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Microbial oceanography in a sea of opportunity

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Plankton use solar energy to drive the nutrient cycles that make the planet habitable for larger organisms. We can now explore the diversity and functions of plankton using genomics, revealing the gene repertoires associated with survival in the oceans. Such studies will help us to appreciate the sensitivity of ocean systems and of the ocean's response to climate change, improving the predictive power of climate models.

The pursuit of knowledge of the oceans has progressed in recent years thanks to the availability of new technologies and tools. Satellites are now equipped with sensors that can measure the optical properties of surface waters; profiling floats in the oceans can collect physical and chemical data from around the world; and fluorescence detectors can provide information about chlorophyll concentrations at depths beyond the reach of satellite-based sensors[1]. Remotely operated autonomous undersea vehicles have also been incorporated into oceanographic research and have been used to explore hydrothermal vents and other remote habitats. These technologies have stimulated a renewed interest in ocean exploration, and the vast quantities of physicochemical data collected have aided in the development of predictive models for some of the major ocean processes[2,3].

By contrast, the integration of cell biology and genomics into oceanographic research is much less developed, even though biological (and especially microbiological) processes are fundamental for maintaining a functional global ecosystem. Microscopic life is ubiquitous in the oceans (Box 1), and functional studies of these organisms are transforming our view of the processes and diversity of life in the world's oceans (see the other articles in this Insight). In this Commentary, we describe the crucial roles of marine microorganisms in maintaining the well-being of our planet, and we discuss how new technologies in the biological sciences can be recruited into oceanography to improve our knowledge of these processes.

Microbial diversity and evolution

Ancient microorganisms that evolved in the oceans helped to create the conditions under which more complex life developed[4]. The appearance of photosynthesis more than two billion years ago helped to shape the chemical environment that allowed the evolution of multicellular organisms and complex biological communities, including human societies. The metabolism of marine microorganisms continues to maintain major biogeochemical cycles that other organisms cannot complete, including significant production of the oxygen required for aerobic life (Box 2). For example, although terrestrial plants make up the vast majority of photosynthetic biomass on the planet, marine phytoplankton carry out almost half of the global net photosynthesis[5]. The relatively high rate of photosynthesis per unit of biomass for marine phytoplankton, compared with terrestrial plants, derives from their rapid rates of metabolism and turnover[6,7]. These facets have implications for the potential response time of microbial assemblages to climate variability and change, and for the neutralization of anthropogenic pollutants.

The oceans contain environments that resemble those that first nurtured life on Earth, such as marine sediments with marked layering of redox potentials, methane seeps from the deep subsurface, elevated heat and pressure around hydrothermal vents, and anaerobic, iron-rich subsurface clays. There is evidence that deep-sea vents have ephemeral features that can arise and disappear on timescales of less than a decade. These structures therefore provide excellent opportunities to monitor community succession and natural selection in real time.

The diversity of marine plankton is enormous, and most of the organisms have yet to be isolated, identified and studied. If the diversity of life in the oceans is to be understood, an assessment is required of how diverse marine microscopic life is, and the driving forces of evolution in the oceans must be identified. The International Census of Marine Microbes (ICOMM; http://icomm.mbl.edu) seeks to generate an inventory of unicellular organisms, but a census is also needed of metabolism and community processes. This inventory should include all the marine microorganisms, including viruses, Bacteria, Archaea and microbial eukaryotes.

Genomics-enabled analysis of the rich diversity of microscopic life in the oceans is now possible, providing a source of information by which to decode previous life histories. The initial phase of the global ocean survey, an ambitious expedition to chart the ocean genome, generated an impressive number of open reading frames (presumed to be genes), equivalent to half of the entire GenBank inventory of known genes[8]. This study of marine bacteria highlighted the vast and previously unknown genetic information contained in extant marine microorganisms, from new protein families to novel metabolic processes. However, many of the open reading frames are unlike any known genes. They could encode metabolic processes that are yet to be discovered or be important in the regulation of cellular activity in the dynamic and variable marine environment. Whole-genome sequences from representative species of major groups are, or soon will be, available (for example, heterotrophic and photosynthetic bacteria, prasinophytes, diatoms, *Emiliania huxleyi*, *Phaeocystis* and copepods). This will not only reveal their genomic content but also provide hints about their evolutionary origin. These genomes offer a complementary understanding of diversity and complexity, and serve as anchors for interpreting ocean processes at the level of the gene.

Microarrays and probes can identify functional groups, species and ecotypes reliably and rapidly[9]. Metatranscriptomics and/or proteomics

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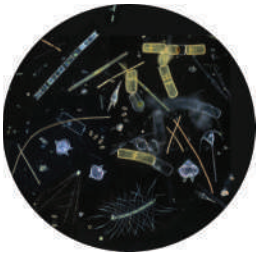
Box 1 | The invisible majority

Plankton are traditionally defined as marine unicellular and multicellular life forms smaller than a few millimetres (see image, courtesy of U. Sacchi and M. Montresor, Stazione Zoologica, Naples, Italy; scale bar 20 μm). This grouping by size combines organisms from all three domains of life (Bacteria, Archaea and Eukarya), despite their distinct evolutionary histories, physiological capabilities and ecological niches. Virus particles and other small, obligate parasites, although lacking a free-living existence, are also considered part of the natural microbial assembla Their common attributes are a high rate of metabolism ar rapid generation time compared with larger organisms. They are invisible to the unaided human eye, but their metabolic capabilities and collective ecosystem service make them vital to the habitability of the planet.



Phytoplankton use solar energy and carbon dioxide to generate oxygen and the organic food that fuels higher trophic levels. Cyanobacteria are the only bacterial members of the phytoplankton; the other members are eukaryotes and comprise diatoms, dinoflagellates, coccolithophores and green algae. Phytoplankton are the main food source of zooplankton, which are composed of unicellular and multicellular organisms, as well as the juvenile stages of non-planktonic adults, which in turn are food for higher animals such as fish. Bacterioplankton are made up of certain types of Bacteria and Archaea; they are ubiquitous in the world's oceans and are the most abundant life form on our planet[38]. Just 1 litre of sea water can contain up to 1 billion bacterial cells, and viruses can be an order of magnitude more abundant. Phytoplankton and zooplankton are much less common, but population densities can increase enormously during blooms.

All microorganisms, regardless of taxonomic or physiological status, require at least three major resources to survive and proliferate: energy, electrons and carbon (and related elements, including nitrogen, phosphorus and sulphur). Depending on how these materials are obtained, microorganisms can be classified into one of three categories: photo- or chemotrophs, litho- or organotrophs, and auto- or heterotrophs[25]. For example, if solar energy is used, the microorganism is a phototroph; if chemical energy is used, it is a chemotroph. Microorganisms that do both are described as mixotrophs. In most natural habitats, there is acute competition for energy, so mixotrophy is a common metabolic strategy. The traditional scheme of autotrophy (for green plants) and heterotrophy (for all other plants) ignores the metabolic complexity of life on Earth, especially within the microbial world. The extraordinary diversity of microbial life in the ocean is due mainly to the sustained availability of energy.

Some metabolic processes occur only in selected groups of microorganisms, termed functional groups. For example, the local balance between denitrification (the removal of biologically available nitrogen) and N_2 fixation (the formation of biologically available nitrogen) can have profound impacts on ecosystem productivity. Because most open-ocean habitats are chronically short of nitrogen, the net gain of fixed nitrogen by N_2 fixation is one of the key ecological processes in the ocean.

Finally, it is well known that microorganisms assemble in a non-random fashion. These microbial assemblages are highly structured and interactive, which facilitates metabolic transformations, and gene activity is highly regulated. Symbiotic associations are also common, for example between diatoms and N_2-fixing bacteria, and self-sufficient microscopic communities can form around a single organism, such as a radiolarian or foraminifer. Some microorganisms are specialists and have streamlined genomes owing to selective gene loss over evolutionary timescales. Others are generalists and have larger and more complex genomes, but this is offset by their greater metabolic plasticity.

can elucidate metabolic activities under different conditions in the ocean in various organisms. They also allow the rapid identification of candidate genes and facilitate the association of genes with specific metabolic and regulatory functions[10] in different organisms spanning hundreds of millions of years of evolution. Metatranscriptomics can also be used to improve our genomic understanding of key organisms such as diatoms, in which recent investigations have revealed the unexpected presence of a urea cycle and hundreds of bacterial genes[11,12] (see also page 185). In this way, genome sequences from model species can be used to identify genes important in regulating ocean processes[13,14].

Looking to the future, genomic sequencing of single cells will soon become routine, and forthcoming sequencing technologies will greatly reduce the cost and extend the depth of coverage to hundreds of megabases in a single run. Metagenomics approaches will be transformed by technologies poised to appear over the next decade that will enable single-molecule sequencing up to 10 kilobases[15]. Miniaturization will allow sequencing in real time on research vessels, and the use of genomic-enabled technologies on moorings, buoys and autonomous undersea vehicles will allow studies in locations where traditional microbial methods cannot be used. The information acquired will challenge

Box 2 | The oceanic carbon cycle

The oceanic reservoir of carbon, approximately 4×10^{19} g, is distributed unequally among dissolved and particulate constituents with various chemical compositions. The largest pool is dissolved inorganic carbon (DIC), which is the most oxidized form of carbon (the valence state is +4), and the smallest pool is that comprising living organisms (mostly microorganisms), which has a much lower oxidation state (a valence state of 0 to −4). This chemical disequilibrium between oxidized and reduced carbon is produced and sustained by biological (mostly microbiological) processes. The reversible interconversion among the various forms of inorganic and organic carbon in the sea is termed the oceanic carbon cycle.

The ocean is a key component of the global carbon cycle. Approximately half of the daily photosynthetic production of organic matter on Earth takes place in the upper 100 m of the marine environment, so the oxygen in every other breath we take can be traced back to the sea. On land, large plants with long generation times (on average 10 years) are the most active contributors to photosynthesis, but in the sea it is nearly exclusively the result of rapidly growing microorganisms (with typical generation times of 1 week). Consequently, organic carbon pools in marine ecosystems are very dynamic.

The distribution of carbon in the sea is governed by two fundamentally distinct processes (termed 'pumps') that have independent controls. The 'solubility carbon pump', which transports mostly DIC, is controlled by CO_2 solubility and large-scale ocean circulation. Superimposed on these physical constraints is the less-well-understood 'biological carbon pump', which includes the production, transport and decomposition of particulate and dissolved matter, and the production and dissolution of calcium carbonate by specialized groups of organisms, including coccolithophores, foraminifers and corals. Furthermore, because particulate matter is, on average, denser than the sea water surrounding it, there is a net downward flux of carbon in the ocean resulting from gravitational settling. This process transfers energy, electrons and carbon to the deep sea and is essential for the survival of all living organisms beneath the sunlit upper portions of the water column.

The biological transfer of particulate carbon from near-surface habitats to great depths, and its subsequent decomposition and dissolution, sustains the characteristic vertical profile of DIC in the open ocean, with highest the DIC concentrations at depths of more than 1,000 m. These biological processes therefore help to sequester carbon in the deep sea, where it is stored for periods ranging from centuries to millennia. The impact of climate variability, especially greenhouse-gas-induced warming, on the efficiency of the ocean's biological carbon pump is not well understood, largely because of the complex, nonlinear behaviour of most ecological processes. Understanding this process is an important challenge for the future.

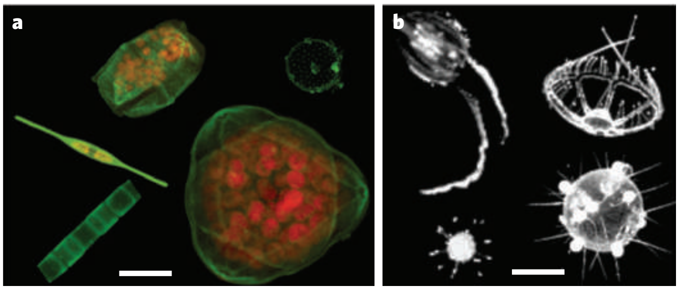


Figure 1 | Methods of visualizing plankton. **a**, Fluorescent labelling of diatoms using fluorescein-isothiocyanate-conjugated silane[37]. The dye labels all silicified structures and can be used directly on samples from the natural environment. The image shows a range of diatoms from surface waters in the Bay of Naples, Italy. Scale bar, 30 μm. (Courtesy of X. Lin and A. Amato, Ecole Normale Supérieure, Paris.) **b**, Plankton recorded *in situ* at a depth of around 500 m using the Underwater Video Profiler constructed at the Oceanography Laboratory of Villefranche-sur-Mer, France, during a cruise carried out for the California Current Ecosystem Long Term Ecological Research site. Scale bar, 1 cm. (Images courtesy of G. Gorsky and M. Picheral, Oceanography Laboratory of Villefranche-sur-Mer, France.)

historical assumptions and lead to fresh breakthroughs.

Advances in imaging technologies have revolutionized cell biology over the past 30 years. Macroscopic and microscopic imaging incorporated into oceanographic studies can connect form with function, notably showing how cell size and shape have been selected in the ocean environment (Fig. 1). Flow cytometry is already widely used in oceanography, and new imaging technologies have recently been developed for *in situ* applications[16–18]. Although the measurement of chlorophyll fluorescence has become routine, the incorporation of fluorescence microscopy into oceanographic analyses is still limited, despite advances in such technologies over recent decades. The analysis of intracellular structures in live or fixed cells by using specific fluorescent probes, revealing differences in function, such as the size of vacuoles or the extent of metabolic activity under different conditions, will be highly informative for microbial oceanography. By incorporating imaging technologies into the marine sciences, and combining them with genomic information, it will be possible to go beyond descriptive oceanography to understand more about the interactions between form, function, genotype and phenotype, and the influence of the environment on each.

The oceans and climate

One of the most serious challenges this century will be to understand how climate change — past, present and future — influences life in the oceans. We lack the adequate baseline data with which to compare contemporary observations to determine whether climate variability alters microbial metabolism and marine ecosystem services. We are in effect conducting a global-scale experiment, but with no control planet.

The oceans redistribute heat, affecting both weather and climate. Greenhouse-gas-induced temperature increases and ocean acidification are expected to have profound consequences on ocean processes. Some effects, such as increased stratification, sea-level rise and changes in ocean mixing caused by severe weather events, are already discernible[19]. Ocean acidification from increased atmospheric carbon dioxide entering the oceans is likely to affect not only calcifying organisms, such as coccolithophores and corals, but also other groups of organisms[20]. Stratification will isolate phytoplankton from the nutrients they need to capture solar energy and grow efficiently, and temperature changes are already causing species migrations over large latitudes[21]. However, the full consequences of climate change on the ocean biome are unknown because it is difficult to carry out rigorous temporal and spatial sampling and to translate laboratory or on-deck experiments to the natural environment. For example, methods such as measuring ocean colour as a proxy for carbon fixation are not ideal because chlorophyll content, biomass and photosynthetic activity are not always correlated.

Experiments that encompass wide spatial scales (from micrometres to thousands of kilometres) with appropriate temporal resolution (from seconds to millennia) have yet to be designed (Boxes 2 and 3). A further necessity is to move from the description of organisms to functional analysis, using methods that measure and monitor biological function and their ecological context (see pages 193 and 200). Genomic-enabled technologies make it possible to define functional groups by the activities of specific genes and to associate suites of gene products to a specific ocean environment (Fig. 2). Reliable biosensors for key biogeochemical processes, such as carbon fixation, nitrogen assimilation and iron bioavailability, are being developed[22–24].

A major investment has been made over several decades to collect ecological data at long-term observatories. Several ocean time-series sites exist worldwide, including locations in the open ocean[25]. Examples

Box 3 | Challenges and opportunities

Microbial oceanography is a relatively new scientific discipline that focuses on the ocean as a habitat for the evolution and regulation of microbial-based processes and their ecological consequences. It combines observation, experimentation and models, and strives to integrate the principles of several otherwise unrelated scientific disciplines[2,3]. It is truly a sea of opportunity, but a few major challenges (technical, conceptual and intellectual) preclude a comprehensive understanding of ocean processes at present. Notwithstanding the clear and urgent need for additional knowledge, the exploration of the biology of the oceans is severely under-resourced at the moment[39].

Major challenges include:

- A lack of conceptual and theoretical ecological models
- Difficulties in four-dimensional sampling of a complex and dynamic habitat because of a lack of suitable microbial and biogeochemical sensors
- Difficulties in knowing how to carry out a ‘census’ of marine microorganisms
- Insufficient numbers of relevant culturable model organisms
- Insufficient development of numerical simulation models for the accurate prediction of changes in microbial processes in response to climate variability
- A lack of understanding of the functional connection between human and ocean health

Responses to these challenges need to include:

- Creating and funding international collaborative research into microbial oceanography
- Recruiting and training new microbial oceanographers
- Developing new tools and methodologies for genomic-enabled oceanography
- Potentiating time-series sites globally by defining and observing functionally relevant ecosystem parameters
- Developing an international, freely accessible database that allows oceanographic and genomic data to be analysed and productively interpreted
- Establishing biologically informed definitions of functional microbial groups based on both community composition and the activities of genes, and defining organic matter using metabolomics
- Using genetically accessible model marine organisms to improve the knowledge of ecologically significant organisms and communities
- Making effective use of knowledge from non-marine model organisms
- Conducting large-scale ecosystem perturbation experiments to test hypotheses concerning microbial processes in the open sea
- Testing existing models of microbial biogeochemical processes, and revising them to evolve according to changing environmental conditions

of the latter include the Hawaii Ocean Time-series programme and the Bermuda Atlantic Time-series Study. Traditionally, physicochemical oceanographic data are collected, usually by batch collection, but more recently bacterial populations have also been monitored[10,26] using metagenomics and functional genomics. The Center for Microbial Oceanography: Research and Education in Hawaii is a recently established US National Science Foundation Science and Technology Center designed to bring about a comprehensive understanding of diverse marine planktonic assemblages. The MarMic initiative from the Max Planck Institute for Marine Microbiology in Bremen, Germany, is a similar example, focusing on marine sedimentary habitats. Such initiatives provide valuable starting points for a global holistic approach to the study of ocean dynamics. Time-series sites also serve as a 'canary in the coal mine,' providing early warning of changes. Sites of special scientific interest (such as regions where the oceans are already acidifying[27], minimal-oxygen zones[28] or locations of ice melts[29]) need to be similarly studied, and single-time-point sampling at many sites can have a complementary value by enriching baseline measurements concerning the potential range of community composition at geographically distributed sites.

Oceanographic physicochemical metadata generated at sampling sites need to be accessible in parallel with sequence data (Fig. 2). This will require the development of new database configurations accepted by the international oceanographic community. The Community Cyberinfrastructure for Advanced Marine Microbial Ecology Research and Analysis (CAMERA) database offers a prototype[30], although the huge amount of information, for example from DNA sequencing and high-resolution imaging, presents a challenge for the future.

The oceans and human health

The balance between marine viruses and their hosts, controls on the dynamics of harmful algae, and the processes that affect nutrient concentrations in marine waters can all influence human health[31]. Destabilizing these fragile equilibria can have serious repercussions for humans and the environment. Changes in water temperature and ultraviolet radiation, two factors known to be affected by human activities, disturb the relative numbers of bacteria, fungi and viruses in the oceans, with consequences for fish and marine mammals. Fishery stocks are critical as food for human populations, especially in developing countries, and diseases caused by pathogenic microorganisms affect food availability. The use of many marine animals for food, including shellfish and many species of fish, depends on the availability of unpolluted sea water and disease-free conditions. Nutrient overloading, for example from agricultural runoff waters, provokes harmful algal blooms that are devastating for fish farms and can also poison humans and wildlife that consume contaminated shellfish. Less widely recognized is that such blooms can introduce new species that outcompete indigenous marine populations[32].

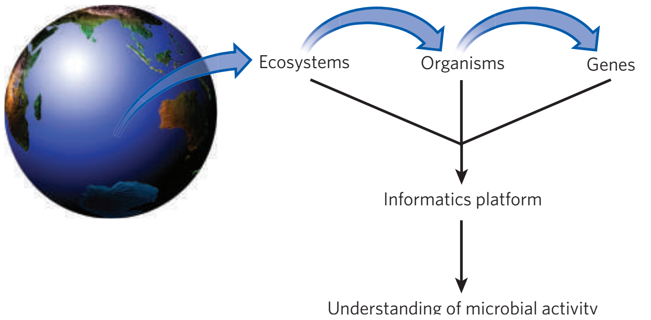


Figure 2 | Proposed framework for assessing oceanic microbial diversity in a functional context. Three levels of data should be collected from each system under study: ecosystem physicochemical data, composition of organisms, and expressed genes. The contextualization of these three sorts of data by dedicated informatics platforms should allow an understanding of microbial activity with respect to the prevailing ocean conditions.

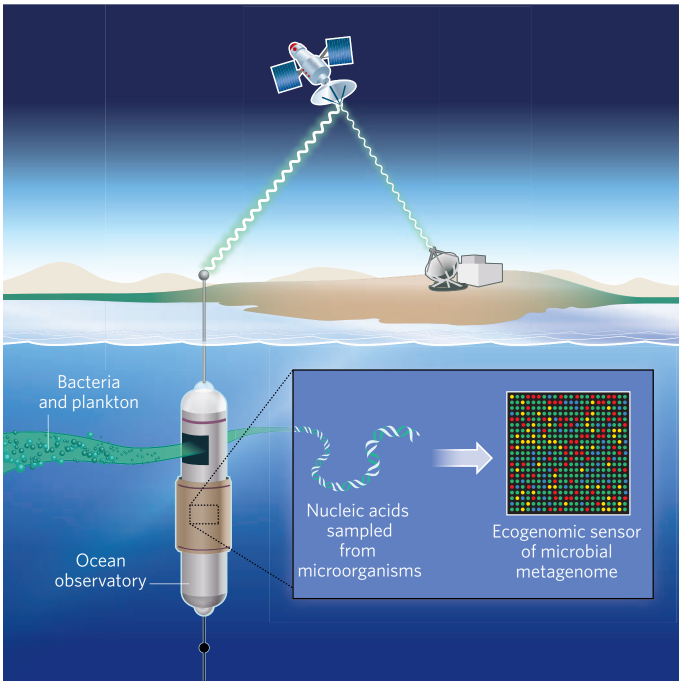


Figure 3 | Miniaturized ecogenomic sensors to measure microbial activity. The sensors could be installed into advanced ocean observatories to monitor DNA and RNA from diverse microbial communities. Subsystems for monitoring, data management and communication, and data modelling would be incorporated for data contextualization. The sensors would report to a worldwide network of laboratories in real time by satellite telemetry.

Coastal zones of the world's oceans are increasingly subjected to the discharge of human waste products, ranging from domestic to industrial effluents. The result is a loss of seagrasses and related estuarine and marine vegetation and the build-up of bacteria and viruses with pathogenic potential. Recreational areas along the coasts become both public health hazards and an aesthetic loss for communities. The extent of plastic debris in several open-ocean regions worldwide, notably the Great Pacific Garbage Patch, is a major threat to ocean life[33].

The human pathogen *Vibrio cholerae*, which causes cholera, is native to coastal and estuarine environments. Coastal temperature is a key determinant of the burden of cholera in coastal waters[34]. Conversely, the life history of this bacterium in Bangladesh is closely linked to the occurrence of planktonic blooms in the Bay of Bengal months before the outbreak of disease[35]. The role of *V. cholerae* in the ecology of the marine environment is extensive: the bacterium can digest chitin, degrade petroleum and carry out denitrification. The links, in evolutionary terms, between human and animal pathogens and their non-pathogenic marine relatives are only now beginning to be analysed[36]. The study of cholera epidemics in human populations represents a useful case study to improve our understanding and prediction of human disease outbreaks. Furthermore, cholera is similar to many other vector-borne human diseases, such as malaria and dengue fever, in being highly sensitive to climate.

In addition to understanding how the oceans affect human health, as a result of infectious disease and ocean pollution, we will need to learn how rising sea levels and altered ocean circulation affect the distribution of microbial populations, because both are affected by human activities and climate events[2]. Marine systems are more highly interconnected than terrestrial systems, so an alteration in microbial equilibria in one part of the ocean can affect a geographically remote area.

Looking forward

Contemporary oceanography, enabled by microbial genomics and other modern technologies, represents a maturation of descriptive biological oceanography. We need to define functional 'keystone' groups by their unique genomic signatures that can be measured and compared across contrasting ecosystems. Traditional nutrient classification schemes, such as dissolved organic matter, will need to be redefined within an ocean metabolome that incorporates knowledge of the metabolic potential of individual components for different species and communities (Box 3). Model microbial systems and laboratory-based experimentation combined with open-ocean observation (Fig. 3) will give us a holistic perspective, moving beyond reductionist science to link descriptive and functional observations, improving the predictive power of oceanography. Realizing such ambitious goals at a time of accelerating global climate change will depend on international collaboration, both to meet these challenges and to educate the next generation of oceanographers. Success will require cross-disciplinary collaborations encompassing and integrating multi-hierarchical and multi-scalar measurements and incorporating databases from each discipline into an inter-operational database. The ultimate goal is the orchestration of a grand synthesis of emergent models that transcends each of its component parts.

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