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Priorities for ocean microbiome research

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Microbial communities have essential roles in ocean ecology and planetary health. Microbes participate in nutrient cycles, remove huge quantities of carbon dioxide from the air and support ocean food webs. The taxonomic and functional diversity of global ocean microbiomes has been revealed by technological advances in sampling, DNA sequencing and bioinformatics. A better understanding of ocean microbiomes could underpin strategies to address environmental and societal challenges, including achievement of multiple Sustainable Development Goals way beyond SDG 14 'life below water'. We propose a set of priorities for understanding and protecting the ocean microbiome, which include delineating interactions between microbiota, sustainable applications of resources from oceanic microorganisms and a need for policy- and funder-friendly ocean education resources, and discuss how to achieve these ambitious goals.

Microbial communities in the oceans are vital for both environmental and human health (Fig. 1). The global ocean comprises an immense biosphere that stretches across more than 70% of the world's surface and averages more than 3.5 kilometres in depth, but its biological properties remain largely underexplored. Remarkably, microscopic organisms represent more than two-thirds of the biomass in the ocean (Fig. 2)[1], performing almost as much photosynthesis as plants do on land[2], locking vast quantities of carbon away from the atmosphere[3,4] and underpinning the ocean food web[5]. Human-driven processes such as increasing greenhouse gas emissions and related warming climate, freshening, deoxygenation and acidification of the ocean represent a huge threat not only to larger flora and fauna but also to microbial communities. Planetary changes are causing altered microbial productivity, shifts in food webs and changes in the rates of transfer of carbon to the deep ocean[6] (Fig. 1).

The ocean microbiome includes bacteria and archaea plus a myriad of single-celled eukaryotes. Besides fungi, these are typically referred to as protists or micro-eukaryotes and include phytoplankton (also known as microalgae). They may act as predators, parasites, pathogens or/and symbionts. Recent genomic studies have revealed the diverse evolutionary trajectories of different phylogenetic groups and highlight complex inter-relationships among them that are not yet fully resolved[7,8]. We also consider viruses to be part of ocean microbiomes. Besides controlling population numbers of their hosts and transferring genes horizontally between different taxa, viruses also facilitate essential ocean processes such as carbon export to the deep ocean, nutrient cycling and primary productivity[9].

The ocean microbiome is estimated to consist of about four gigatons of carbon (the unit used to calculate biomass), which is four times the global biomass of all insects on Earth (Fig. 2)[1]. Ocean protists contribute the most biomass, whereas viruses represent only a small proportion of the total. Nevertheless, marine viruses are the most diverse, with recent analyses using metagenomic data collected during the *Tara* Oceans expedition (2009–2013) identifying a remarkable 200,000 different types of virus compared with 35,000 different taxa of bacteria and archaea, and 150,000 taxa of micro-eukaryotes[10]. These numbers are current best estimates; however, there are some limitations. The metrics used to determine diversity in each group are different, the full extent of diversity is not yet known and we still struggle to relate species concepts defined molecularly in unicellular organisms with macroscopic animals and plants, where sexual boundaries are clearer. Nevertheless, overall estimates placing the total species richness of the ocean microbiome at a few million taxa are similar to the estimated five million to nine million macroscopic species on Earth.

Recent environmental genomics initiatives, beginning with Craig Venter's shotgun sequencing of microbes from the Sargasso Sea reported in 2004[11], have shed light on the number of genes in the ocean. Around 50 million prokaryote and 100 million micro-eukaryote genes have so far been described by *Tara* Oceans, the project that has so far performed the largest global survey[10]. To put these numbers in perspective, the total number of prokaryotic genes identified in the ocean is similar to that in the human gut. However, the proportion of genes with unknown versus known functions in ocean prokaryotes is more than five times higher than in the human gut microbiome. This difference probably reflects the enormous disparities in scale and complexity of ocean versus human microbiomes, as well as in research funding for the ocean compared with human healthcare[12]. Conversely, protists are hugely understudied across all biomes, despite the importance of *Plasmodium*, Trypanosomes and *Phytophthora* to human and plant health. The vast diversity and often complex genomes of protists make their study challenging[7], but nonetheless vital because protists seem to dominate many aspects of the ocean microbiome.

It is increasingly evident that our understanding of a microbiome must go beyond identifying its members (termed the microbiota, that is, what is present), but also understanding members' habitats and functions. For the ocean microbiome, this is extremely complex and must include not only marine water but also sediments, coral reefs, hydrothermal vents, fragments of plastics and so on, as well as within all larger organisms—from copepods to fish, penguins, kelp and whales.

Ocean microbiome research dates back centuries (Fig. 3), with aquatic microorganisms first observed in the late 1600s and first cultured in the early 1900s[8]. In the past 20 years[13], multidisciplinary approaches combining multiple omics technologies (metagenomics,

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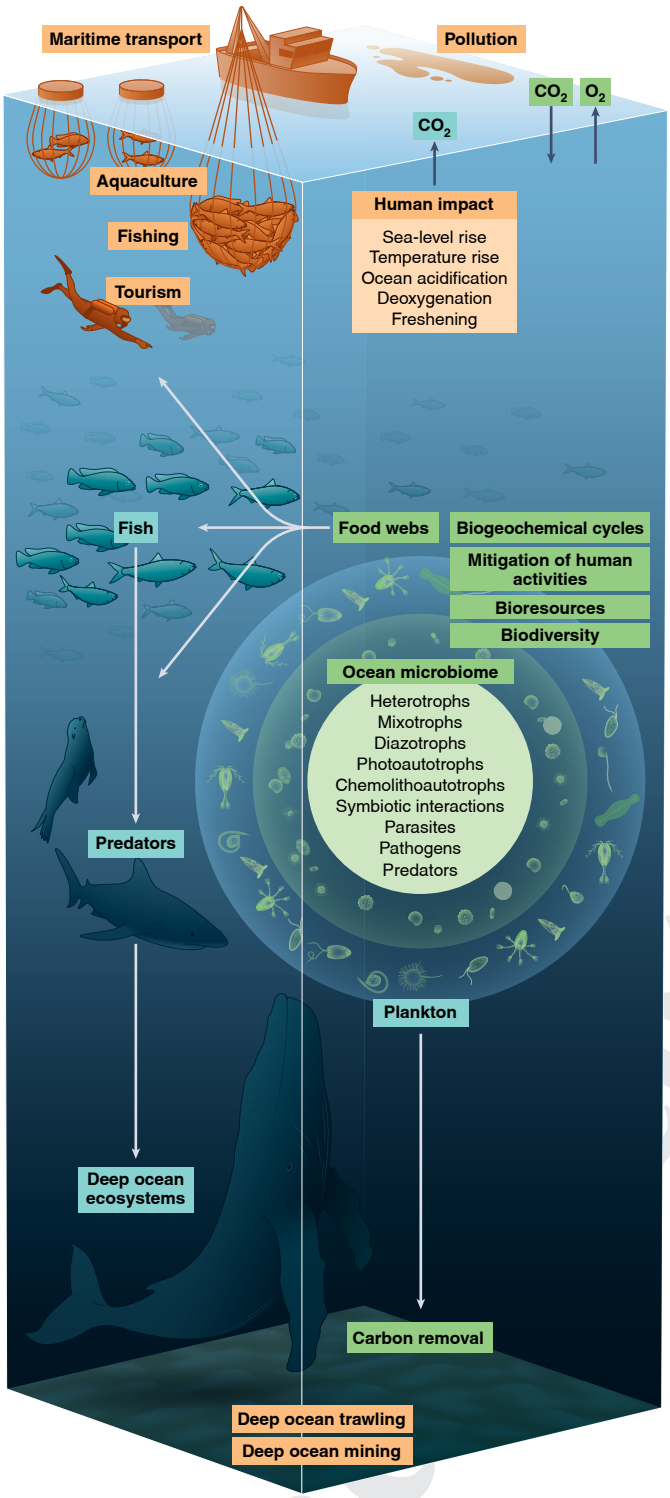

Fig. 1 | Roles of ocean microbiomes. The ocean microbiome (centre) is composed of a range of prokaryotes, eukaryotic microbes and viruses, which have a range of different lifestyles driving microbial interactions. The essential ecosystem services they provide, such as biogeochemical cycling (for example CO_2 capture, O_2 generation and carbon removal), mitigation of human activities, bioresources, biodiversity and resources for the entire ocean food web, are shown in green. Human impacts on the ocean are indicated in orange. Other aspects of the ocean environment are indicated in blue and interconnections between different components are shown with arrows. Image credits: boat, jellyfish, whale and killer whale from Freepik.

metatranscriptomics, metaproteomics and metabolomics) applied to environmental samples with cell biology, imaging, ecosystem modelling, remote sensing and oceanography have enabled improved understanding of individual microbes and their roles in the oceans (see Fig. 3 for major milestones).

While progress has been made, especially for coastal ecosystems[14], there are still major knowledge gaps and vast regions of the ocean remain largely underexplored (as outlined in Fig. 4). Our understanding of marine ecosystems in the surface (top 200 m) of the ocean far exceeds that of deeper ecosystems that make up most of the volume of the ocean. The majority of ocean microorganisms remain uncharacterized, but their populations are changing rapidly. For example, large shifts in the range and community composition of marine species, driven by anthropogenic climate change, have been observed in microbial communities[15]. Other threats to ocean habitats such as microplastics are also altering or even creating new habitats for microorganisms. A better understanding of these microbiomes would allow us to improve predictions of anthropogenic impacts on microbiome composition, resilience, evolution and productivity.

In this Perspective, we propose the ocean microbiome as a window of opportunity for enhancing our knowledge of the ocean's role in biogeochemical cycling and climate regulation, as well as our understanding of evolutionary and ecological processes that underpin the functioning of the entire ocean ecosystem. To aid this ambitious endeavour, a framework of priorities to understand and protect the ocean microbiome is outlined below (Fig. 5).

Composition and functions of the ocean microbiome

Separate searchable repositories for ocean microbiome datasets exist (Table 1). Recent advances, such as genome-resolved approaches that place genes in their whole-genome context (Fig. 3)[16,17], present further opportunities to develop a comprehensive view of the parts-list underlying microbial activities. However, efforts need to be centralized and harmonized to be fully exploitable by a wide range of end-users (Box 1). An ambitious programme—on the scale of the Human Genome Project—is now required to build a comprehensive inventory of genes, genomes, proteins, structures and molecular machineries associated with the ocean microbiome that also incorporates the morphological diversity of cells, symbioses and community structures. To achieve this, the research community will need to secure funding, coordinate and deliver this programme. An ocean microbiome inventory must be accessible online to all and include multiple search options to enable a wide range of questions to be addressed.

One key challenge is how to characterize genes of unknown function, especially when they are only present in uncultivated microbial lineages. One exciting possibility will be to extend genome-resolved approaches to address structural dynamics, for example, to explore how individual genomes respond to intimate symbioses between evolutionarily divergent species living in ultra-close proximity. This will require the adoption of long-read DNA sequencing and technologies to explore genome structure (for example, ref. [18]), as well as the use of high-throughput phenotyping platforms to detect microbial activities in single cells and in tractable representatives of key microbes and symbioses. The tracking of cellular fluxes of energy and matter (for example, ref. [19]) is equally crucial.

An ocean microbiome inventory needs to be accompanied by an atlas, designed to explore microbial functions in space and time. To achieve this, enhanced ocean observation systems and intensive data collection are needed. These data could be collected by cruise-based missions, in particular to less-studied parts of the ocean such as polar regions, areas beyond national jurisdiction, the deep ocean, the Global South and key biodiversity hotspots (Fig. 4). Long-term microbial observatories in the open ocean[20] are also critical for integration with data from coastal stations, and sampling

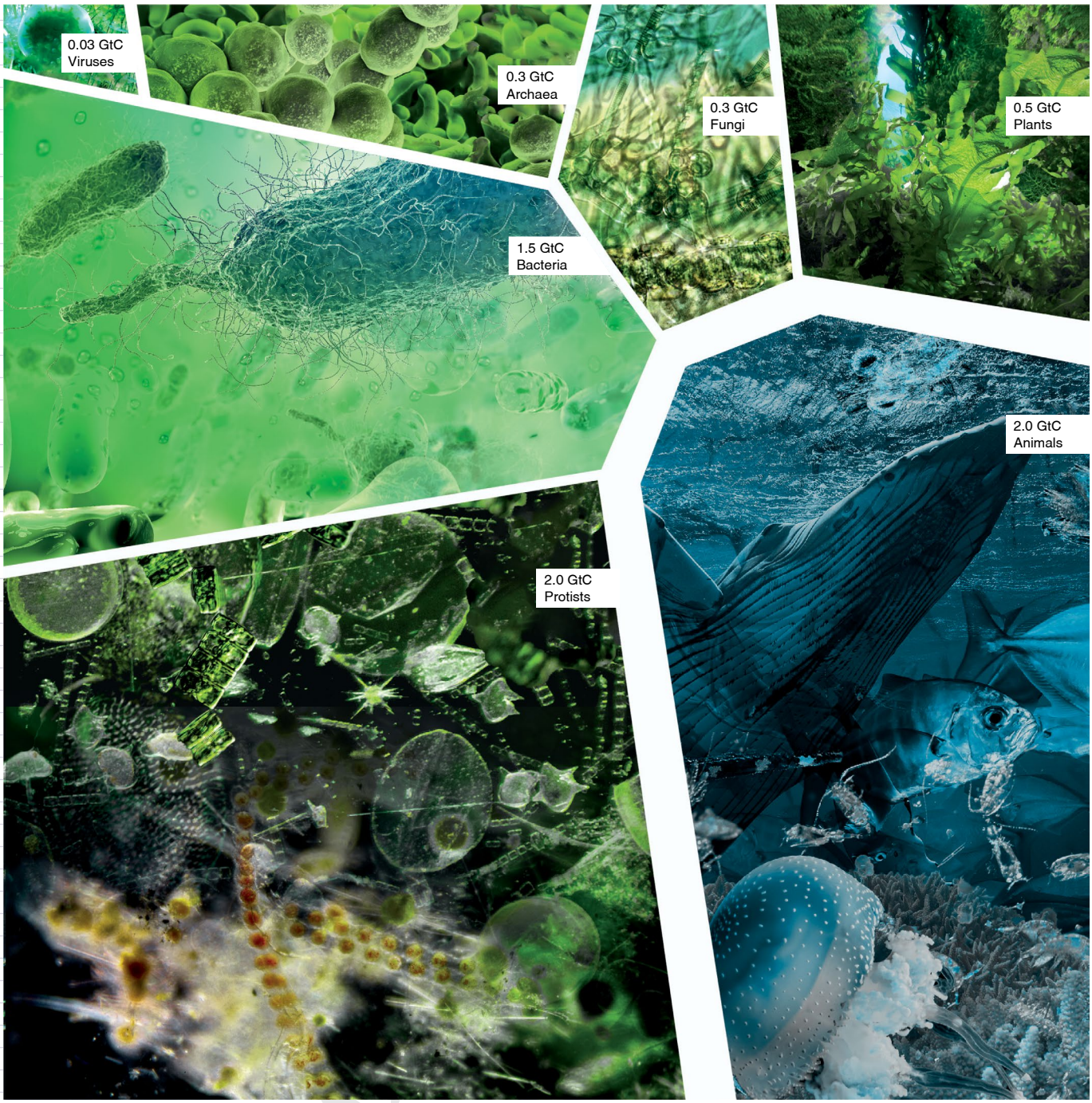

Fig. 2 | Estimates of total biomass in the ocean. Images are based on ref. [1]. Current knowledge of the ocean biome indicates that its microbiome represents at least two-thirds of its collective biomass, massively outweighing macroscopic animals and plants. Note that 'Plants' includes seaweeds and seagrasses, as well as green algae. For uncertainties, see ref. [1]. Data from ref. [1]. Bacteria image credit: University of Hawaii at Manoa. Other images from Adobe Stock.

protocols need to be standardized to cover the breadth of marine microbial communities[21]. Technological innovation of remote and autonomously operated instruments in areas such as automation[22] and miniaturization should continue, and artificial intelligence approaches must be developed to assist in data interpretation[23].

Given the scale of the endeavour, the development of complementary toolkits that empower citizen scientists and researchers to sample and study the ocean microbiome will be essential. For instance, the Ocean Sampling Day initiative proposed specially designed protocols to enable citizen scientists across the world to collect water samples alongside a minimal set of environmental metadata[24]. Conversely, the Planktoscope offers an open, user-friendly and cheap modular platform to image plankton quantitatively (https://www.planktoscope.org/). Inspired by the continuous plankton recorder deployed since the 1930s, we need to develop affordable instruments and protocols that can be used by sailors and others in maritime industries to generate global, reliable, long-term data[25].

A coordinated approach will be needed to ensure that microbial inventory and atlas data are findable, accessible, interpretable

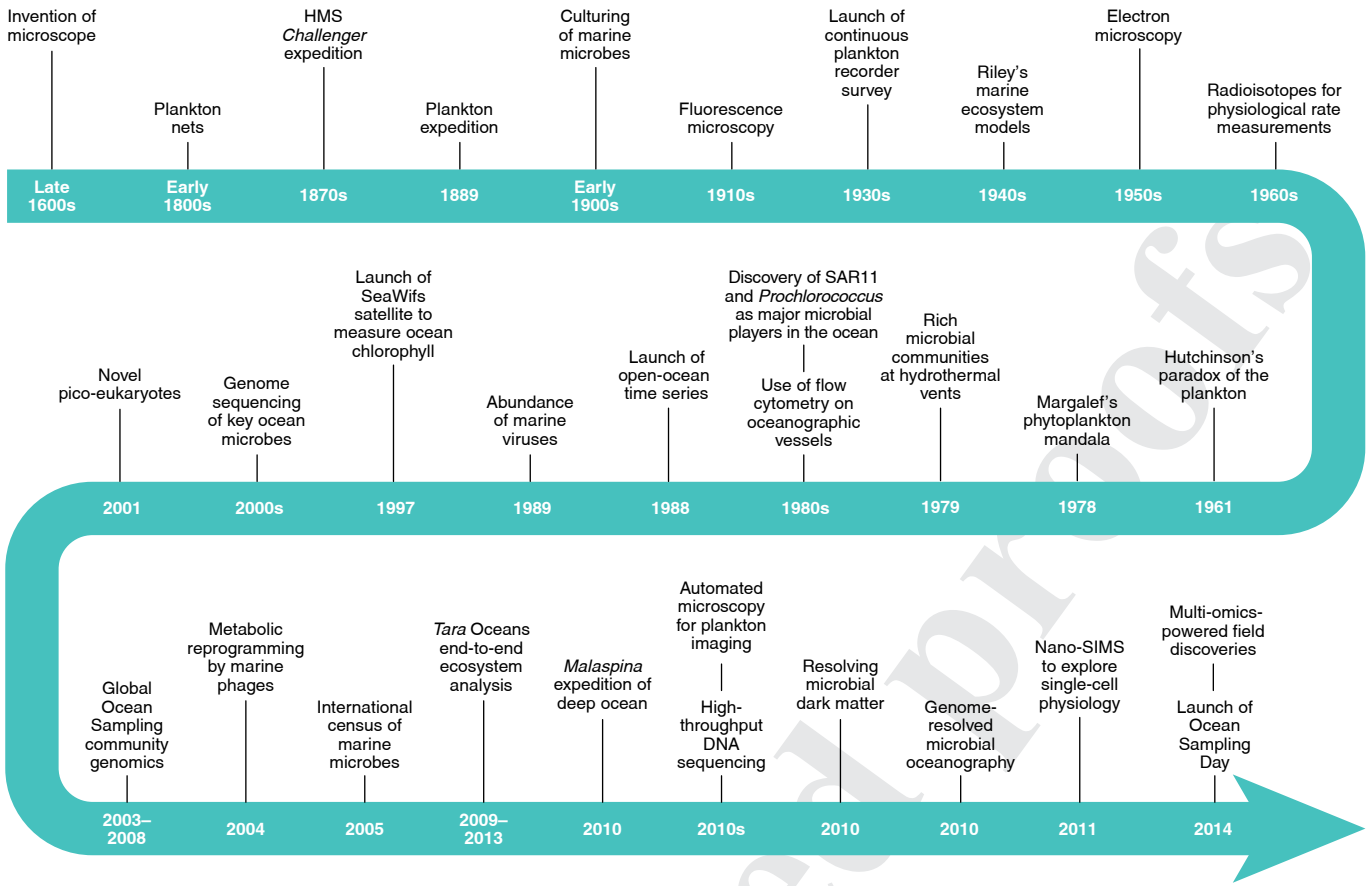

Fig. 3 | Timeline of ocean microbiome research. Data from refs. [8,16,17,48–67]. Image credits: 1870s, 1889, 1961, 1979, 1980s (left), 1988, 2009–2013 and 2010 (far right), Wikipedia; 1930s, David Johns, Marine Biological Association, UK; 1950s, Pixabay; 1980s (right), Isabel Romero Calvo; 1989, *Tara* Oceans; 2000s and 2010s (left), Christian Sardet and the *Tara* Ocean Foundation; 2011, Rachel A. Foster; 2014 (right), European Marine Biological Resource Centre. Other images from Adobe Stock.

and reusable, as well as interoperable (Box 1). Building on existing infrastructures such as MGnify and the National Microbiome Data Collaborative[26,27], a global scientific network dedicated to studying the ocean microbiome would bring different scientific expertise and communities together and might serve as an international benchmark for the study of all biomes.

Ecosystem-level ocean microbiology

Ecosystem-level biology combines the study of molecules, cells, populations and communities to assess their ecosystem impacts and the multidirectional connections between them. This is needed to bridge the gaps between molecular-level mechanisms, ecosystem processes and global-scale Earth system function. Integration of the ocean microbiome inventory and atlas—at both taxonomic and gene levels—with ecosystems research, including macroorganisms, will allow exploration of how microbes compete, collaborate and connect across ocean regions, ultimately aiding our appreciation of microbial functions and outputs at a global scale.

Ecosystems approaches will further reveal how the organization of marine and terrestrial ecosystems differ. This is crucial because our current conceptual framework for exploration of marine ecosystem function is based on studies of terrestrial ecosystems[28]. We are currently unable to incorporate biological diversity into Earth system models due to our lack of comprehension of its relation with ecosystem function. Understanding organization in the ocean is important not least because physics and chemistry are more likely to constrain the biology of the ocean than they do on land. Life probably evolved in the ocean, so a holistic view of the ocean as a dynamic bio-physico-chemical system might answer fundamental questions about the evolution, organization, adaptive capacities, and transfer of energy and matter within an ecosystem.

Safeguarding the ocean microbiome

Given the increasing number of threats to the ocean environment (Fig. 1), there is an urgent need to characterize the ocean microbiome in a relatively healthy state. This would provide a baseline to understand how these microbial communities might respond to global change, identify tipping points that could permanently change the composition of ocean microbiomes and determine potential broader impacts on ecosystem services[6]. One approach to achieve this is the identification of microbial diagnostic markers of change, akin to Essential Biodiversity Variables (EBVs) in macroecology. EBVs use genetic composition, species populations, community composition and ecosystem structure as tools to support the study, reporting and management of biodiversity change. The development of EBVs for the ocean microbiome would need to be based on acquisition of longitudinal time series data at a network of sites (particularly in understudied regions; Fig. 4), using standardized quantitative methodologies for fully automated sampling, sample processing and analysis that permit semi-real-time monitoring. The European Marine Omics Biodiversity Observation Network (EMO BON) provides one model for how this can be achieved (https://www.embrc.eu/emo-bon).

In addition, the development of hindcasting approaches to explore changes in the ocean microbiome in past centuries and

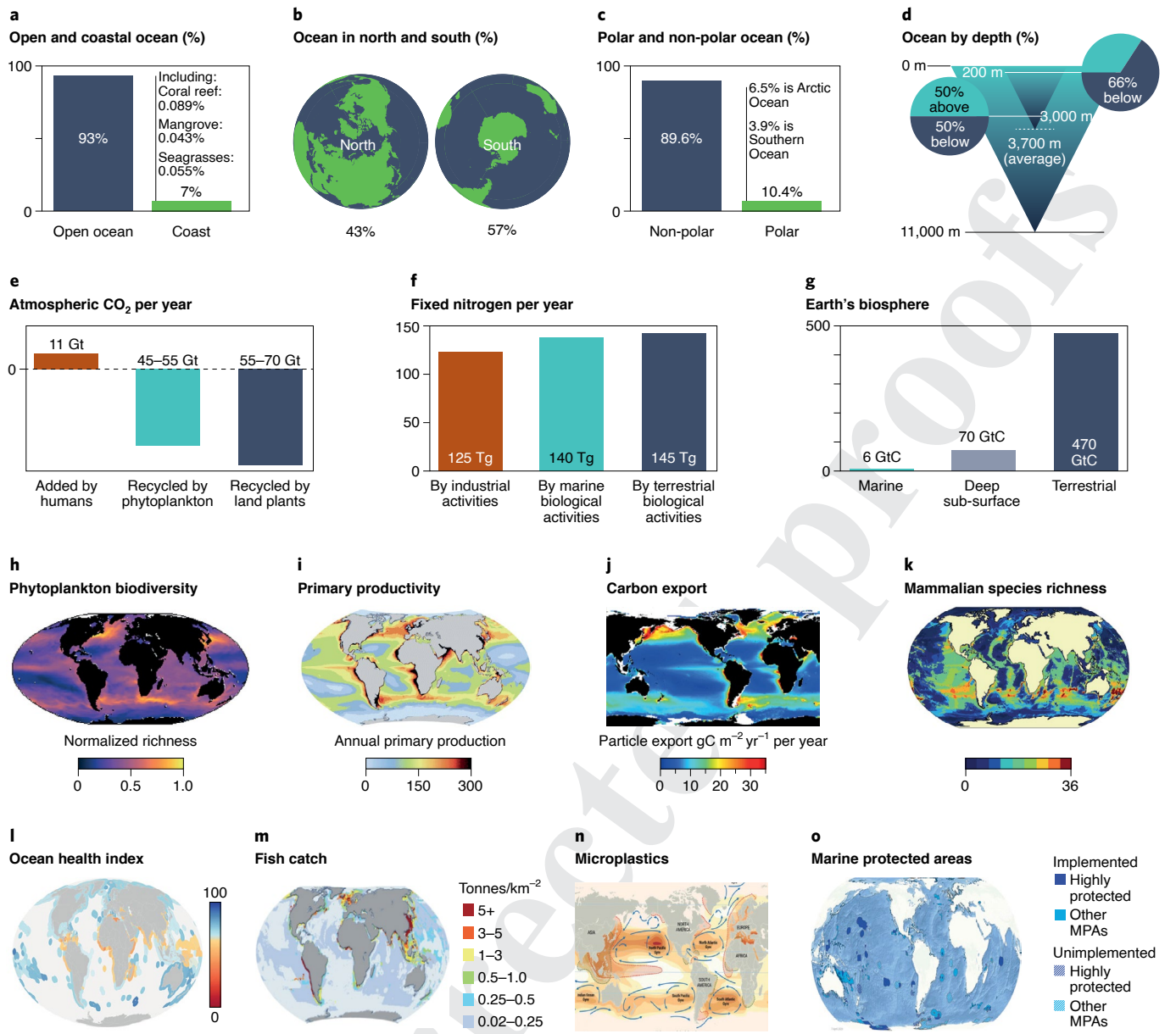

Fig. 4 | Key features related to the ocean microbiome. a–g, The extent of open ocean (**a**), particularly in the Southern Hemisphere (**b**) and in polar regions (**c**), is particularly understudied, as is the deep ocean (**d**), even though they represent huge extents of the ocean. In terms of global biogeochemical cycling, the ocean microbiome participates in almost as much removal of atmospheric CO_2 by photosynthesis as all land plants combined (**e**). The ocean microbiome also fixes as much nitrogen as terrestrial ecosystems (**f**), despite contributing a much smaller biomass to the Earth's biosphere (**g**). For comparison, human contributions to atmospheric CO_2 and fixed nitrogen are indicated in **e** and **f**. **h–o**, Global maps show phytoplankton biodiversity (eukaryotic and prokaryotic groups combined; data from ref. [68]) (**h**), primary productivity (data from https://www.grida.no/resources) (**i**), carbon export (data from ref. [69]) (**j**), marine mammal species richness (ref. [70]) (**k**), ocean health index (data from http://www.oceanhealthindex.org/) (**l**), fish catch (data from https://www.grida.no/resources) (**m**), microplastics distribution (data from https://www.grida.no/resources) (**n**) and coverage of marine protected areas (MPAs) (data from https://www.grida.no/resources) (**o**). Other data sources: **a**, percent of open ocean versus coastal waters (https://www.grida.no/resources) (for seagrasses, mangroves and coral reefs[71–73]); **b**, percent of ocean in Northern and Southern hemispheres[74]; **c**, percent of polar ocean[75]; **d**, percent of ocean at different depths[76]; **e**,**f**, carbon and nitrogen fixation[2,77,78]; and **g**, Earth's biosphere[1,79]. Panels **a–c**, **l** and **n** consider only surface area. Panels reproduced with permission from: **b**, ref. [74] under a Creative Commons license CC BY 4.0; **h**, ref. [68] under a Creative Commons license CC BY 4.0; **j**, ref. [69], American Geophysical Union; **l**, ref. [71], Springer Nature Limited. Credit: **i**,**m**, Hugh Ahlenius, UNEP/GRID-Arendal; **k**, Nordpil.com; **n**, Riccardo Pravettoni and Philippe Rekacewicz/GRID-Arendal; **o**, Kristina Thygesen/GRID-Arendal. Other images from Adobe Stock.

millennia could be incorporated, on the basis of the application of palaeogenomics techniques to explore ancient DNA in sediments from the ocean floor[29]. Further technological advances will be required to achieve these objectives, for example, to distinguish intracellular from extracellular DNA, and DNA derived from living and dead organisms—issues that also need to be addressed urgently in eDNA research[30]. To help researchers predict change at local, regional and global scales, the development of sophisticated computational approaches—such as multivariate statistics, niche modelling, graph analysis, deep learning and constraint-based

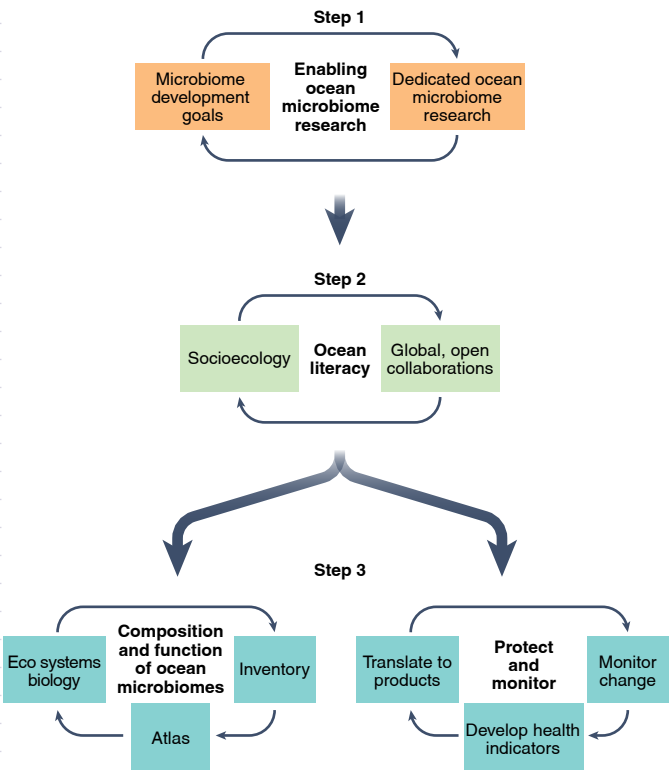

Fig. 5 | Connections between ocean microbiome priorities. For more details, see main text.

modelling—will also be required. Ultimately, these efforts will enable scientists to go from hindcasting to forecasting, and understand how microbial diversity and activities that drive local interactions translate to wider system impacts.

Given the centrality of ocean microbes for ocean health (Fig. 1), they can act as natural biosensors[13], providing a diagnosis of the local ecosystem services they provide and the state of ocean health. Identifying microbial indicators of ocean health, such as genes and metabolic pathways, is a key research goal for monitoring ocean health but is challenging because the ocean exposome (the 'ensemble' of biotic and abiotic stimuli that organisms are exposed to throughout their life[31]) encompasses a wide variety of factors. It will require a multidisciplinary approach using, for instance, ecotoxicology to determine responses of individual organisms or simplified microbial communities to single or multiple stresses, and statistical techniques to make sense of the vast amounts of data within the ocean microbiome inventory and atlas described above as a function of environmental exposures[4].

The development of a microbiome health index, most probably based on modules of diagnostic taxa and genes, would furthermore be highly complementary to existing ocean indicators, such as those based on macro-organisms[32]. It could also provide a boost to current attempts to define an ocean health index, which bring together diverse observations of the global ocean relating to areas such as water quality, biodiversity and carbon sequestration to support policy decision-making[32]. A microbiome health index could be harnessed to develop roadmaps in the fight against climate change, ocean acidification, chemical pollution and other environmental threats; and to conceive plans to return the ocean to a healthy state, or achieve other beneficial outcomes. Because the regions most exposed to anthropogenic impacts are coastal areas, it will be essential to include all countries, including those currently underrepresented in global ocean research (see below).

Bioactive resources from the ocean microbiome

Most marine microbes may be uncharacterized, but their potential for economically valuable breakthroughs is enormous, for example, new medicines[33], antibiotics[34], CRISPR-Cas[35] systems, bioremediation of pollution and plastics[36], breeding of nutrient-rich microalgae as a food source or for carbon sequestration[37], aquaculture[38], and compounds for industrial applications including glues, gels, nanomaterials and biofuels[39]. Infrastructure for culturing individual species, experimental systems to study symbioses and communities, and the development of genetically tractable model systems will be required to develop high-throughput screening platforms for molecules of interest and is one of the key objectives of the European Marine Biological Resource Centre (EMBRC).

In addition to establishing programmes to support discovery, it will be necessary to provide incentives for researchers, engineers, medical organizations and entrepreneurs to drive 'blue' products to the marketplace. Impact could be leveraged by bringing together different fields of research, government agencies, private enterprise and foundations to advance the science and its application, as well as answer important questions relating to intellectual property, sustainability and standards for open innovation. Besides the well-known DNA polymerases used in PCR that are derived from hydrothermal vent bacteria, the marine-derived antitumoral dolastatin 10, a linear non-ribosomal peptide synthetase-polyketide synthase (NRPS-PKS) hybrid natural product derived from Cyanobacteria—and marketed as Ascentris[40]—is one of several success stories. However, the huge commercial interest associated with the development of new medicines remains a significant challenge for developing new marine products equitably (see below).

Enabling ocean microbiome research

An opportunity exists to set out ambitious international goals to promote research and awareness of the ocean microbiome, inspired by the United Nations Sustainable Development Goals, to integrate microbial oceanography with other aspects of ocean sciences such as biogeochemistry, conservation and climate.

A set of ocean microbiome development goals could include meeting the skills and training requirements specific to ocean microbiome research, including collection, curation and exploration of the vast quantities of information generated from omics, microscopy, remote sensing and other data-heavy approaches, as well as promoting interdisciplinary collaborations. Ultimately, these goals would inform the creation of marine protected areas, the effective integration of the ocean microbiome into climate and sustainability models, and guide the sustainable use of marine resources. Establishment of a working group dedicated to creating microbiome development goals by the Scientific Committee on Oceanic Research (SCOR) would be a crucial step towards the delivery of such goals.

Dedicated multi-scale funding programmes are needed to promote a wide range of initiatives to specifically accelerate our understanding of the ocean microbiome, for example, analogous to the US Joint Global Ocean Flux Study (JGOFS), GEOTRACES (an international study of the marine biogeochemical cycles of trace elements and isotopes) and the European Union's Joint Programming Initiative on Healthy and Productive Seas and Oceans (JPI Oceans), all of which have been focused largely on physical and chemical oceanography.

Large-scale projects focused on the ocean microbiome are needed to organize the sampling and to disseminate advanced tools to less-developed countries, a task beginning to be addressed by the European Union-funded AtlantECO project. Research infrastructures are key to support biobanking, cloud computing, data visualization and exploitation (Box 1 and Table 1). So too are innovative ways of integrating the data—notable examples include initiatives to create a Digital Twin of the Ocean, which aim to bring together

Table 1 | Repositories for ocean microbiome datasets

Name	Description	URL
MGnify	Database for submission, analysis, discovery and comparative microbiome data, including from marine environments, and for prokaryotes and micro-eukaryotes	https://www.ebi.ac.uk/metagenomics/
PATRIC	Bacterial Bioinformatics Resource Center	https://www.patricbrc.org/
Phycocosm	An algal genomics resource from the Joint Genome Institute	https://phycocosm.jgi.doe.gov/phycocosm/home
Pico-PLAZA	A comparative genomics resource for marine microalgae	https://bioinformatics.psb.ugent.be/plaza/versions/plaza_pico_03/
Marine Metagenomics Portal	Collection of richly annotated and manually curated contextual and sequence databases for marine prokaryotes	https://bio.tools/mmp
Ocean Gene Atlas	Exploration of prokaryotic and eukaryotic gene expression in *Tara* Oceans metagenomes and metatranscriptomes	https://tara-oceans.mio.osupytheas.fr/ocean-gene-atlas/
Ocean Barcode Atlas	Web service to explore the biodiversity and biogeography of marine organisms in *Tara* Oceans	https://oba.mio.osupytheas.fr/ocean-atlas/
Tara Oceans genomic resources	A series of downloadable datasets from *Tara* Oceans, including eukaryotic and prokaryotic metagenomes and metatranscriptomes, metagenome assembled genomes (MAGs) and single-cell amplified genomes (SAGs)	https://www.genoscope.cns.fr/tara/ https://microbiomics.io/ocean/ http://ocean-microbiome.embl.de http://ocean-microbiome.org
Malaspina Deep Datasets	Collection of the *Malaspina* Gene Database (M-GeneDB) and Malaspina Deep MAGs catalogue (MDeep-MAGs) from the deep ocean	https://malaspina-public.gitlab.io/malaspina-deep-ocean-microbiome/page/data/
Global Ocean Reference Genomes Tropics (GORG-Tropics) database	Prokaryotic SAGs from prokaryotes derived from the Bermuda Atlantic Time Series sampling station	https://osf.io/pcwj9/
efam	An expanded metaproteome-supported HMM profile database of viral protein families	https://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/Zayed_efam_2020.1
Ocean Protein Portal	A proteomics-based database to explore localization and abundance of proteins in the global ocean, principally for prokaryotes	https://proteinportal.whoi.edu/
MAREDAT	A global atlas of non-genomic marine ecosystem data, for example, from microscopy, phytoplankton pigment analysis and flow cytometry	https://www.pangaea.de/?q=maredat
EcoTaxa	Web application for the visual exploration and the taxonomic annotation of images of marine plankton, principally eukaryotes	https://ecotaxa.obs-vlfr.fr/
Ocean Biodiversity Information System	A global open-access data and information clearing-house on marine biodiversity for science, conservation and sustainable development	https://obis.org/
SeaDataNet	An international oceanography resource whose main goal is to enable the scientific community to access historical datasets owned by national data centres	https://www.seadatanet.org
Blue Cloud	Infrastructures for marine research and the blue economy, including plankton genomics	https://www.blue-cloud.org/

new and existing observations and data to develop high-resolution models of the global ocean—from the surface to the seabed to allow continuous and timely monitoring for both research and policy decision-making. However, further efforts are required to integrate biological data, and in particular to understand interactions of the ocean microbiome with the Earth system as a whole through modelling. In addition to advancing knowledge, there is a need to fill gaps between individual grants and large-scale projects: one approach would be to develop programmes akin to the European Research Council's synergy grants, which enable small groups of researchers to bring teams together to address ambitious research problems.

Socioecology of the ocean microbiome

Advances in science and a growing awareness of the importance of microbes—especially in medical contexts—provide an opportunity to broaden discussions on how the ecosystem services provided by the ocean microbiome impact societies. Linking ocean and social sciences can both improve ocean literacy and provide direction for future ocean microbiome research. Studies show that many of the areas with high microbiome biodiversity, ecosystem productivity and importance in biogeochemical cycling are also sites of intense human activities and are not protected for species conservation (Fig. 4). The solutions to many of the stresses that the ocean microbiome faces, such as climate change and plastic pollution, must also be driven by major societal and cultural changes[41], and addressing deficits in microbial literacy[42]. Although many initiatives exist to integrate socioecology in marine decision-making, they tend to be modest in scope, are often not coordinated with each other and are not inclusive of regions underrepresented in ocean research. Socioecological research can add new dimensions to ocean

Box 1 | Initiatives to characterize Earth's microbiome

Following the advent of DNA sequencing from environmental samples, numerous initiatives have attempted large-scale exploration of Earth's microbiomes. These generally come in two forms, focused either on the use of amplicon sequencing to provide taxonomic information and assess the biodiversity of a sample, or whole-genome or shotgun metagenomic sequencing to assess genetic potential in an ecosystem context. Biodiversity assessments are most pronounced in environmental studies and have typically focused on prokaryotic and fungal diversity due to their importance in nutrient cycling, for example, in agricultural or forest soils. A predictive understanding of ecosystem response to environmental and climate change has become a pressing societal need, hence these projects are now integrating a functional approach[80]. For example, the National Science Foundation-funded EMergent Ecosystem Responses to ChanGE (EMERGE) Biology Integration Institute aims to develop such a framework. More generally, the crowd-sourced foundation-funded Earth Microbiome Project (a massively collaborative effort to characterize microbial life on the planet; https://earthmicrobiome.org/) has also shifted focus from a systematic attempt to characterize global microbial taxonomic diversity[81], to functional aspects based on gene abundances and expression. Data repositories are also available to interrogate environmental sequence data both from taxonomic and functional perspectives (see Table 1 for some examples). Human microbiome research is nonetheless much more advanced and better organized because of its links with healthcare. The International Human Microbiome Consortium (IHMC) has a coordinating function for the different international programmes and spinoffs spanning different research questions, and provides a recommendation of standards in human microbiome research[82]. The US National Microbiome Data Collaborative[27] is a new initiative to support microbiome data exploration and discovery through a collaborative, integrative data science ecosystem going beyond biome-specific studies. These existing efforts provide a model for other microbiomes, including the ocean. An important topic that spans all biomes is the need to generate a unifying taxonomic framework and integrated reference gene database for micro-eukaryotes beyond fungi, to fully explore their biology, ecology and evolution. The UniEuk initiative is working towards this ambitious goal (https://unieuk.org/).

microbiome research by documenting aspects such as uses, benefits, values, rights and culture. They can guide actions to manage and govern the oceans, support assessments of conservation activities and identify factors that influence human behaviours[43].

Nevertheless, qualitative approaches associated with social science research do not always translate into effective policy and there is a need to understand the value of diverse approaches to socioecological research before integrating it into the broader picture[43]. Therefore, another major opportunity is to develop research programmes that bring experts together from fields as diverse as law, ethics, history, culture, philosophy and human rights, as well as initiatives to engage members of the public from broad sectors of society, internationally. This includes identifying how everyday human activities interconnect with the ocean microbiome, how the ocean microbiome supports lives and livelihoods around the world, and the related social costs of an unhealthy ocean microbiome. Concepts based on biodiversity economics, such as natural capital accounting and deliberative monetary valuation, could provide an interesting path forward[44,45]. Moreover, the potential to manipulate the ocean microbiome, for example, to protect the environment or mitigate the impact of climate change, raises considerable ethical questions. Of concern are unexpected collateral effects on the environment and equitable sharing of benefits, both of which require upstream engagement of scientists, policymakers and the public. By connecting human societies, lives and livelihoods as an integral part of ocean microbiome research, it will be possible to achieve a truly holistic appreciation of the ecosystem. Major hurdles must be overcome to achieve these goals, but the increased appreciation of the importance of soil microbiome health in agriculture can provide a valuable roadmap[46].

International collaboration in ocean microbiome research

The Open Science Framework[47], an open-source software platform that facilitates open collaboration in research, should be used as a basis for developing research programmes with countries currently underrepresented in global ocean research, many of which are in the Global South. This should be done with a view to enhance capabilities, share technology, scientific methods, data and expertise, and widen support for ocean microbiome research—and thus contribute to fair and equitable sharing of the benefits and understanding of the ocean. However, current national regulations that restrict access to biodiversity hamper marine scientific research in territorial seas and exclusive economic zones. The levying of custom duties on instrumentation designed to study the oceans is an additional impediment to international collaboration that should be lifted.

While promoting the protection of biodiversity and ensuring a fair sharing of benefits resulting from its use, the Nagoya Protocol of the Convention on Biological Diversity (CBD) has nevertheless created heavy administrative barriers for biodiversity exploration and basic research by demanding a difficult diagnosis of compliance before undertaking scientific activities. The CBD has rendered research activities focused on the global ocean microbiome dependent on the sovereign rights of countries over their biodiversity. Therefore, current discussions on the adoption of a benefit-sharing scheme for data extracted from biological resources, such as digital sequence information (DSI) and access to genetic resources in the high seas, must ensure that data is open to all through existing data repositories (for example, refs. [26,27]; https://www.ncbi.nlm.nih.gov/genbank/metagenome/), an objective best achieved by inclusion of all interested parties in the negotiations, including scientists active on the ground. In this way, ocean microbiome research can serve not just as a basis for collaboration but also as a foundation for inclusion of all countries across the world. Failure to resolve current access issues will significantly limit the impact of the priorities laid out in this Perspective.

Outlook

As our ability to explore the ocean microbiome grows, so too does our knowledge of how marine microbial communities impact environmental and human health (Fig. 1). The United Nations Decade of Ocean Science for Sustainable Development (2021–2030) is a major opportunity to further develop our understanding of ocean microbes and raise general awareness of their importance. Efforts to characterize, understand and protect the ocean microbiome should complement global efforts to protect the ocean, its inhabitants and its vital ecosystems. Several initiatives are now underway that place the microbiome at the heart of ocean exploration. They include AtlantECO, *Tara* Mission Microbiomes (https://oceans.taraexpeditions.org/en/m/science/news/mission-microbiomes/), the Marine Biodiversity Observation Network (MBON) (https://geobon.org/bons/thematic-bon/mbon/), EMO BON (https://www.embrc.eu/emo-bon), the Atlantic Ocean Research Alliance (AORA)[48] (https://simbaproject.eu/wp-content/uploads/2020/02/AORA_Marine-Microbiome-Roadmap_v-final.pdf), BioGeoScapes (https://www.biogeoscapes.org/), Ocean Carbon and Biogeochemistry

(https://www.us-ocb.org/), Bio-GO-SHIP[21] (https://biogoship.org/), the GOOS Biology and Ecosystem panel (https://goosocean.org/index.php?option=com_content&view=article&layout=edit&id=289&Itemid=438) and BIOceans5D that builds on EMBL's Traversing European Coastlines (TREC) expedition. These initiatives are allowing researchers around the world to network, share ideas and resources, and build collaborations, thus providing a solid basis for the future.

Studying the ocean microbiome is a grand challenge for humankind. It is a vital endeavour because the knowledge gained can inform international policies related to ocean governance, tackling climate change, ocean acidification and pollution. It is essential for addressing sustainable development goal 14 'life below water', and the ocean microbiome's multiple roles also make it highly relevant for multiple other sustainable development goals.

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