Marine microbes in 4D — using time series observation to assess the dynamics of the ocean microbiome and its links to ocean health

Pier Luigi Buttigieg¹,², Eduard Fadeev¹,², Christina Bienhold¹,², Laura Hehemann¹, Pierre Offre³ and Antje Boetius¹,²,⁴

Microbial observation is of high relevance in assessing marine phenomena of scientific and societal concern including ocean productivity, harmful algal blooms, and pathogen exposure. However, we have yet to realise its potential to coherently and comprehensively report on global ocean status. The ability of satellites to monitor the distribution of phytoplankton has transformed our appreciation of microbes as the foundation of key ecosystem services; however, more in-depth understanding of microbial dynamics is needed to fully assess natural and anthropogenically induced variation in ocean ecosystems. While this first synthesis shows that notable efforts exist, vast regions such as the Southern Oceans, the open ocean, the polar oceans, and most of the Southern Hemisphere lack consistent observation. To secure a coordinated future for a global microbial observing system, existing long-term efforts must be better networked to generate shared bioindicators of the Global Ocean’s state and health.

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Introduction
Despite decades of effort, the oceans remain strongly undersampled in space, hampering the estimation of global element fluxes and assessments of the diversity and distribution of marine life. Well-structured and sustained temporal sampling is also limited, despite its central importance in detecting changes in ocean productivity, food webs, biodiversity, and habitat structure. Strategically distributed ocean time series are thus key to the detection and quantification of ecosystem change, and for assessing anthropogenic impacts across decadal time scales. Unfortunately, these efforts are rare in the marine realm, do not follow concerted international strategies (as done by physicochemical observatories), and typically do not measure biological phenomena in the deep (see Table 1 and [1*]). The need to advance the status quo has never been more pressing: ocean ecosystems are rapidly warming and acidifying, effects compounded by the influence of pollutants, eutrophication, and the spread of hypoxia [2]. Additionally, industries such as mineral, gas and oil extraction, tourism, international shipping, and large-scale fisheries are further impacting marine ecological assemblages and food webs at every scale [3*,4]. Microbial observation has a large role to play in revealing the biogeochemical and biotic structure and functioning of the ocean, but must transition into a spatiotemporally coherent and comprehensive activity to realise its full potential.

Taxonomically and functionally diverse microbial assemblages from all three domains of life, along with their viruses, are the primary contributors to ocean productivity, biomass, and diversity. They are the core drivers of ocean biogeochemical cycles, control the emission of radiatively active gases, and constitute the foundations of many marine ecosystem services. Further, they are essential to the functioning of other trophic levels, providing animals with access to essential lipids and vitamins while supporting organismal health (e.g. [5–7]). These essential marine microbes respond to both natural and anthropogenic stressors; however, assessing how responses on the population and community level will contribute to ecosystem functions remains a challenging research target [8]. Pioneering studies, such as the TARA Oceans expedition [9*] and Ocean Sampling Day (OSD; [10]), have shown that the large-scale assessment of microbiome variations in space can be achieved when sampling, sequencing, and data flows are thoroughly coordinated. Further, these studies have made clear that synchronised observations must be temporally extended
Table 1
Overview of currently active long-term microbial observatories around the world. This overview table was generated based on search results in Google and Web of Science. Combinations of keywords for ‘Microbial Observatory’ OR ‘Genomic Observatory’ OR ‘Long Term Ecological Research’ OR ‘Microbial LTER’ OR ‘Long Term Microbial Research’ were used to initiate searches. In addition, we included (1) marine LTERs with microbial research programmes participating in LTER network initiatives (e.g. LTER and iLTER) and (2) phytoplankton monitoring observatories found using the NOAA Time Series Metabase. All information was manually collected from the website of each observatory or from direct contact with the corresponding researcher. These results are almost certainly incomplete, underscoring the need for the microbial observatory community to create a central registry to better align our collective efforts.

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<td>40</td>
<td>IEO-RADMED monitoring program</td>
<td>Western Mediterranean Sea (Balearic Sea)</td>
<td>36.5</td>
<td>−3</td>
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<td><a href="http://www.ba.ieo.es/investigacion/grupos-de-investigacion/coplamed/proyectos/263-radmed">http://www.ba.ieo.es/investigacion/grupos-de-investigacion/coplamed/proyectos/263-radmed</a></td>
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<td>41</td>
<td>Tohoku Ecosystem-Associated Marine Sciences —TEAMS —Manazuru</td>
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<td>35.12</td>
<td>139.22</td>
<td>Yes</td>
<td>Unknown</td>
<td>Unknown</td>
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<td>42</td>
<td>Tohoku Ecosystem-Associated Marine Sciences —TEAMS —Sagami Bay</td>
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<td>139.20</td>
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<td>Unknown</td>
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<td>43</td>
<td>California Current Ecosystem (CCE-LTER)</td>
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<td>33.90</td>
<td>−120.30</td>
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<td>44</td>
<td>San Pedro Ocean Time series (SPOTS)</td>
<td>Eastern North Pacific Ocean (San Pedro Channel)</td>
<td>33.30</td>
<td>−118.30</td>
<td>Yes (Transect)</td>
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<td>Monthly</td>
<td>1998</td>
<td>Active</td>
<td><a href="http://dornsife.usc.edu/labs/usc-microbial-observatory">http://dornsife.usc.edu/labs/usc-microbial-observatory</a></td>
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<td>45</td>
<td>Texas A&amp;M —University of Haifa Eastern Mediterranean Observatory —THEMO</td>
<td>Eastern Mediterranean Sea (Levant Basin)</td>
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<td>34.85</td>
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<td>Monthly</td>
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<td>46</td>
<td>CENCOOS Scripps Pier</td>
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<td>32.87</td>
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<td>47</td>
<td>Georgia Coastal Ecosystems LTER</td>
<td>Western Atlantic Ocean</td>
<td>31.5</td>
<td>−81.1</td>
<td>Yes</td>
<td>Unknown</td>
<td>Unknown</td>
<td>2000</td>
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<td><a href="http://gce-lter.marsci.uga.edu/">http://gce-lter.marsci.uga.edu/</a></td>
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<td>48</td>
<td>Oceanic Microbial Observatory — BIOS-SCOPE</td>
<td>Western North Atlantic Ocean (Sargasso Sea)</td>
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<td>−64.10</td>
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<td>Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m)</td>
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<td><a href="https://labs.eemb.ucsb.edu/carlson/craig/research/oceanic-microbial-observatory">https://labs.eemb.ucsb.edu/carlson/craig/research/oceanic-microbial-observatory</a></td>
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<td>49</td>
<td>JAMSTEC — S1 LTER RAPROCAN Time Series</td>
<td>Western North Pacific Ocean</td>
<td>30.00</td>
<td>145.00</td>
<td>No</td>
<td>Unknown</td>
<td>Unknown</td>
<td>2010</td>
<td>Unknown</td>
<td><a href="https://ebcrpa.jamstec.go.jp/k2s1/en/index.html">https://ebcrpa.jamstec.go.jp/k2s1/en/index.html</a></td>
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<td>50</td>
<td>RAPROCAN Time Series</td>
<td>Eastern Atlantic Ocean (Canary Islands)</td>
<td>29.5</td>
<td>−25</td>
<td>Yes (Transect)</td>
<td>Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m)</td>
<td>2 cruises/yr</td>
<td>2007</td>
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<td><a href="http://www.oceanografia.es/raprocan/">http://www.oceanografia.es/raprocan/</a></td>
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<td>51</td>
<td>ANTARES-Ubatuba</td>
<td>Western South Atlantic Ocean</td>
<td>23.75</td>
<td>−45</td>
<td>No</td>
<td>Epipelagic Zone (0–200 m)</td>
<td>Monthly</td>
<td>2004</td>
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<td>52</td>
<td>Hawaii Ocean Time-series (HOT)</td>
<td>Western North Pacific Ocean (Hawaii)</td>
<td>22.75</td>
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<td>53</td>
<td>Cape Verde Ocean Observatory</td>
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<td>2007</td>
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<td>Yes</td>
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<td>Darwin</td>
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<td>70 King Sejong</td>
<td>Station (KOPRI)</td>
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<td>–62.2</td>
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<td>Unknown</td>
<td>2 cruises/yr</td>
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<td>71 PALMER Antarctica</td>
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<td>–64.05</td>
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<td>Unknown</td>
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</table>
Holistic evaluations of ecosystem state require complex, community-level insight integrating taxonomic and functional information over time [20**,21**]. For example, studies on phytoplankton assemblages have detected compositional change tracking environmental variation [22–24], while broader microbial community shifts have been detected in a rapidly warming Arctic Ocean [25,26]. This class of MIs can be fully utilised only if they allow the differentiation of baseline, natural variation (e.g. by seasonality, El Niño, or the North Atlantic Oscillation) from deviations explained by other factors, a challenge even for mature time series (e.g. [25]). Applications of advanced anomaly and gradient detection analyses (e.g. [27]) and tuning of sampling strategies to better resolve events [28] are needed to advance this domain, and would greatly benefit from aligning methodologies to emerging efforts in global biodiversity monitoring [29]. Unfortunately, the scarcity of automated sensing and sampling systems fosters heterogeneous and asynchronous observations, preventing advancements such as the continuous sensing of microbial responses to hydrocarbon pollution [30] and heavy-metal contamination [31] on a global scale. Anticipating the emergence of such systems, credible baseline data and frameworks for integrated reporting (e.g. see [32]) are needed now to transition individual studies and time series into globally coherent diagnoses of marine ecosystem state and health.

The past decade has shown that multi-omic technologies and techniques will be central to emerging microbial observation networks, allowing insight into the metabolic capacities and behaviours of the uncultivable majority. These technologies have undergone rapid transformations every 4–5 years in the past 20 years, and a growing body of expertise in handling community metagenomes, metatranscriptomes, and environmental DNA (eDNA) has ushered in a new generation of MIs [33,34,35**]. Concurrently, omics approaches are increasing the efficiency and cost-effectiveness of MIs already in operation (e.g. [36]) and have encouraged established macroecological indicators such as the AZTI (Centro Tecnológico Experto en Innovación Marina y Alimentaria) Marine Biotic Index (AMBI) to extend into the microbial realm (microgAMBL [37]). Importantly, some of these approaches allow the use of functional genes as indicators, thus allowing MIs to target a wide range of processes that shape the composition of microbial communities. For example, the genes of sulphur-oxidisers like SUPO5 trace the spread of dead zones [38]; increased proportions of antibiotic resistance genes indicate anthropogenic impacts [39–41]; and the enrichment of hydrocarbon-degrading genes mark the impact of oil spills [42]. Together, these indicators can permit sensitive assessment of environmental change [43] alongside its impact on the ecosystem services supported by microbial life. Sequence-based approaches will be a prime focus of future marine microbial observation, fuelled by progress.
in autonomous sampling and omic technologies [44**], context provided by large-scale sampling campaigns (e.g. [9**,10,45]), and the application of techniques such as machine learning to omics data (e.g. [46]).

However, regardless of what technologies can be applied to individual samples, the problem of meaningfully linking MIs to environmental change remains an issue of spatiotemporal coverage (see references in Table 2). In most regions, too little is measured to reliably discriminate background microbial dynamics from all but a few, pronounced responses to natural and anthropogenic perturbations. Consequently, we struggle to detect less obvious changes with profound consequences. For example, we lack sampling efforts to detect the slight increases in the degradation rate of dissolved organic carbon induced by warming, or the adaptive responses to ocean acidification, expected to profoundly impact the ocean’s capacity to take up CO₂ [47]. Effort is needed to develop MIs to consistently report on functional changes (e.g. in primary productivity and nutrient recycling) caused by the synergistic action of multiple marine stressors [48**]. Long-term marine microbial observatories, with their sustained multidisciplinary focus and developed understanding of their locale, represent our best chance to advance this front. For example, the Hawaii Ocean Time-series (HOT; est. 1988) has sampled its ALOHA (A Long-term Oligotrophic Habitat Assessment) station monthly, investigating the North Pacific Subtropical Gyre (NPSG) for three decades [49]. In this region, HOT has characterised the foundational relationship between sea surface irradiance, chlorophyll a concentration, and oxygen production [50,51] and links between local primary production, large-scale climatic variation influencing the North Pacific Gyre Oscillation, and monthly to annual mesozooplankton dynamics [52]. Moreover, monitoring the concentration of potent greenhouse gases in the system’s euphotic zone (5–175 m) has detected a link between methane cycling

Table 2

<table>
<thead>
<tr>
<th>MI target</th>
<th>Reference(s)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pollution (general)</td>
<td>[30,31,36]</td>
<td>Methods to assess microbial responses to pollution are increasingly using community structure and functional profiles (obtained via metagenomics) to detect genes associated with various forms of anthropogenic pollution. Specifically for hydrocarbon pollution a variety of marker genes and marker microbes have been identified, for example, from the Deep Water Horizon accident.</td>
</tr>
<tr>
<td>Pathogens (including wastewater contamination)</td>
<td>[13,14,61,75]</td>
<td>Screening for taxonomic marker genes and functional genes can readily detect pathogenic threats. However, many pathogen are uncharacterised and determining when organisms will display pathogenicity requires further work.</td>
</tr>
<tr>
<td>Invasive taxa</td>
<td>[4]</td>
<td>Readily identifiable by taxonomic marker genes from community or eDNA samples, methods which can also reveal cryptic invaders. Determining thresholds for action or alarm — based on the proportion of the invader or its persistence in the community — often involves sustained observation. Identification of species known to form HABs (using molecular and traditional approaches) during periods when blooms are likely, has shown some success in predicting hazardous events. Community-level indicators of imminent HABs are also emerging.</td>
</tr>
<tr>
<td>Harmful algal blooms</td>
<td>[60]</td>
<td>Repeated sampling tracking periodic events and the occurrence of short-term perturbations are being coupled with both taxonomic and functional gene profiling strategies to establish community-level indicators of ecosystem state. Efforts to link these assessments to the objectives of policies such as the EU’s Marine Strategy Framework Directive are also underway.</td>
</tr>
<tr>
<td>Antibiotic resistance</td>
<td>[39,40]</td>
<td>Screening for antibiotic resistance genes in metagenomic datasets readily identifies risks.</td>
</tr>
<tr>
<td>Ecosystem status, seasonality, resilience, and food webs integrity</td>
<td>[8,17,20**,21**,24,25,32,35**, 37,44**,46,62,63]</td>
<td>Repeated sampling tracking periodic events and the occurrence of short-term perturbations are being coupled with both taxonomic and functional gene profiling strategies to establish community-level indicators of ecosystem state. Efforts to link these assessments to the objectives of policies such as the EU’s Marine Strategy Framework Directive are also underway.</td>
</tr>
<tr>
<td>Ocean warming and acidification</td>
<td>[22,53,55,57,61]</td>
<td>Long-term studies tracking warming and acidifying seas and their associated microbial communities are demonstrating a biotic signal to planetary-scale changes in the ocean microbiome. Some of these changes, for example, in the cycling of greenhouse gases, feedback into these global processes. For example, changes in calcification rates, growth, community composition and primary production in planktonic communities provide foundations for indicators of acidification.</td>
</tr>
<tr>
<td>Marine fauna health status</td>
<td>[5–8,41,74]</td>
<td>Similar to microbiome-health associations in humans, taxonomic and functional gene profiles of marine animal microbiomes (e.g. Cetaceans) are providing insights into their health and environmental associations.</td>
</tr>
</tbody>
</table>
and phosphate availability [53,84]. Analogously, the only open-ocean long-term ecological research station in the Arctic, HAUSGARTEN (est. 1999; now operated under the Frontiers in Arctic Marine Monitoring programme; [25]), has investigated: the dynamics and handling of marine particles (e.g. [54]), the coupling of deep ecosystem responses to surface variability [25]; the interactive effects of temperature, acidification, and organic matter on bacterioplankton biomass production and extracellular enzyme activity [55]; punctuated pico- and nanoplanktonic turnover during warm water anomalies nestled within decadal increases in chlorophyll a concentration [23]; and the biological control of microbially derived transparent exopolymeric particle (TEP) concentrations, which transport carbon to deeper ecosystems and influence regional climatic conditions by nucleating cloud and ice formation [56].

Many more examples exist (e.g. responses in coccolithophore abundance due to increased dissolved inorganic carbon at the Bermuda Atlantic Time-series Study [57]), driving home the value of these sites in registering ecosystem changes relevant to global challenges. To face these challenges, the natural corollary for the next 5–10 years is two-part: (1) microbial observatories would need to form a coordinated and well-integrated observation system and (2) observation variables would need to be synthesised into a well-documented and consistent set of microbial indicators, serving as stable and widely approachable sentinels of ocean health.

**Building a network for marine microbial observation**

As illustrated above, long-term ocean observatories — as instituted and standardised acts of multidisciplinary observation — offer an ideal context to bring prototypical MIs to maturity. Observatories provide the baselines needed to qualify short-term microbial dynamics [20**], and characterise an MI’s behaviour and relevance within a well-examined ecosystem. On this basis, MIs can be transferred to and tested in other contexts. Should MIs prove generalisable, they would then be viable for adoption by the international observatory community. In the marine realm, and spurred by initiatives such as the Genomic Observatories Network [58**], a growing collection of observatories are now conducting regular microbial sampling. However, to be sustainable, extant efforts must seek to integrate under a common, mutually reinforcing observatory framework (see [39] for an analogous case). In this contribution, we have assembled the first overview of existing oceanic microbial observatories to initialise a more formal community registry and observatory framework (Table 1; Figure 1). During our survey, we noted that most microbial observatories augment one of the three major types of physicochemical ocean observatories, each with their strengths and weaknesses. Traditional observatories operated by ship-based transects (e.g. the Global Ocean Ship-based Hydrographic Investigations Programme, GO SHIP) provide the best opportunities for biological sampling due to the flexibility of ships as sampling platforms; however, they often lack temporal resolution due to uncertainties in securing ship time. Moorings and anchored buoys provide fixed platforms for autonomous observation through time, but lack sufficient energy stores to operate advanced in situ sensors and samplers. Lastly, tagged marine mammals and drifting Lagrangian observatories — including Argo profiling floats, gliders, and buoys — have considerable spatial reach and resolution, accessing depths of ca. 2000 m, but have limited capacities to carry equipment for handling microbial samples [60]. All these options are challenged by high maintenance costs [1**], yet present our only options in detecting environmental trends and their links to microbial community structure and function. Encouragingly, many of these physicochemical frameworks have already established common practices and shared governance strategies, a feature that can be used to catalyse similar progress in the microbial observation domain.

The now global network of Continuous Plankton Recorder (CPR; www.globalcpr.org) sites presents an excellent example of interconnected and harmonised ecological and physicochemical observation. The CPR network has used collecting instruments with conserved design and standardised processing protocols for many decades, which now act as a stable platform upon which new technology can be mounted. The integrity and coverage of this system has allowed the detection of numerous signals in the plankton, such as population dynamics of invasive *Vibrio* species linked to warming waters [61], interannual variability in herring populations [62], and planetary-scale regime shifts [63]. This knowledge has allowed the CPR community to identify essential, ecosystem-specific variables to improve global assessments [64**] and channel their collective outcomes into a wide array of policy development organisations. Of equal importance, the network is able to buffer loss of capacity by any of its members by, for example, maintaining sample records or stepping in when tows cannot be performed. At many levels, from governance to community engagement, the CPR network is a viable model upon which a global consortium of microbial observatories can be based; however, a phased approach to this goal is needed to progressively align initiatives in this complex and active domain.

The lack of long-term, internationally coordinated support is not the only major challenge to realising an integrated network of microbial observatories: Immense methodological and technological variability reduces the comparability of biological and biogeochemical parameters between and within existing efforts. Thus, at the initial stages, networking microbial observatories
Map of marine long-term ecological time series sites which measure microbial variables. Single sites are marked with yellow circles and regions where multiple sites are clustered are marked with pink triangles. Sites are identified by numbers, corresponding to row labels in Table 1. Note that this map should not be treated as exhaustive or authoritative. This map shows a lack of observation in large ocean realms, especially in upwelling zones containing intensive fisheries, in polar zones, in coastal regions containing intense aquaculture, and in the Southern Ocean. The map features chlorophyll data from the GlobColour project, generated by merging Level-3 ocean colour sensor products at a resolution of 4.6 km. The chlorophyll-a concentration (mg/m³), case 1 waters (CHL1) was derived from 2016 Sentinel-3 sensors: SeaWIFS, MERIS, MODIS AQUA, VIIRS and OLCI-A. Data was merged using a weighted average and a GSM model method. The data was further averaged over a 1-year period by AWI FRAM Remote-Sensing. Continent data sourced from ESRI.

will be a question of aligning information flows via interoperable reporting standards and principles (notably, [65]). In this manner, frequent exchange between existing and new initiatives could become more normalised, increasing the potential to perform meta-analyses and synthesis studies. In turn, this is likely to drive greater alignment at all levels to promote globally impactful studies. Some success is already visible through the grassroots development of standards for sequence-derived data (e.g. the BIOM format [66]) and its metadata (e.g. MiXS [67]). The latter is converging with more general biodiversity standards such as Darwin Core [68] and Humboldt Core [69] as well as resources in domains such as Earth sensing through shared semantic technologies (e.g. [70]). The time is ripe for microbial observatories to interface by adopting and developing such standards, collectively shaping them to be fit for purpose. Subsequently, the community can approach integrative reporting mechanisms aimed at a far broader base of stakeholders, including researchers from other domains, policy analysts, decision makers, educators, and the general public. Similar paths leading to standardised information flows have been followed by the marine oceanographic and geoscientific communities (e.g. in the Argo or Integrated Ocean Drilling Programme communities), offering further examples for the microbial sciences. The latter steps, that is, integration with other stakeholders, are also happening through international
programmes, debates, and policy meetings, but have not yet resulted in sustainable international funding for coordinated long-term observations of marine ecosystems.

Three prominent foci — which could orient and facilitate integration activities — are emerging from debates relevant to the international ocean observation community: The Essential Ocean Variables (EOVs), the Essential Biodiversity Variables (EBVs) [71,72], and the Ocean Health Index (OHI; [12]). The EOVs, championed by the Global Ocean Observing System (GOOS), are a developing mixture of low-level (i.e. raw or minimally processed data) and high-level (involving several steps of processing and quality control) variables deemed necessary to report on the state of the ocean. Microbiological variables, as most biological/ecological variables in this scheme, currently exist in a conceptual state with no established guidelines on measurement or assessment. The EBVs, promoted by the Group on Earth Observations Biodiversity Observation Network (GEO BON), play a somewhat different role: they aim to offer an intermediary layer of abstraction between raw biodiversity measurements, such as genetic beta diversity, and high-level ecological indicators (e.g. ‘connectivity/fragmentation of ecosystems’) used to monitor adherence to agreements such as the Convention of Biological Diversity. With careful handling, this abstraction layer may allow harmonisation of biodiversity data, preserving rationale-driven methodological differentiation while promoting unified reporting. Researchers who operate and utilise microbial observatories are well-poised to report on some EBVs, such as ‘Taxonomic diversity’ and ‘Physiological traits’ through methods including pigment, lipid and marker gene analysis, cell counts, enzymatic activity assays, and metagenomic approaches. However, there is a great need to build consensus on how data generated by local methodologies can be credibly merged across sites to provide global reporting. In our opinion, observatories should take stock of how their data streams can report on relevant essential variables, documenting caveats as appropriate and accounting for uncertainties. Subsequently, these strategies should be made publically available, allowing review and comment prior to standardisation by a task group of data analysts charged with formulating a robust set of aggregate indicators. Naturally, activities of this kind must be accompanied with diagnostic studies, continually testing whether integrative approaches centred on essential variables and indices adequately and accurately capture ecological signals. While this may sound daunting, similar activity reported almost a decade ago has provided the broader biodiversity community with a common basis to highlight increasingly urgent issues on a global scale and simultaneously conduct fascinating research (e.g. [73]). In this vein, the OHI [12] — now in its fifth year of operation — provides another framework which may benefit from harmonised microbial insight and novel MIs. The OHI integrates information about the ecological, social, and economic benefits that a healthy ocean provides to humans. Relatively low-level components of the OHI — including the counts of alien species and the degree of habitat destruction — are organised into the dimensions of status, resilience, pressures, and trend. Microbial indicators would have a natural home in the OHI’s framework, but, as discussed above, need firmer scientific foundations and consensus within the observing community before they can be globally applied. For example, thresholds for declaring the detection of invasive species in molecular data are likely to vary across systems (due to varying degrees of natural turnover) and technologies (e.g. due to variation in error rates). Thus, well-documented and reproducible expert intervention is required prior to integration. Together, these reporting frameworks exemplify a challenging, but feasible, route towards global integration of marine microbial observation, especially when compared to the incredibly cumbersome and currently unsustainable option of attempting to standardise the use of samplers, filters, extraction technologies, primers and sequencing pipelines at a global scale. If taken up, we believe that this vital task of harmonised reporting will nucleate a tightly coordinated network of observatories, laying a solid foundation for further alignment.

Conclusion: realising the societal relevance of marine microbial observatories

Ocean biodiversity and its relationship to ocean health and human well-being has never been a more pressing target for research, with sustained observation being central in disentangling human impacts from natural variation (e.g. [74–77]). This urgency will only increase with the rapid growth of human settlements in coastal zones, which is increasing dependence on the ocean’s resources and exposure to its biotic hazards. Indeed, the UN Environment Chief, Erik Solheim, has recently called for the elevation of biodiversity monitoring to the same level as climate monitoring by 2020, and stressed the central importance of functioning ecosystems to societal well-being (COP12, Manila, 2017-10-25). Bolstering the capacity of long-term ocean observatory networks to coherently monitor microbes — the greatest store of biodiversity in the oceans — would do much to accomplish this target and enhance reporting on many components of the UN’s Sustainable Development Goals (esp. SDGs 14: ‘Life Below Water’ [78,79]). Indeed, much in the same way that the human microbiome is becoming increasingly relevant in monitoring human health, the ocean microbiome must be integrated into monitoring the health of marine ecosystems [80].

Microbial observing efforts at all scales can accelerate this mission if they are able to harmonise their outputs and function as a consolidated system capable of generating coherent, spatiotemporally comprehensive indicators and assessments tuned to societal priorities. Observatories,
projects, programmes, and consortia such as the Genomic Observatories Network (GON), DNAqua-Net [81], the ‘Optimising and Enhancing the Integrated Atlantic Ocean Observing Systems’ (AtlantOS) project, and the Association of European Marine Biological Laboratories Expanded (ASSEMBLE+) have an immense opportunity to align efforts and collectively interface with broader coordination mechanisms offered by organisations such as GOOS and the Marine Biological Observation Network (MBON). This convergence would greatly promote analyses and syntheses with greater coverage across time and space, which already draw from the findings of long-term observation efforts (e.g. [20**]). Lastly, as societal needs associated with healthy marine ecosystems frequently cross the land–ocean interface, it is important to create operationalised links to observation infrastructures targeting more terrestrial systems (e.g. NEON [82**]). The scale of this challenge is immense; however, a concerted effort to establish sustained microbial observation with global coverage will vastly enhance our ability to understand the role of microbial interactions as a key driver and indicator of ecosystem dynamics. At an even larger scale, international microbiologists have already called for a unified microbiome initiative, with the overarching goal to take the next step from microbial monitoring to prediction of how Earth’s microbiome will respond to the challenges of the 21st century [83]. Marine microbiology must rally its capacities and prepare for the key role it will play in this process.

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- of outstanding interest


The authors present the second global assessment of the Ocean Health Index, first reported in 2012. The index integrates variables to report on 10 societal goals for healthy oceans and aims to inform the public as well as international and regional policy makers in support of the management of ocean ecosystem health.


This publication, resulting from the Tara Oceans Expeditions, is a good example of a concerted effort that included the systematic collection of samples for genetic and environmental analyses at the global scale using standardised protocols. The consortium generated an ocean microbial reference gene catalog for the water column and identified patterns of vertical stratification as well as environmental drivers at an unprecedented global scale, thus contributing to a baseline against which future changes can be assessed.


This review paper shows that the composition of ocean microbial communities follows predictable patterns even at the level of complex network associations, and points out key natural dynamics in time, from hours to decades.


As in [20**], this paper examines time-series data with graph-theory approaches and examines seasonal and bloom-linked dynamics and resilience of surface water communities sampled at high temporal density. This is an approach that may aid baseline characterisation at long-term observatories.


Provides a recent overview of the advantages and challenges of using DNA sequencing in monitoring ecological status in the context of the EU Marine Strategy Framework Directive.


The authors, from the HOTs and MBARI observatories, provide insight into ocean microbiome dynamics based on in situ data, and discusses future opportunities for new technologies.


The authors of the response of the microbes responsible for carbon and nitrogen cycling to anthropogenic global change. The authors note that microbiologists must develop improved predictions, integrating diverse biological and physicochemical data, on how these changes will impact global element cycles.


This chapter provides a model that holds great relevance in facing the challenges we identify in this Opinion and describes a network which will likely be a major part of a global microbial observing system.


60. Seegers BN, Birch JM, Marin R, Scholin CA, Caron DA, Seubert EL, Howard MDA, Robertson GL, Jones BH: Subsurface seeding of surface harmful algal blooms observed through the integration of autonomous gliders, moored environmental sample processors, and satellite remote sensing in southern California. Limnol Oceanogr 2015, 60:754-764.


The authors discuss the development of 'ecosystem Essential Ocean Variables' (eEOVs) motivated by the lack of adequate EOVs for monitoring (Southern Ocean) ecosystems. The reference points out the important role played by the ocean observing community in the development and tuning of standards for the observation of marine ecosystems and biodiversity.


The authors discuss the concept of Essential Biodiversity Variables (EBVs) and some of the major challenges related to their implementation. The authors identify the interoperability of existing biodiversity research infrastructures (e.g., including the development of openly shared standards, protocols, and workflows) as key to the integration of biodiversity data to calculate EBVs.


This call expresses the value of developing a holistic understanding of microbiomes across ecosystems to provide insights into organismal health and biosphere processes. The authors identify key issues in realising global efforts and propose routes to their resolution, centred on breaking down disciplinary silos.


