Title
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Permalink
https://escholarship.org/uc/item/0t7079dj

Journal
Scientific data, 8(1)

ISSN
2052-4463

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Publication Date
2021-04-16

DOI
10.1038/s41597-021-00889-9

Peer reviewed
High spatial resolution global ocean metagenomes from Bio-GO-SHIP repeat hydrography transects

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Detailed descriptions of microbial communities have lagged far behind physical and chemical measurements in the marine environment. Here, we present 971 globally distributed surface ocean metagenomes collected at high spatio-temporal resolution. Our low-cost metagenomic sequencing protocol produced 3.65 terabases of data, where the median number of base pairs per sample was 3.41 billion. The median distance between sampling stations was 26 km. The metagenomic libraries described here were collected as a part of a biological initiative for the Global Ocean Ship-based Hydrographic Investigations Program, or "Bio-GO-SHIP." One of the primary aims of GO-SHIP is to produce high spatial and vertical resolution measurements of key state variables to directly quantify climate change impacts on ocean environments. By similarly collecting marine metagenomes at high spatiotemporal resolution, we expect that this dataset will help answer questions about the link between microbial communities and biogeochemical fluxes in a changing ocean.

Background & Summary

A growing list of coordinated scientific efforts have produced deep metagenomic libraries of the surface ocean. Projects such as the Global Ocean Survey, Tara Oceans, and bioGEOTRACES\(^1,2\) have significantly advanced our understanding of marine microbial biogeography and biodiversity. However, this ever-increasing abundance of metagenomic data raises the question of how do we move beyond analyses of biodiversity to linking microbial traits with ecosystem function and elemental fluxes\(^4\). In oceanography, it has been widely acknowledged that sparse sampling results in high noise and error rates that in turn prevent the characterization of dynamic chemical balances and limit biogeochemical models\(^5\). Thus, we propose that an increased emphasis on high resolution spatio-temporal sampling of marine microbial communities would allow for a more mechanistic understanding of the relationship between microbes and ocean biogeochemistry.

The Global Ocean Ship-based Hydrographic Investigations Program (GO-SHIP) seeks to produce high spatial and vertical resolution measurements of physical, chemical, and biological parameters over the full water column. This internationally-organized program coordinates a network of sustained hydrographic sections that are repeatedly measured on an approximately decadal time scale. Compared to autonomous programs such as Argo, which has significantly increased the spatial and temporal resolution of ocean observations\(^6\), ship-based programs have the advantage of a much broader range of biogeochemical measurement capabilities and full water column coverage. To date, repeat hydrography programs have largely focused on physical (light, currents, water column thermohaline structure, etc.) and chemical (nutrients, oxygen, dissolved organic and inorganic carbon, pH, etc.) state variables. This work has significantly improved our understanding of the response of oxygen\(^7\), pH\(^8\), calcium carbonate saturation depth\(^9\), and sea level rise\(^10\) to global warming and anthropogenic carbon accumulation\(^11\). By

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comparison, systematic and sustained biological measurements of the microbial component of ocean ecosystems has lagged far behind.

We present a dataset of 971 ocean surface water metagenomes collected at high spatio-temporal resolution in an effort to more mechanistically link marine microbial traits and biodiversity to both chemical and hydrodynamic ecosystem fluxes as a part of a novel Bio-GO-SHIP sampling program. Samples were collected in the Atlantic, Pacific, and Indian Ocean basins (Fig. 1, Table 1). This effort has been supported by GO-SHIP, SOCCOM, the Plymouth Marine Laboratory Atlantic Meridional Transect (PML AMT), and three National Science Foundation (NSF) Dimensions of Biodiversity funded cruises (AE1319, BVAL46, and NH1418) (Table 2). Whereas the median distance between Tara Oceans sampling stations was 709 km and the median distance between bioGEOTRACES sampling stations was 191 km, the median distance between sampling stations in the current Bio-GO-SHIP dataset is 26.5 km (Fig. 2). In addition, the majority of Bio-GO-SHIP samples were collected every 4–6 hours, allowing for analysis of diel fluctuations in microbial composition and gene content. We anticipate that our high-resolution sampling scheme will allow for a more detailed examination of the relationship between the broad range of geochemical parameters alone and microbial diversity and traits.

Due to their rapid generation times and high diversity, microbial genomes integrate the impact of environmental change and can be used as a ‘biosensor’ of subtle biogeochemical regimes that cannot be identified from physical parameters alone. Thus, the fields of microbial ecology and oceanography would benefit from coordinated, high resolution measurements of marine ‘omics products (i.e., metagenomes, metatranscriptomes, metaproteomes, etc.). This dataset provides an important example of the benefits of a high spatial and temporal resolution sampling regime. In addition, our data highlights the need for increased sampling of marine metagenomes in the Central and Western Pacific Ocean (Fig. 1), areas above 50°N and 50°S (Fig. 2), and below the euphotic zone. We hope and expect that these challenges will be addressed by the scientific community in the coming decade.

### Methods

On all cruises, whole (i.e., no size fractionation) surface water was collected via either the Niskin rosette system (depth ~3–5 m) or the ship’s circulating seawater system (depth ~7 m). Between 2–10 L of surface water (Table 1) was collected in triple-rinsed containers and gently filtered through a 0.22 μm pore size Sterivex filter (Millipore, Darmstadt, Germany) using sterilized tubing and a Masterflex peristaltic pump (Cole-Parmer, Vernon Hills, IL). DNA was preserved with 1620 mM sodium dodecyl sulfate (SDS) and stored at 20 °C before extraction.

### Table 1. Sampling protocols and read counts for global Bio-GO-SHIP surface ocean metagenomes.

| Cruise/Year     | DNA Collection | DNA Volume | Station Count | Total Reads | Total Bases | Median Bases Per Sample | Range of Bases Per Sample | Total Pre-Filter Reads ≥ Q25 |
|-----------------|----------------|------------|---------------|-------------|-------------|-------------------------|---------------------------|-----------------------------|
| I07N 2018       | Underway, CTD  | 4 L, 2–4 L | 248           | 6.20 × 10⁸  | 9.36 × 10⁹  | 3.27 × 10⁷              | 2.47 × 10⁸–1.42 × 10⁸   | 4.65 × 10⁸                   |
| I09N 2016       | Underway       | 10 L       | 242           | 5.73 × 10⁸  | 8.64 × 10⁹  | 3.10 × 10⁷              | 4.71 × 10⁸–1.22 × 10⁸   | 4.15 × 10⁸                   |
| C13.5 2020      | Underway       | 5–10 L     | 229           | 5.94 × 10⁸  | 8.96 × 10⁹  | 2.94 × 10⁷              | 3.98 × 10⁸–2.14 × 10⁸   | 4.17 × 10⁸                   |
| P18 2016-17     | CTD            | 2 L        | 104           | 3.22 × 10⁹  | 4.86 × 10¹⁰ | 4.46 × 1⁰              | 6.14 × 1⁰–1.77 × 1⁰     | 2.55 × 1⁰                   |
| AMT-28 2018     | CTD            | 2 L        | 63            | 2.18 × 10⁹  | 3.29 × 10¹⁰ | 4.95 × 1⁰              | 1.62 × 1⁰–1.22 × 1⁰     | 1.71 × 1⁰                   |
| NH1418 2014     | CTD            | 2 L        | 23            | 5.41 × 10⁹  | 8.17 × 10¹⁰ | 3.03 × 1⁰              | 2.42 × 1⁰–1.08 × 1⁰     | 4.02 × 1⁰                   |
| AE1319 2013     | CTD            | 2 L        | 13            | 2.01 × 10⁹  | 3.03 × 10¹⁰ | 4.69 × 1⁰              | 2.15 × 1⁰–7.43 × 1⁰     | 1.63 × 1⁰                   |
| BVAL46 2011     | CTD            | 2 L        | 12            | 2.01 × 10⁹  | 3.04 × 10¹⁰ | 2.73 × 1⁰              | 2.33 × 1⁰–4.88 × 1⁰     | 1.61 × 1⁰                   |
To extract DNA (modified from Bostrom et al. 2004) Sterivex filters were incubated with 180 μL lysozyme (3.5 mM) at 37 °C for 30 minutes followed by an overnight 55 °C incubation with 180 μL Proteinase K (0.35 mM) and 100 μL 10% SDS buffer. DNA was extracted from the Sterivex with 1000 μL TE buffer (10 mM Tris-HCl, 1 mM EDTA), precipitated in an ice-cold solution of 500 μL isopropanol (100%) and 1980 μL sodium acetate (3 M, pH 5.2), pelleted via centrifuge for 30 mins at 4 °C, and resuspended in TE buffer in a 37°C water bath for 30 min. DNA was purified using a genomic DNA Clean and Concentrator kit (Zymo Research Corp., Irvine, CA). Finally, DNA concentrations were quantified using a Qubit dsDNA HS Assay kit and Qubit fluorometer (ThermoFisher, Waltham, MA).

A total of 971 metagenomic libraries from 932 locations were prepared using Illumina-specific Nextera DNA transposase adapters and a Tagment DNA Enzyme and Buffer Kit (Illumina, San Diego, CA, cat. no. 20034197) (modified from Baym et al. 2015). Nextera adapter sequences to be used for bioinformatic quality trimming are: 5′-TCG TCG GCA GGG TCA GAT GTG TAG AAG AGA CAG-3′ and 5′-TCG TCG TGC TGG GCT CGG AGA TGT GTA TAA GAG ACA G-3′. Custom Nextera DNA-style 8 bp unique dual index (UDI) barcodes I7 (5′-CAA GAA GAC GCC ATC CGA GAT [NNN NNN NNN]G TCT CGT GGG CTC GG-3′) and I5 (5′-AAT GAT AGC GGC ACC GAG ATC TAC ACG [N NNN NNN N]TCG TGC GGC AGC GTC-3′) were used to multiplex the metagenomic libraries. A total of 10 ng of 2 μM DNA was added to 1.5 μL tagmentation reactions (1.25 μL TD buffer, 0.25 μL TDE1) and incubated at 55°C for 10 minutes. After tagmentation, product (2.5 μL) was immediately added to 22 μL reactions (1.02 μM per UDI barcode, 204 μM dNTPs, 0.0204 U Phusion High Fidelity DNA polymerase and 1.02X Phusion HF Buffer [ThermoFisher, Waltham, MA] final concentrations). Barcodes were annealed to tagmented products using the following polymerase chain reaction (PCR): 72°C for 2 min, 98°C for 30 s., followed by 13 cycles of 98°C 10 s., 63°C 30 s., 72°C 30 s., and a final extension step of 72°C for 5 min.

To quality control tagmentation products, dimers that were less than 150 nucleotides long were removed using a buffered solution (1 M NaCl, 1 mM EDTA, 10 mM Tris–HCl, 44.4 M PEG–8000, 0.055% Tween–20 final concentration) of Sera-mag SpeedBeads (ThermoFisher, Waltham, MA). Metagenomic libraries were quantified using a Qubit dsDNA HS Assay kit (ThermoFisher, Waltham, MA) and a Synergy 2 Microplate Reader (BioTek, Winooski, VT). Libraries were then pooled at equimolar concentrations. Pooled library concentration was verified using a Qubit fluorometer (ThermoFisher, Waltham, MA) and a Synergy 2 Microplate Reader (BioTek, Winooski, VT).

A total of 666 samples were sequenced on three Illumina NovaSeq S4 flowcells and an additional 251 samples were sequenced on a combination of S1 and SP flowcells using 150 bp paired-end chemistry with 300 cycles (Illumina, San Diego, CA). A total of 1010 reads, or 3.65 × 10^{12} bp. The sequencing strategy produced a total of 2.42 × 10^{10} reads, or 3.65 × 10^{12} bp. The
The median number of bases per sample was 3.41 billion (range: 61,400,000–21.4 billion). Prior to read trimming and quality filtering, 74% of all forward and reverse reads had an average quality score ≥ Q25 (Table 1). The sequencing cost per bp in US dollars was $8.2 \times 10^{-9}.

Data Records
The majority of the samples here were collected under the auspices of the international GO-SHIP program and the national programs that contribute to it\textsuperscript{21–24}. Links to publicly available metadata variables collected via CTD cast are provided in Table 2. A comprehensive data directory of all metadata resources, including those that were collected and may be requested from individual PIs, is available through GO-SHIP and the Carbon and Climate Hydrographic Data Office (CCDHO) under a Public Domain Mark (PDM).

Metadata variables from the AMT-28 cruise are hosted by the British Oceanographic Data Centre (BODC)\textsuperscript{25} and the Southern Ocean Carbon and Climate Observations and Modeling project (SOCCOM).

The BVAL46, AE1319, and NH1418 cruises were collected as a part of the “Biological Controls on the Ocean C:N:P Ratios” project funded by the NSF Division of Ocean Sciences\textsuperscript{26–29}. Data associated with these deployments are hosted by the NSF Biological and Chemical Oceanography Data Management Office (BCO-DMO) under Project 2178 and are archived by the Woods Hole Open Access Server (WHOAS) under a Creative Commons BY 4.0 (CC BY 4.0) license.

All sequencing products associated with the Bio-GO-SHIP program can be found under BioProject ID PRJNA656268 hosted by the National Center for Biotechnology Information Sequence Read Archive (SRA)\textsuperscript{30}. SRA accession numbers associated with each metagenome file are provided in Supplementary Table 1.

Technical Validation
To ensure that no contamination of metagenomes occurred, negative controls were used. To ensure optimum paired-end short read sequencing, a 2100 Bioanalyzer high sensitivity DNA trace (Agilent, Santa Clara, CA) was used for each library to confirm that ~90% of the sequence fragments were above 200 bp and below 600 bp in length (Table 3). A Qubit (ThermoFisher, Waltham, MA) and a KAPA qPCR platform (Roche, Basel, Switzerland) were used to ensure that all pooled libraries were submitted for sequencing at a concentration > 15 nM.
Table 3. Sequencing run breakdown of Bio-GO-SHIP metagenomes including technical validation statistics.
*Run 1 was concentrated via SpeedVac to 15 nM and bead size-selected such that 90% of fragments were between 200–600 bp by the UC Davis Genome Center DNA Technologies Core prior to sequencing. Final values for this run are not available.

Usage Notes
The genomic data described here have not been pre-screened or processed in any way. We recommend quality control parameters. Prior to our sequence analysis in subsequent projects, we removed adapter sequences, performed sequence quality control, and ensured there was no contamination from common genomic add-ins such as Phi-X using the following code parameters:

```
Trimmomatic (v0.35): PE ILLUMINACLIP:NexteraPE-PE.fa:2:30:10 SLIDINGWINDOW:4:15 MINLEN:36
```

Nutrient data (NO₃, NO₂, PO₄, SiO₄) collected by SOCCOM and funded by the National Science Foundation are available from the AMT-28 transect through the CCHDO (http://cchdo.ucsd.edu, search on SOCCOM).

Code availability
Custom scripts were not used to generate or process this dataset. Software versions and non-default parameters used have been appropriately specified where required.

Received: 9 December 2020; Accepted: 12 March 2021; Published online: 16 April 2021

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Acknowledgements
We would like to thank the captains and crew of the R/V Atlantic Explorer, R/V New Horizon, NOAA Ship Ronald H. Brown, R/V Roger Revelle, and the R.R.S. James Clark Ross. Our additional thanks go to Michael Lomas (Bigelow Laboratory for Ocean Sciences) and Andy Rees (Plymouth Marine Laboratory). Financial support for this project was provided by the National Science Foundation (OCE-1046297, 1559002, 1848576, and 1948842 to ACM). LJU was supported by the National Institutes of Health (T32AI114346). LB and DLY were supported in part under the auspices of the Cooperative Institute for Marine and Atmospheric Studies (CIMAS), a cooperative institute of the University of Miami and NOAA (cooperative agreement NA10OAR4320143). The PML AMT is funded by the UK Natural Environment Research Council through its National Capability Long-term Single Centre Science Programme, Climate Linked Atlantic Sector Science (grant number NE/R015953/1). This study contributes to the international IMBeR project and is contribution number 357 of the AMT program. SOCCOM nutrient sampling (LDT) on AMT-28 was supported by the National Science Foundation (OCE-PLR-1425989). GO-SHIP is supported in part by the NOAA Global Ocean Monitoring and Observation program (U8R1SE3-PRF) and by the National Science Foundation (OCE-1437015). P18, I07N, and A13.5 (aborted) were NOAA-led cruises and I09N was an NSF-led cruise.

Author contributions
A.A.L. wrote the manuscript, designed metagenomic protocols, coordinated sample collection, collected/processed samples, performed and/or supervised all metagenomic sequencing, and compiled metadata. C.A.G. coordinated sample collection, collected/processed samples, performed metagenomic sequencing, and compiled metadata. M.L.B. performed metagenomic sequencing and compiled metadata. J.A.L. collected/processed samples and performed metagenomic sequencing, and compiled metadata. R.E.S., L.D.T. and D.L.V. coordinated GO-SHIP and SOCCOM (L.D.T.) collection and collaboration efforts. G.T. coordinated PML AMT/GO-SHIP collection and collaboration efforts. A.C.M. designed and supervised the study, secured funding, and coordinated GO-SHIP collection. All authors contributed to manuscript editing and revision.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41597-021-00889-9.

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