habitats, the content of carbon dioxide in the atmosphere has increased by ca. 50% during the last two centuries, one-quarter of which is absorbed by the oceans [96,106]. This oceanic uptake of CO₂ has resulted in a reduction in pH and changes in the carbonate chemistry of the oceans from the surface to the deep ocean [14,23], with expected significant impacts on cold-water coral reefs [107,108]. At the same time, the rise of sea-surface temperature, due to the increase of greenhouse gases in the atmosphere, by enhancing water stratification and reducing mixing, is expected to reduce primary productivity of the ocean surface and the export of carbon to the ocean floor with severe consequences on the structure, function and biodiversity of deep-sea ecosystems [32,109–112]. Structural and functional alterations of deep-sea biodiversity can also occur due to temperature shifts of the deep-water masses [113]. Direct and indirect global climate change impacts will likely exacerbate all the other impacts on deep-sea ecosystems [14,23,32,96,106–113]. Moreover, at present, the actual extension of marine ecosystems impacted by human activities is still largely unknown [114], especially that in the deep sea [22]. Due to our scarce knowledge of the deep-sea functioning, cumulative consequences of all the impacts are not easy to assess [115].

2. Planning the “restoration” of deep-sea ecosystems

The Society of Ecological Restoration (SER) defines the International Standards for the Practice of Ecological Restoration and clearly distinguishes between “ecological restoration” and other forms of ecosystem repair. Although restoration is the process of “assisting the recovery of ecosystems that have been degraded, damaged or destroyed” [116], the “recovery” of an ecosystem refers to the achievement of a target environment similar to an appropriate local native model or reference ecosystem, in terms of its specific compositional, structural, and functional ecosystem attributes [117,118]. “Restoration” includes an action or multiple actions that jumpstart recovery and place a degraded ecosystem on a trajectory for recovery [119,120], regardless of the period required to achieve the recovery outcome [118]. Ecosystem restoration principally aims to establish a self-supporting habitat similar to the ‘original’ habitat prior to the impact. Restored ecosystems can be resilient to perturbations, including the capacity for the ecosystem to adapt to existing and anticipated environmental change [117,121,122]. The selection of the desired reference system guides ecological restoration and should be both historically inspired and grounded in social processes that include multi-party stakeholders and restoration scientists and practitioners [120]. Application of a group of restoration actions at a site can help achieving restoration goals, including remediation, reparation, and rehabilitation. As a restoration goal, rehabilitation is less ambitious in not necessarily achieving full recovery of processes and a return to “pre-disturbance”

conditions [120,123]. It simply replaces structural or functional characteristics damaged by an impact, and aiming to enhance the social, economic, and ecological value of the new ecosystem [117,118,123].

SER states that the reference ecosystem, as a model for all of these kinds of actions, should resemble a near undamaged site. In alternative, the reference ecosystem can be derived from multiple sources of information on diverse ecological and biological variables (e.g. biodiversity, life cycles, functional variables, food webs) supported by abiotic measurements [6,117]. In any case, ecosystem baselines should be clearly defined. Full recovery requires several steps, each encompassing several interventions (e.g. removal of the disturbance, removal of invasive species, enhancement of native species reproduction; [118]). Ecological experts in restoration have abandoned the idea of total recovery, recognising the dynamic nature of ecosystems, and restoration may not follow the appropriate ecological trajectory to re-establish over time, especially considering the need for ecosystems to adapt and evolve over time in response to climate change [124].

Regarding the deep sea, some new industrial projects, such as the pipeline deployment in the deep Mediterranean Sea and the exploitation of mineral ores in Papua New Guinea, include mitigation actions for reducing the environmental impact. For example, the mitigation plan for the exploitation of deep-sea mineral ores in Papua New Guinea includes the selection of an area similar in size and characteristics to the mining one, as a possible source for natural repopulation of the impacted site (i.e., natural unassisted recovery; [68]). Despite this, if deep-sea mining will be realized in the next future, restoration actions are needed to remediate and compensate the habitat degradation induced by such activities [120,123]. Managers may sometimes consider replacement, re-creation or creation of new undamaged habitats that can compensate for the loss of another [118,119].

Furthermore, for most deep-sea ecosystems, we lack information on ecosystem baselines to establish an appropriate reference for effective restoration, an attribute that most terrestrial restoration efforts can provide through experimental ecology. We require robust information on biodiversity, trophic interactions, distribution ranges, dispersal distance and connectivity [112]. The scientific community recognizes an urgent need to increase knowledge on deep-sea ecosystem functioning prior to deep-sea resource exploitation [100,125,126]. The limited information on deep-sea ecosystems (less than 0.0001% of the deep ocean's surface has been investigated [112]) precludes the assessment of restoration effectiveness in case of degradation due to future possible activities such as deep-sea mining [32]. Even when baselines are better known, like for some deep-sea habitats (e.g. cold-water coral reefs and seamounts) or for certain areas of the oceans (e.g. some areas of the north-east Atlantic Ocean), restoration actions will be a major challenge, especially due to the need of sophisticated technologies and infrastructures (e.g. autonomous underwater vehicles, remotely operated vehicles, oceanographic vessels) and high costs [5,112]. In addition, the prolonged timeframe for natural recovery of threatened deep-sea ecosystems by slow rates of recruitment and growth of resident fauna will further constrain deep-sea restoration efforts [22,127,128]. Thus, in parallel with monitoring ecosystem recovery following anthropogenic disturbances, we need to develop and apply restoration strategies to degraded/damaged deep-sea ecosystems.

2.1. Passive restoration: the natural unassisted recovery of deep-sea ecosystems

Multiple studies have investigated anthropogenic impacts on deep-sea ecosystems and the natural recovery capacity of benthic fauna (Table 1) with passive restoration, i.e. unassisted natural recovery of ecosystems following cessation of an activity. Although the unassisted restoration can be considered the less expensive practice, economic resources should be allocated by governments, research institutions, academia, industries, and non-governmental organizations for monitoring activities aiming to assess the natural recovery of the

Table 1
Benthic fauna recovery capacity in different deep-sea habitats. n.a. = not available.

Type of action	Habitat	Depth	Biotic component	Duration	Spatial scale	Result/Efficacy	References
Natural recovery	Soft bottom	1760 m	Macrofauna	2 years	< 10 m ²	no significant recovery	[129]
Fertilisation with kelp powder		1525 m	Macrofauna, meiofauna	3 months	≈ 200 m ²	no recovery	[84]
Natural recovery	Seamount and coral mounds	1300 m	Macrofauna	5 months	< 10 m ²	low colonisation rates, no effects of enrichment	[130]
		ca. 1200 m	Stony corals, associated megafauna	5 years	≈ 0.002 km ²	no significant recovery	[131]
Natural recovery	Manganese-nodule fields	from 750 to 1600 m	Macrofauna	about 20 years	≈ 0.006 km ²	no recovery of community composition	[132]
		from 750 to 1600 m	Megafauna	5–10 years	n.a.	no complete recovery	[133]
		ca. 4000 m	Prokaryotes	6 months	< 10 m ²	abundances similar to undisturbed sites	[138]
			Megafauna, macrofauna, meiofauna	3 years	< 10 m ²	high abundances but no completely recovery of community structure	
			Polychaeta	7 years	≈ 0.05 km ²	differences in taxa and functional group composition	[136]
		4140 and 4160 m	Soft-bottom megafauna	7 years	< 10 m ²	differences in abundance and taxa composition	
		from 4122 to 4201 m	Hard-bottom megafauna	7 years	< 10 m ²	no recovery due to hard-bottom removal	[137]
		ca. 5000 m	Macrofauna	26 years	< 10 m ²	recovery of the overall abundances, no recovery of community structure	
		ca. 5000 m	Meiofauna (Nematoda)	26 years	< 10 m ²	abundance, biomass and biodiversity significantly lower within dredging tracks	[141]
		ca. 5000 m	Macrofauna	44 months	< 10 m ²	recolonization in progress but at slow rates	[143]
		200–800 m	Epifauna	37 years	≈ 0.02 km ²	no significant recovery	[142]

investigated ecosystems, including funding for ship time, personnel involved and sampling activities [6]. For restoration/rehabilitation/conservation practices, a global strategy could be the principle of “polluter pays”: stakeholders who are responsible for the damage should fund deep-sea ecosystem recovery actions [31]. Despite ISA could allocate a part of the money derived from the payment of licences for funding future protection projects on mined areas, activities like high seas fishing and oil extraction have free access to deep-sea resources and are not obliged to fund such programs. In these cases, a tax corresponding to the 1% of their revenues will generate a big fund to support actions for deep-sea conservation in any form [31]. In addition to the very high costs, the long-time scale needed for the recovery of degraded deep-sea ecosystems will further constrain restoration efforts [22,127,128].

The first assessments of the natural unassisted recovery of deep-sea assemblages in the early 1970s compared rates of macrofaunal re-colonisation of defaunated sediments placed in boxes at 1760 m depth (using the submersible Alvin) to those at shallow depths (10 m depth; [129]). This experiment provided the first evidence of much slower recovery rates of macrofauna in benthic deep-sea ecosystems compared to shallow environments (years vs. few months). A similar study in the Santa Catalina Basin (California) at 1300 m depth used defaunated sediments to explore the potential of organic enrichment using kelp algae (*Macrocystis pyrifera*) powder to enhance deep-sea macrofaunal recovery [130]. Colonisation rates in the enriched sediments were i) lower than those in the un-enriched deep-sea sediments and ii) an order of magnitude lower than rates at shallow depths. Moreover, several time-series observations of seamount benthic communities impacted by bottom trawling [49,131–134] revealed no consistent signs of recovery in megafauna or macrofauna 5–10 years after fishing cessation, again suggesting very slow recovery for these benthic organisms.

Recovery of deep-sea benthic assemblages was also investigated in a manganese nodule area of the deep South Pacific (Peru Basin) after a simulated disturbance in 1989 [135–137]. Researchers simulated mining impacts by intensively ploughing manganese nodules near the sediment surface with a plough-harrow disturber designed to mimic manganese extraction. Half a year later, only prokaryote abundances resembled those of the undisturbed sites [138]. After 7 years, neither macrofaunal nor megafaunal abundances had completely recovered [136,137] and after 26 years there are still no evidence of complete recovery of the ecosystem functioning [139,140]. In the Clarion Cliperton Zone (North-eastern Pacific), the most commercially attractive deep-sea deposit of manganese nodules, several experiments simulated mining operations using benthic disturbers: meiofauna had not recovered 26 years after the experiment [141], and epifauna had not recovered after 37 years [142]. In the Central Indian Basin, 44 months after researchers' simulated disturbance by manganese nodule collection, the sedimentary macrofauna still had not recovered [143]. A recent meta-analysis suggested impacts and recoveries from deep-sea mining comparable to those associated with bottom fisheries or volcanic eruptions [144]. This study reinforces expectations of slow recovery rates in benthic deep-sea assemblages [22,76] and that deep-sea mining, by removing the hard substrates on which associated fauna depends, can significantly impact assemblage composition and result in long-term community changes [142,144]. Recovery rates of disturbed taxa differ widely, with some taxa increasing above pre-disturbance abundance and others that do not recover even in the long term [144]. Other studies of recovery of benthic deep-sea fauna examined impacts of oil and gas exploitation. For example, oil dispersal from the Gulf of Mexico Deepwater Horizon blowout resulted in slow recovery of deep-sea invertebrate assemblages [84], supporting previous findings obtained after the Amoco Cadiz oil spill off France in 1978 [145].

Therefore, multiple lines of evidence indicate (very) delayed recovery of altered deep-sea ecosystems, principally because of slow rates of faunal recruitment and growth [22,112]. Thus, the establishment of Marine Protected Areas and Marine Reserves in high seas is needed not

Table 2
Proposed methods for the restoration of damaged deep-sea habitats. Evaluation of the costs for the first year has been made using data from literature [30,161,162]. The time required for the recovery is based on the data/opinion of the authors reported in the reference list. n.e. = not estimated.

Habitat	Impact	Type of recovery	Proposed method	Costs for the 1st year (in millions USD x ha ⁻¹)	Time for recovery	References
<i>Soft bottoms</i>	trawling, dredging, bottom longlines	Passive restoration	Protected Areas to enhance natural recovery	1.2	> 40 years	[142]
		Passive restoration	Protected Areas to enhance natural recovery	1.2	> 10 years	[49,131–133,144]
	mining of Fe–Mg crust	Active restoration	Increasing of the rugosity of mined substrata to promote larval settlement	n.e.	n.e.	[163]
<i>Coral mounds</i>	trawling, dredging, bottom longlines	Passive restoration	Protected Areas to enhance natural recovery	1.2	at least one decade to reach the same proportion of dead/alive corals of control areas	[34,43,164]
		Active restoration	Rearing and transplant of nubbins of deep corals	≥ 15	several decades	[30]
<i>Manganese nodules fields</i>	mining	Active restoration	Electrified artificial reefs to enhance survival/growth/recruitment rate of Cold-Water Corals	4.4	n.e.	[41,152]
		Passive restoration	Recruitment of larvae in shallow depths and translocation in deeper areas	3.3	n.e.	[30]
		Passive restoration	Transplanting fragments from donor colonies	3	n.e.	[30,39,40]
		Active restoration	Protected Areas to enhance natural recovery	1.2	> 40 years	[142]
		Active restoration	Networks of Areas of Particular Environmental Interest where mining is not allowed	5	n.e.	[36]
<i>Hydrothermal vents</i>	mining	Active restoration	Deployment of hard artificial substrata	n.e.	n.e.	[163]
		Passive restoration	Addition of artificial sponges to enhance recruitment of associated fauna	n.e.	n.e.	
		Active restoration	Recreating nodule moulding mined sediments	n.e.	n.e.	
		Passive restoration	Protected Areas to enhance natural recovery	1.2	n.e.	[36,71,147]
		Active restoration	3D structures for the recruitment and/or transplant of vent fauna/enhancement of sulphides precipitation and eventually drilling of the seafloor to recreate the vent	≥ 15	several decades	[30,163]

only to protect deep-sea habitats from human exploitation activities, but also to favour the natural recovery of already degraded habitats. More areas with restrictions for resource exploitations, like APEIs and Mediterranean FRAs, should be established for preserving deep-sea habitats. If specific exploitation activities will be allowed, they should be strongly regulated asking to the industries to provide specific environmental management plans that includes baseline assessment, monitoring and mitigation measures. This kind of management will be crucial to assess and reduce the impacts [146]. Finally, the application of restoration tools will be necessary to remediate and compensate unavoidable human impacts on deep-sea ecosystems [31].

2.2. Active restoration of deep-sea ecosystems

Active restoration of deep-sea ecosystems has received little attention, and until now lack any discussion on how to enhance natural recovery [30]. One major scientific research challenge is to develop new approaches and methodologies to support and accelerate natural recovery of deep-sea habitats affected by trawling and oil exploitation, and in the future by mining. Researchers have proposed several methods for deep-sea habitat restoration (Table 2), but all of these approaches require testing and evaluation of costs with applications in the field [147]. In some cases, however, active restoration (e.g., transplantation of artificial nodules in polymetallic nodule fields) can be unfeasible. For example, assuming mining within a contract area (75,000 km²) removes nodules over an area of 15,000 km² and the average nodule density prior to removal is 15 nodules m⁻², it would require 2.25×10^{11} nodules to be produced and carefully deposited at the seafloor. Assuming each nodule costs 0.1 USD to produce, it would equate to 22.5 billion USD to produce the nodules required to restore the hard habitat in 1 claim area.

The maintenance of deep-sea species in aquaria has significantly advanced in the last decade through technological improvements that allow researchers to manipulate deep-sea organisms, avoiding damage caused by pressure variations during transportation and manipulation [148,149]. High-pressure tanks can maintain deep-sea organisms at *in situ* pressures, facilitating laboratory experiments to test recovery potential (e.g. in terms of growth rates, budding rates, larval settling and growth) from damage/*ex-situ* transplantation. Laboratory experiments on the cold-water coral *L. pertusa*, reveal high recovery potential because of its capacity to regenerate coenosarc tissue after skeletal damage caused by physical disturbance actions, for example, from mining or trawling [150]. One study advocates that young polyps of fragments of Mediterranean *L. pertusa* maintained in aquaria can have higher growth rates than *in-situ* [151]. Moreover, mineral accretion technology (based on the seawater electrolysis induced by low voltage and a low intensity electric field; [152]) that has proven to be effective for tropical coral restoration [153] can significantly enhance the survival and growth of *L. pertusa*, opening new possibilities for rehabilitating and restoring cold-water coral habitats [41]. Pilot transplantation experiments of nubbins of *L. pertusa* were carried out in the Gulf of Mexico and in the North Sea. Other transplantation experiments off the south-eastern coast of Florida were carried out with *Oculina varicosa*. These experiments provided evidence of high survival rates of both species [39,40,42], suggesting that transplantation of nubbins from healthy colonies to degraded habitats can be an effective method for cold-water coral reef restoration [42].

The MERCES project (Marine Ecosystem Restoration in Changing European Seas; www.merces-project.eu) aims to provide additional evidence that deep-sea restoration is feasible, either using coral nubbins transplantation techniques or using artificial habitats enabling a better recruitment of the larvae of some deep-sea species. In this way, it will be possible to assist regeneration and aid the recovery of areas impacted by human activities, although the long-term efficacy of these transplants has yet to be assessed. MERCES is an EU-funded project started in 2016 which focuses on developing new restoration actions of some

specific kinds of degraded deep-sea habitats (hard bottoms). New technologies and approaches are now available to quantify the returns of restoration either in terms of ecosystem services and socio-economic impacts and defining the legal-policy and governance frameworks needed to optimize the effectiveness of the different restoration actions. In the framework of this project, active restoration experiments are focused on deep-water corals (in the Condor Seamount located in the north-eastern Atlantic Ocean) and compared with coral garden restoration at shallower depths. In the framework of the Work Package 4 (“Restoration of deep-sea habitats”), fragments of *Dentomuricea meteor* were collected, maintained in aquaria and transplanted with the use of benthic landers. Analyses of survival rate, growth rate and success of the experiment are still ongoing.

Further studies on active restoration protocols are needed, especially because the majority of available studies is focused only on cold-water corals that are also the most well mapped European deep-sea habitats [154]. Funding of scientific projects (as MERCES) could improve the comprehension of how restoration can be applied in the deep sea, how much time restoration actions could require to be effective and successful, how pilot experiments could be transposed at a broader spatial scale, which can be the criteria to establish the level of success of a restoration action.

Although the development of some promising tools to restore deep-sea degraded areas without compromising pristine habitats are in progress, the costs for scaling-up these pilot experiments are still uncertain. In addition, the long-term success of these experiments is unknown yet and we need to monitor the restored habitats to assess the efficiency and efficacy of the restoration action.

2.3. Deep-sea restoration: costs and benefits

Restoration of deep-sea ecosystems will surely challenge future decision makers evaluating the costs and benefits of maintaining ecosystem functioning and provisioning of goods against the economic benefits of exploitation activities. The costs required for restoration and major uncertainties of the outcomes raise major concern, in that restoration of deep-sea ecosystems might be 3–4 orders of magnitudes more expensive than for shallow water ecosystems [31]. As an example, the costs for the restoration of coastal habitats range from 0.8 to 1.6 million USD per hectare [155]. Despite these high costs, it appears that restoration in coastal areas can be successful and can provide tangible and social-economic benefits [156]. Both costs and benefits are more difficult to evaluate for deep-sea ecosystems [12].

Previous studies have considered hypothetical restoration actions in two impacted deep-sea ecosystems: the Darwin Mounds (UK) and Solwara I (Papua New Guinea) [30]. Economic estimates highlighted that restoring “Darwin Mounds” would cost about 75 million USD per hectare, whereas restoring “Solwara I” would cost about 740 million USD per hectare [30]; these estimates for the deep sea exceed by orders of magnitude the average cost of restoring one hectare of marine coastal habitats [30]. In particular, for restoration of deep-sea ecosystems, the use of ships and equipment such as remotely operated vehicles would account for approximately 80% of these costs [30].

As far as the duration of the restoration action is concerned, restoration projects in coastal areas often last less than five years (due to the duration of grants, academic thesis, experimental trials; [155]). However, the expected lower recovery rates in the deep sea let to hypothesise decades for reaching comparable results (Table 2). Another problem is how to determine the success of restoration efforts. For example, restoration programs in saltmarshes and coral reefs demonstrate high survival rates of transplanted organisms that promote habitat recovery [155]. However, it is difficult to evaluate the real success of these operations because most of these restoration actions have been carried out on a spatial scale of few hectares or less, whereas the spatial scale of human impacts on coastal habitats is in the order of several thousands of hectares [119]. Clearer criteria for assessing the success of

restoration actions should be established either for coastal (e.g., survival rate of transplanted seagrasses and corals; [119]) and deep-sea ecosystems, where in addition we need to expand our knowledge on the baseline conditions needed to establish the success of the recovery [30,157].

3. Conclusions and future perspectives

Despite high costs and uncertainties of the success, restoration of degraded habitats is considered as a priority for the next decades. On March 2019, the UN General Assembly has declared 2021–2030 as UN Decade on “Ecosystem restoration” [158]. In 2015, the United Nations defined a list of 17 Sustainable Development Goals (SDGs) for 2030. One of these goals (SDG14, life below water) is specifically dedicated to the conservation and sustainable management of marine life, including restoration of marine degraded habitats [159].

The IUCN (International Union for Conservation of Nature) has provided guidelines for restoration practices of coastal marine ecosystems [160]. To date, no guidelines have been established for the restoration of the deep sea. As a step toward such guidelines, scientists have proposed that governments and the UN should commit to the development of a global Deep-Sea Ecosystem Monitoring Network (DEMNs) that can provide new scientific knowledge to inform sustainable management of the deep ocean [6]. DEMNs will require a high level of funding to sustain the research that will support development of effective conservation and restoration actions.

Policy makers, before making decisions on exploitation of deep-sea resources, should take into consideration the following: i) avoid actions of irreversible degradation, ii) plan in advance the mitigation of the impacts caused on deep-sea ecosystems and iii) assess the costs for restoring the degraded deep-sea habitats [30,38]. It is also evident that restoration (both passive and active) actions for the deep sea should be identified before exploitation, and when restoration actions are deemed unrealistic or inconvenient after a cost-benefit analysis, the society should be properly informed. Policy makers should also consider that a loss of ecosystem functions could cause long-term loss of goods and services and have negative economic consequences. If the costs of restoration overtake the benefits obtained by exploiting activities, policy makers should consider carefully the convenience of such activities. Protection alone can be insufficient to reverse the degradation of deep-sea habitats so that restoration will be increasingly required in the future. Finally, policy makers should require the adoption of common internationally standardised guidelines for the restoration of the deep sea. We also need to improve and share our knowledge through international cooperative research and understand that ecosystem restoration will be the priority action for the compensation of the environmental impacts caused by the exploitation of natural resources in the deep sea. With global imperatives to restore marine ecosystems, accumulating knowledge from scientific research, environmental baseline studies, and other sources, an optimistic view is that the science of deep-sea restoration will mature rapidly and that application of restoration actions in the deep sea may be an opportunity for a new and competitive blue-growth sector.

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Author contributions

All authors equally contributed to this work.

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