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

Pier Luigi Buttigieg[1,2], Eduard Fadeev[1,2], Christina Bienhold[1,2], Laura Hehemann[1], Pierre Offre[3] and Antje Boetius[1,2,4]

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 ocean depths, 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.

**Addresses**
[1] Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Am Handelshafen 12, D-27570 Bremerhaven, Germany
[2] Max Planck Institut für Marine Mikrobiologie, Celsiusstr. 1, D-28359 Bremen, Germany
[3] NIOZ Royal Netherlands Institute for Sea Research, Department of Marine Microbiology and Biogeochemistry, and Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands
[4] MARUM — Center for Marine Environmental Sciences, University of Bremen, Leobener Str. 8, D-28334 Bremen, Germany

Corresponding authors: Buttigieg, Pier Luigi (pier.buttigieg@awi.de), Boetius, Antje (antje.boetius@awi.de)

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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.**

| Labels | Observatory name | Region | Latitude (N) | Longitude (E) | Multiple sampling sites? | Sampling depth | Sampling frequency | Year of establishment | Status | Website |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | LTER HAUSGARTEN | Arctic Ocean (Fram Strait) | 79.00 | 4.00 | Yes | Epipelagic Zone (0–200 m) and Benthos (sediment) | Annually | 1999 | Active | https://www.awi.de/en/science/special-groups/deep-sea-research/observatories/lter-observatory-hausgarten.html |
| 2 | Adventfjorden Time Series (IsA) | Arctic Ocean (West Spitsbergen) | 78.26 | 15.53 | Unknown | Unknown | Unknown | Unknown | Unknown | Unknown |
| 3 | Icelandic monitoring programme | North Atlantic Ocean (Iceland) | 63.33 | −21.58 | Yes | Unknown | Annually | 1960 | Active | https://www.st.nmfs.noaa.gov/copepod/time-series/is-30101/ |
| 4 | Marine phytoplankton monitoring in Sweden (Svenskt HavsARKiv) | Baltic Sea | 61 | 19 | Yes | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | Monthly | 1983 | Active | https://www.smhi.se/en |
| 5 | Marine Scotland Science (MSS) Coastal Ecosystem Monitoring Programme | Eastern North Atlantic Ocean | 60.1 | −1.4 | Yes | Unknown | Unknown | 2002 | Active | http://www.gov.scot/Topics/marine/science/MSInteractive/Themes/Coastal |
| 6 | Northern Gulf of Alaska (NGA) LTER | North Pacific Ocean | 59.05 | −148.70 | Yes | Epipelagic Zone (0–200 m) | Monthly | 2017 | Active | https://lternet.edu/node/84415 |
| 7 | Linnaeus Microbial Observatory | Baltic Sea | 56.91 | 17.05 | Yes | Epipelagic Zone (0–200 m) | Weekly | 2011 | Active | https://lnu.se/en/research/searchresearch/linnaeus-microbial-observatory-lmo/ |
| 8 | Cooperative Monitoring in the Baltic Marine Environment (COMBINE) | Baltic Sea | 56.8 | 11.5 | Yes | Unknown | Unknown | 1992 | Unknown | http://www.helcom.fi/action-areas/monitoring-and-assessment/manuals-and-guidelines/combine-manual |
| 9 | Atlantic Zone Off-Shelf Monitoring Program (AZOMP) | Western North Atlantic Ocean | 55 | −55 | Yes (Transect) | Unknown | Annually | 1998 | Active | http://www.bio.gc.ca/science/monitoring-monitorage/azomp-pmzao/azomp-pmzao-en.php |
| 10 | Helgoland Roads | North Sea (German Bight) | 54.20 | 7.90 | No | Epipelagic Zone (0–200 m) | Daily | 1962 | Active | https://www.awi.de/en/science/biosciences/shelf-sea-system-ecology/working-groups/long-term-observations-lto.html |

**Table 1** (*Continued*)

| Labels | Observatory name | Region | Latitude (N) | Longitude (E) | Multiple sampling sites? | Sampling depth | Sampling frequency | Year of establishment | Status | Website |
|---|---|---|---|---|---|---|---|---|---|---|
| 11 | Phytoplankton Monitoring Programme of Marine Institute in Ireland | Eastern North Atlantic Ocean | 52.79 | −6.1 | Unknown | Unknown | Unknown | 1980 | Active | https://www.marine.i.e./Home/site-area/areas-activity/marine-environment/phytoplankton-monitoring |
| 12 | UK Colne estuary microbial LTER | Eastern North Atlantic Ocean (English Channel) | 51.78 | 0.98 | Yes | Epipelagic Zone (0–200 m) | Unknown | and | Unknown | http://www.sciencedirect.com/science/article/pii/S0065250416300198?via%3Dihub |
| 13 | Western Channel Observatory | Eastern North Atlantic Ocean (English Channel) | 50.25 | −4.20 | Yes | Unknown | Weekly | 1988 | Active | http://www.westernchannelobservatory.org.uk |
| 14 | Line P Program | Eastern North Pacific Ocean | 49.00 | −135.00 | Yes (Transect) | Unknown | 3 cruises/yr | 1950 | Active | https://www.waterproperties.ca/linep/index.php |
| 15 | SOMLIT coastal network | Eastern North Atlantic Ocean (English Channel) | 48.72 | −3.98 | Yes | Epipelagic Zone (0–200 m) | Bi-weekly | 1997 | Active | http://somlit.epoc.u-bordeaux1.fr/fr/ |
| 16 | VENUS Saanich Inlet cabled observatory | Eastern North Pacific Ocean (Strait of Georgia) | 48.65 | −123.48 | Unknown | Unknown | Daily | 2007 | Active | https://www.oceannetworks.ca/saanich-inlet-and-science-dead-zones |
| 17 | Northwest Enhanced Moored Observatory (NEMO) | Eastern North Pacific Ocean (Strait of Juan de Fuca) | 48.22 | −123.41 | Yes | Unknown | 2 cruises/yr | 2011 | Active | https://sites.google.com/site/aplwavechasers/projects/active-projects/nemo |
| 18 | JAMSTEC — K2 LTER | Western North Pacific Ocean | 47.00 | 160.00 | No | Unknown | Unknown | 2010 | Unknown | https://ebcrpa.jamstec.go.jp/k2s1/en/index.html |
| 19 | Bay of Fundy | Western North Atlantic Ocean | 45.04 | −66.84 | Yes | Epipelagic Zone (0–200 m) | Monthly | 1988 | Active | https://www.st.nmfs.noaa.gov/copepod/time-series/ca-50501/ |
| 20 | Bedford Basin Monitoring Program | Western North Atlantic Ocean | 44.6 | −63.6 | Yes | Unknown | Weekly | 1999 | Active | http://www.bio.gc.ca/science/monitoring-monitorage/bbmp-pobb/bbmp-pobb-en.php |
| 21 | Booth Bay | Western North Atlantic Ocean | 43.84 | −69.64 | Yes | Epipelagic Zone (0–200 m) | Weekly | 2000 | Active | https://www.st.nmfs.noaa.gov/copepod/time-series/us-10401/ |
| 22 | REPHY | Western Mediterranean Sea (Ligurian Sea) | 43.68 | 7.31 | Yes (Transect) | Unknown | Monthly | 1995 | Active | http://envlit.ifremer.fr/surveillance/phytoplancton_phycotoxines |
| 23 | AZTI Station D2 | Eastern North Atlantic Ocean | 43.45 | −1.91 | No | Epipelagic Zone (0–200 m) | Monthly | 1986 | Unknown | https://www.st.nmfs.noaa.gov/copepod/time-series/es-30201/ |
| 24 | DYFAMED Time Series | Western Mediterranean Sea (Ligurian Sea) | 43.45 | 7.8 | Yes | Unknown | Monthly | 1991 | Unknown | http://dyfbase.obs-vlfr.fr/ |
| 25 | Thau Lagoon | Western Mediterranean Sea (Balearic Sea) | 43.4 | 3.6 | No | Unknown | Weekly | 1971 | Active | https://www.st.nmfs.noaa.gov/copepod/time-series/fr-10201/ |

**Table 1** (*Continued*)

| Labels | Observatory name | Region | Latitude (N) | Longitude (E) | Multiple sampling sites? | Sampling depth | Sampling frequency | Year of establishment | Status | Website |
|---|---|---|---|---|---|---|---|---|---|---|
| 26 | RADIALES Time Series | Eastern North Atlantic Ocean (Southern Bay of Biscay) | 43.34 | −3 | Yes (Transect) | Unknown | Monthly | 2007 | Active | http://www.seriestemporales-ieo.com/en/index.htm |
| 27 | Atlantic Zone Monitoring Program (AZMP) | Western North Atlantic Ocean | 43 | −60 | Yes | Unknown | Bi-weekly | 1998 | Active | http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html |
| 28 | Microbial Observatory of the Laboratoire Arago | Western Mediterranean Sea | 42.50 | 3.12 | Unknown | Unknown | Unknown | 2001 | Unknown | http://collection.obs-banyuls.fr/ |
| 29 | Les Medes Islands | Western Mediterranean Sea | 42.00 | 3.23 | Unknown | Unknown | Unknown | Unknown | Unknown | Unknown |
| 30 | Blanes Bay Microbial Observatory (BBMO) | Western Mediterranean Sea (Blanes Bay) | 41.66 | 2.90 | Yes | Epipelagic Zone (0–200 m) | Monthly | 1992 | Active | http://www.icm.csic.es/bio/projects/icmicrobis/bbmo/ |
| 31 | The Operational Observatory of the Catalan Sea (OOCS) | Western Mediterranean Sea (Blanes Canyon) | 41.66 | 2.91 | Yes | Epipelagic Zone (0–200 m) | Weekly | 2009 | Active | http://www2.ceab.csic.es/oceans/index.html |
| 32 | Martha's vineyard observatory — MVCO | Western North Atlantic Ocean | 41.33 | −70.56 | Yes | Epipelagic Zone (0–200 m) | Daily | Unknown | Active | http://www.whoi.edu/mvco/publications |
| 33 | Gulf of Naples — LTER-MC | Eastern Mediterranean Sea (Gulf of Naples) | 40.80 | 14.25 | Yes | Unknown | Weekly | 1984 | Active | http://www.st.nmfs.noaa.gov/copepod/time-series/it-30101/ |
| 34 | Northeastern U.S. Shelf (NES) LTER | Western North Atlantic Ocean | 40.75 | −70.65 | Yes | Unknown | Unknown | 2017 | Active | https://nes-lter.whoi.edu/ |
| 35 | Tohoku Ecosystem-Associated Marine Sciences — EAMS — Otsuchi | Western North Pacific Ocean | 39.31 | 142.09 | Yes | Unknown | Unknown | 2011 | Active | http://www.i-teams.jp/e/ |
| 36 | Tohoku Ecosystem-Associated Marine Sciences — TEAMS — Onagawa | Western North Pacific Ocean | 38.44 | 141.64 | Yes | Unknown | Unknown | 2011 | Active | http://www.i-teams.jp/e/ |
| 37 | PROTEUS-LMER | Western North Atlantic Ocean (Chesapeake Bay) | 37.52 | −76.10 | Unknown | Unknown | Unknown | 1994 | Not active | http://news.lternet.edu/article1507.html |
| 38 | ECOMÁLAGA time-series | Western Mediterranean Sea (Alboran Sea) | 36.8 | −4.25 | Yes | Epipelagic Zone (0–200 m) | 2 cruises/yr | 2010 | Active | https://www.st.nmfs.noaa.gov/copepod/time-series/es-50301/ |

**Table 1** (*Continued*)

| Labels | Observatory name | Region | Latitude (N) | Longitude (E) | Multiple sampling sites? | Sampling depth | Sampling frequency | Year of establishment | Status | Website |
|---|---|---|---|---|---|---|---|---|---|---|
| 39 | Monterey Bay MBARI (Monterey Bay Microbial Observatory (MBMO)) | Eastern Pacific Ocean (Monterey Bay) | 36.60 | −121.89 | Yes (Transect) | Epipelagic Zone (0–200 m) | Monthly | 1989 | Active | http://www.mbari.org/ |
| 40 | IEO-RADMED monitoring program | Western Mediterranean Sea (Balearic Sea) | 36.5 | −3 | Yes (Transect) | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 2007 | Active | http://www.ba.ieo.es/investigacion/grupos-de-investigacion/coplamed/proyectos/263-radmed |
| 41 | Tohoku Ecosystem-Associated Marine Sciences — TEAMS — Manazuru | Western North Pacific Ocean | 35.12 | 139.22 | Yes | Unknown | Unknown | 2011 | Active | http://www.i-teams.jp/e/ |
| 42 | Tohoku Ecosystem-Associated Marine Sciences — TEAMS — Sagami Bay | Western North Pacific Ocean | 35.00 | 139.20 | Yes | Unknown | Unknown | 2011 | Active | http://www.i-teams.jp/e/ |
| 43 | California Current Ecosystem (CCE-LTER) | Western North Pacific Ocean | 33.90 | −120.30 | Yes | Unknown | Monthly | 1996 | Active | http://cce.lternet.edu/ |
| 44 | San Pedro Ocean Time series (SPOTS) | Eastern North Pacific Ocean (San Pedro Channel) | 33.30 | −118.30 | Yes (Transect) | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | Monthly | 1998 | Active | http://dornsife.usc.edu/labs/usc-microbial-observatory |
| 45 | Texas A&M — University of Haifa Eastern Mediterranean Observatory — THEMO | Eastern Mediterranean Sea (Levant Basin) | 33.15 | 34.85 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | Monthly | 2017 | Active | http://themo.haifa.ac.il/ |
| 46 | CENCOOS Scripps Pier | Western North Pacific Ocean | 32.87 | −117.25 | No | Unknown | Unknown | Unknown | Active | http://www.cencoos.org/data/parameters/blooms |
| 47 | Georgia Coastal Ecosystems LTER | Western Atlantic Ocean | 31.5 | −81.1 | Yes | Unknown | Unknown | 2000 | Active | http://gce-lter.marsci.uga.edu/ |

**Table 1** (*Continued*)

| Labels | Observatory name | Region | Latitude (N) | Longitude (E) | Multiple sampling sites? | Sampling depth | Sampling frequency | Year of establishment | Status | Website |
|---|---|---|---|---|---|---|---|---|---|---|
| 48 | Oceanic Microbial Observatory — BIOS-SCOPE | Western North Atlantic Ocean (Sargasso Sea) | 31.40 | −64.10 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | Monthly | 1996 | Active | https://labs.eemb.ucsb.edu/carlson/craig/research/oceanic-microbial-observatory |
| 49 | JAMSTEC — S1 LTER | Western North Pacific Ocean | 30.00 | 145.00 | No | Unknown | Unknown | 2010 | Unknown | https://ebcrpa.jamstec.go.jp/k2s1/en/index.html |
| 50 | RAPROCAN Time Series | Eastern Atlantic Ocean (Canary Islands) | 29.5 | −25 | Yes (Transect) | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | 2 cruises/yr | 2007 | Active | http://www.oceanografia.es/raprocan/ |
| 51 | ANTARES-Ubatuba | Western South Atlantic Ocean | 23.75 | −45 | No | Epipelagic Zone (0–200 m) | Monthly | 2004 | Active | http://www.coastcolour.org/site_23.html |
| 52 | Hawaii Ocean Time-series (HOT) | Western North Pacific Ocean (Hawaii) | 22.75 | −158.00 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | 10 cruises/yr | 1988 | Active | http://hahana.soest.hawaii.edu/hot/hot_jgofs.html |
| 53 | Cape Verde Ocean Observatory | Eastern North Atlantic Ocean | 17.6 | −24.3 | Yes | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | Monthly | 2006 | Active | http://cvoo.geomar.de/index.php?id=23 |
| 54 | Arabian Sea Time-Series (ASTS) | Indian Ocean (Arabian Sea) | 17 | 68 | Unknown | Unknown | 6 cruises/year | 2007 | Active | http://www.nio.org/ |
| 55 | Candolim Time-Series (CaTS) | Indian Ocean (Arabian Sea) | 15.52 | 73.63 | Unknown | Unknown | Monthly | 1997 | Active | Unknown |
| 56 | CARIACO Ocean Time-Series Program | Western Atlantic Ocean | 10.5 | −64.67 | Yes | Unknown | Monthly | 1995 | Active | http://www.imars.usf.edu/cariaco |
| 57 | IMARPE Time Series | Eastern South Pacific Ocean | −4.8 | −82 | Yes | Unknown | 4cruises/yr | Unknown | Active | https://www.st.nmfs.noaa.gov/copepod/time-series/pe-30101/ |
| 58 | Darwin | Eastern Indian Ocean (Timor Sea) | −12.40 | 130.77 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) |  | Unknown | Unknown | http://imos.org.au/facilities/nationalmooringnetwork/nrs/nrsdeployments/ |

Table 1 (*Continued*)

| Labels | Observatory name | Region | Latitude (N) | Longitude (E) | Multiple sampling sites? | Sampling depth | Sampling frequency | Year of establishment | Status | Website |
|---|---|---|---|---|---|---|---|---|---|---|
| 59 | Moorea — MCR LTER | South Pacific Ocean (Moorea Island) | −17.50 | −149.88 | No | Epipelagic Zone (0–200 m) and Benthos (sediment) | Monthly | 2004 | Active | http://mcr.lternet.edu/about/overview |
| 60 | Australian National Mooring Network — IMOS — Yongala | South Pacific Ocean (Coral Sea) | −19.31 | 147.62 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 2006 | Active | http://imos.org.au/facilities/nationalmooringnetwork/nrs/nrsdeployments/ |
| 61 | Australian National Mooring Network — IMOS — North Stradbroke Island | South Pacific Ocean (Coral Sea) | −27.34 | 153.56 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 2006 | Active | http://imos.org.au/facilities/nationalmooringnetwork/nrs/nrsdeployments/ |
| 62 | Australian National Mooring Network — IMOS — Rottness Island | Eastern Indian Ocean | −32.00 | 115.42 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 2006 | Active | http://imos.org.au/facilities/nationalmooringnetwork/nrs/nrsdeployments/ |
| 63 | Australian National Mooring Network — IMOS — PS Hacking | Tasman Sea | −34.08 | 151.25 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 2006 | Active | http://imos.org.au/facilities/nationalmooringnetwork/nrs/nrsdeployments/ |
| 64 | Australian National Mooring Network — IMOS — Kangaroo Island | Eastern Indian Ocean (Great Australian Bight) | −35.83 | 136.45 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 2006 | Active | http://imos.org.au/facilities/nationalmooringnetwork/nrs/nrsdeployments/ |
| 65 | COPAS Time Series | Eastern South Pacific Ocean | −36.5 | −73.13 | Yes | Unknown | Monthly | 2002 | Active | http://www.ocean-partners.org/sites/ocean-partners.org/files/public/attachments/295_Ocean_observing_article_COPAS.pdf |
| 66 | Estacion Permanente de Estudios Ambientales (EPEA) | Western South Atlantic Ocean | −38.46 | −57.68 | No | Epipelagic Zone (0–200 m) | Monthly | 2000 | Active | https://www.st.nmfs.noaa.gov/copepod/time-series/ar-10201/ |

**Table 1** (*Continued*)

| Labels | Observatory name | Region | Latitude (N) | Longitude (E) | Multiple sampling sites? | Sampling depth | Sampling frequency | Year of establishment | Status | Website |
|---|---|---|---|---|---|---|---|---|---|---|
| 67 | Australian National Mooring Network — IMOS — Maria Island | Tasman Sea | −42.60 | 148.23 | No | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 2006 | Active | http://imos.org.au/facilities/nationalmooringnetwork/nrs/nrsdeployments/ |
| 68 | Munida Time Series | South Pacific Ocean | −45.77 | −170.72 | Yes (Transect) | Epipelagic Zone (0–200 m) | 6 cruises/yr | Unknown | Unknown | http://www.st.nmfs.noaa.gov/copepod/time-series/nz-10101/ |
| 69 | Bay of Bengal Time-Series (BBTS) | Indian Ocean (Bay of Bengal) | −50.4 | 68.25 | Unknown | Unknown | 6 cruises/year | 2010 | Active | http://www.nio.org/ |
| 70 | King Sejong Station (KOPRI) | Southern Ocean | −62.2 | −58.8 | Unknown | Unknown | 2 cruises/yr | 2012 | Active | https://eng.kopri.re.kr/home_e/contents/e_3110000/view.cms |
| 71 | PALMER Antarctica | Southern Ocean | −64.77 | −64.05 | Yes | Unknown | Annually | 1990 | Active | http://pal.lternet.edu/ |
| 72 | Rothera Oceanographic and Biological Time Series (RaTS) | Southern Ocean | −67.34 | −68.13 | Yes | Epipelagic Zone (0–200 m) and Mesopelagic Zone (200–1000 m) | | 1997 | Active | https://www.bas.ac.uk/project/rats/ |

to expand on their exciting findings. As autonomous technologies extend the spatiotemporal reach of marine sampling, archiving, and measurement [11], we must establish a sustained and integrated system with which to provide novel microbiological insights into the changing state of the oceans.

Hence, in this contribution, we have assembled the first global map of long-term microbial observatories which provide insight into the dynamics of marine microbial life. We highlight the great potential that these efforts have in persistently assessing the microbial contribution to ocean 'health': the state of the oceans' constituent ecosystems and their support of ecosystem services such as the provisioning of biological resources, climatic regulation, and myriad other benefits [3••]. To realise this potential, we call for increased scientific activities to develop robust microbial indicators to enhance the understanding and assessment of oceanic ecosystems (see, e.g., [12]).

## The microbial role in assessing ocean health

Given the composition of the oceanic web of life, microbial dynamics should be an essential indicator of ocean state and health. The metabolic and compositional responses of microbial assemblages to variations in light, temperature, and a vast host of substances (e.g. oxygen, nutrients, metabolites, xenobiotics) make them prime candidates for biosensing and bioindication of both short- and long-term ecological variations. Thus, microbes have been used in the production of biosensors to detect, among other stimuli, the presence of organic substances (e.g. biofouling-linked compounds and toxins) and heavy metals. Further, microbial indicators (MIs), such as those examples listed in Table 2, have been developed for monitoring of environmental pressures and hazards, primarily based on the detection of invasive or pathogenic taxa (e.g. [13]). For example, the close association of bacteria such as *E. coli* with untreated sewage allows effective screening for faecal contamination in aquatic systems [14], while the temperature-dependent ranges and activity of pathogenic *Vibrio* strains can be predicted across global change scenarios [15,16]. Eukaryotic MIs, which typically report on flagellates, ciliates, and diatoms [17], are also being developed to detect the occurrence of harmful algal blooms. The emergence of new microbial functions, such as the metabolism of plastics [18], promises to steadily increase this sensing repertoire, tracking the diversification of anthropogenic stressors. Undoubtedly useful, MIs of this kind have a narrow focus, centred on risks to human health and well-being. To fully report on *ocean* health, a suite of MIs, integrated into broader observational frameworks is urgently needed to fill pronounced gaps in marine assessment strategies, while accounting for the wide range of benefits the oceans provide (e.g. [19]).

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 (microgAMBI, [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

**Table 2**

**Examples of phenomena which mature or emerging microbial indicators (MIs) may inform on. We restrict this listing to references discussed in the main text, as a complete review is beyond our scope. References to mature indicators (bold) and work which can seed new MIs are noted. In many cases, background levels of the target phenomenon are required to draw confident conclusions regarding change, stressing the need for local, long-term microbial observatories.**

| MI target | Reference(s) | Description |
|---|---|---|
| Pollution (general) | [**30**,31,36] | 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 |
| Pathogens (including wastewater contamination) | [**13**,**14**,61,75] | Screening for taxonomic marker genes and functional genes can readily detect pathogenic threats. However, many pathogens are uncharacterised and determining when organisms will display pathongenicity requires further work. |
| Invasive taxa | [4] | 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. |
| Harmful algal blooms | [60] | 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. |
| Antibiotic resistance | [39,40] | Screening for antibiotic resistance genes in metagenomic datasets readily identifies risks |
| Ecosystem status, seasonality, resilience, and food webs integrity | [8,17,20••,21••,24,25,**32**,35••, **37**,44••,**46**,**62**,63] | 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. |
| Ocean warming and acidification | [22,53,55,57,61] | 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. |
| Marine fauna health status | [5–8,41,74] | 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. |

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 $CO_2$ [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 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 nested 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.

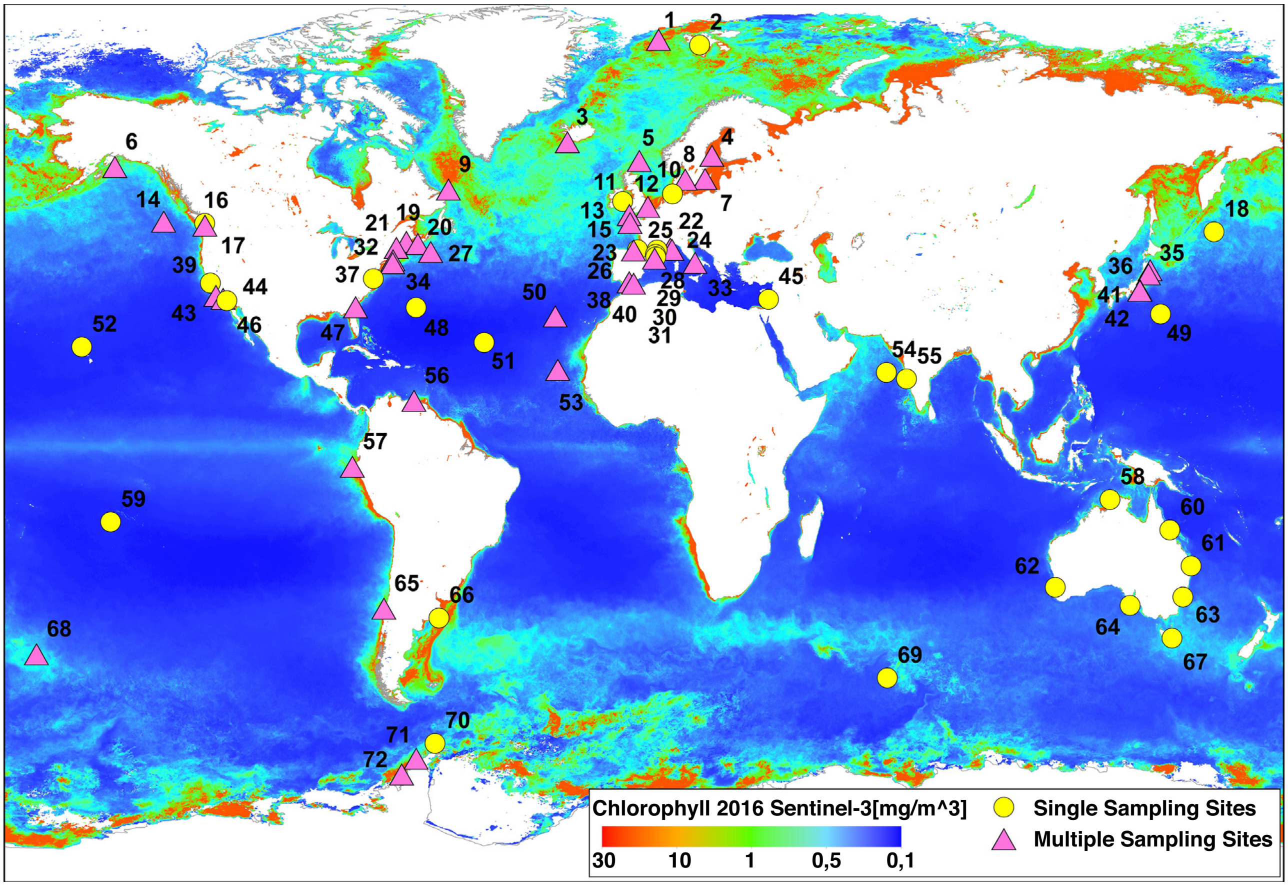
## Building a network for marine microbial observation

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 [59] 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

**Figure 1**



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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/m$^3$), 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 meta-omic 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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