

Bio-GO-SHIP: the time is right to establish global repeat sections of ocean biology

Sophie Clayton^{1,*}, Harriet Alexander^{2,*}, Jason Graff³, Nicole Poulton⁴, Luke R. Thompson^{5,6}, Heather Benway⁷, Emmanuel Boss⁸, Adam Martiny^{9,10}

¹ *Department of Ocean and Earth Sciences, Old Dominion University, Norfolk, VA, USA*

² *Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, MA, USA*

³ *Oregon State University, Corvallis, OR, USA*

⁴ *Bigelow Laboratory for Ocean Sciences, East Boothbay, ME, USA*

⁵ *Northern Gulf Institute, Mississippi State University, Mississippi State, MS, USA*

⁶ *Ocean Chemistry and Ecosystems Division, Atlantic Oceanographic and Meteorological Laboratory, National Oceanic and Atmospheric Administration, Miami, FL, USA*

⁷ *Department of Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, MA, USA*

⁸ *School of Marine Sciences, University of Maine, Orono, ME, USA*

⁹ *Department of Earth System Science, University of California, Irvine, CA, USA*
¹⁰ *Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, USA*

Correspondence*:

Corresponding Authors

sclayton@odu.edu; halexander@whoi.edu

2 ABSTRACT

3 Ocean plankton is an essential component of the earth system. Despite its importance, ocean
4 biology is largely under-sampled in time and space compared to physical and chemical properties.
5 This lack of information hampers our ability to understand the role of plankton in regulating
6 biogeochemical processes, now and in future oceans. Traditionally, many of the methods used
7 to quantify biological and ecosystem essential ocean variables (EOVs) have been expensive
8 and labor- and time-intensive, limiting their large-scale deployment. In the last two decades,
9 new technologies have been developed and matured, making it possible to greatly expand our
10 biological ocean observing capacity. These technologies, including cell imaging, bio-optical
11 sensors and 'omic tools, can be combined to provide overlapping measurements of key biological
12 and ecosystem EOVs. New developments in data management and open sharing can facilitate
13 meaningful synthesis and integration with concurrent physical and chemical data. We argue that
14 the time is right to incorporate systematic and consistent biological observations into global ocean
15 repeat surveys, and present Bio-GO-SHIP, a new global biological ocean observing program.

16

17 **Keywords:** biological oceanography, ocean observing, plankton ecosystems, GO-SHIP program, repeat hydrography

1 INTRODUCTION

The physics, chemistry, and biology of the ocean system are irrevocably interlinked. Marine life and biological processes, particularly within plankton, drive the global biogeochemical cycling of climatically-important elements (e.g. C, O, N, P, Si, Fe). The measurement and chronicling of physical (e.g. salinity and temperature) and chemical ocean properties (e.g. dissolved oxygen, the carbonate system and nutrients) have been broadly and systematically incorporated into global repeat surveys for many decades. By comparison, ocean life and biological processes are chronically under-sampled in both time and space, with the notable exception of ocean color-derived surface ocean chlorophyll (McClain, 2009; Siegel et al., 2013). As a result of this under-sampling, many important questions and observations in oceanography remain poorly constrained, and our ability to observe and detect marine ecosystem responses to global climate change is restricted (Mieszkowska et al., 2014).

A globally consistent effort to quantify and study plankton communities across ocean basins will transform our understanding of plankton biogeography, marine food webs, and the biological regulation of elemental cycles. To date, the majority of survey programs have focused on "bio-discovery", targeting unique ocean environments in order to generate a catalog of ocean life, leading to the discovery of new biodiversity by the Global Ocean Sampling Expedition (Rusch et al., 2007), Tara Oceans (Carradec et al., 2018), and Malaspina (Acinas et al., 2019; Salazar et al., 2015). We propose that a central need exists to coordinate and merge observations of biology with concurrently measured physical and chemical properties across large spatial and temporal scales in order to study and model feedback loops between plankton ecosystems and chemical and physical ocean processes. Consistent and fully integrated observations will provide a beyond-baseline understanding of global plankton and pelagic organism biogeography, the biological regulation of particle composition and elemental stoichiometry, linking surface plankton diversity with the downward particle flux and C storage, and the regulation of deep ocean biodiversity. We also envisage that biological tracers such as microbial community composition in the deep ocean will help to uncover physical transport pathways that are not well constrained by hydrographic observations alone. With sustained observations, we will be able to identify how characteristic shifts in ocean plankton communities may act as 'biosensors' for ocean changes (Ustick et al., 2021).

In this paper, we outline a plan for **Bio-GO-SHIP**¹, a globally consistent biological ocean observing program that integrates the latest observing technologies into the existing repeat hydrography program (Sloyan et al., 2019). Integrating Bio-GO-SHIP within the existing GO-SHIP program naturally bridges physical, chemical, and biological measurements. This synergy has the potential to progressively inform our understanding of plankton biodiversity, the impacts of plankton community structure and activity on chemical inventories, and the physical connectivity between communities residing in apparently distinct oceanic provinces. Below we highlight existing and new technologies that meet the demands of Bio-GO-SHIP and discuss aspects of data management and community access. Finally, we describe how repeat biological sections fit into and augment existing ocean observing systems, and how they will support future developments of autonomous observing platforms.

2 GLOBAL REPEAT HYDROGRAPHIC SURVEYS

2.1 Physical and biogeochemical oceanographic surveys

GO-SHIP is the most recent iteration in a series of global hydrography programs dating back to the Geochemical Ocean Sections Study in the 1970s (GEOSECS; Moore, 1984), followed in the late 1980s by the Joint Global Ocean Flux Study (JGOFS; Fasham et al., 2001), and the World Ocean Circulation

¹ <https://biogoship.org/>

Experiment in the 1990s (WOCE; Woods, 1985). The principal scientific objectives for long-term ship-based repeat hydrography programs have two closely linked components. Firstly, they aim at understanding and documenting the large-scale distribution of ocean properties, their changes, and the drivers of those changes. Secondly, they assess the functioning of a warmer and more stratified ocean with increased dissolved inorganic carbon (DIC), lower pH, changes in circulation and ventilation processes, altered water cycle, and shrinking sea-ice. GO-SHIP organizes a global repeat-occupation effort, whereby most major ocean regions are sampled every decade in order to observe global changes. The program coordinates measurements of a suite of key physical and chemical essential ocean variables (EOVs) throughout the full ocean water column, and in areas of the ocean inaccessible to other platforms. While GO-SHIP is an international program, it is funded and executed nationally. Key to GO-SHIP's success is international agreement between the national partners on standard data collection and curation methods and protocols.

GO-SHIP's repeat decadal observations of ocean physics and chemistry have provided critical constraints on anthropogenic changes in ocean heat content (Roemmich et al., 2007; Waugh et al., 2013; Purkey and Johnson, 2010), penetration of carbon (Gruber et al., 2019), shoaling of the calcium carbonate saturation depth (Feely et al., 2004) and loss of oxygen (Schmidtko et al., 2017), all of which have direct and serious implications for ocean life. Unfortunately, routine measurements of EOVs to characterize life in the ocean - including its composition, abundance, and changes in distribution - which are fundamental to our understanding of marine ecosystems (Lombard et al., 2019; Boss et al., 2020) are missing. Integrating routine measurements of biological and ecosystem EOVs into global repeat sections represents an important step forward for developing both a holistic understanding of the functioning of marine ecosystems, and a baseline from which changes over the coming decades can be observed.

2.2 Recent scientific advances enabled by biological sampling on GO-SHIP sections

The increasing availability of mature technologies to measure key biological EOVs offers a unique opportunity for a truly integrated global repeat sampling program. There have been a number of biological efforts in collaboration with the GO-SHIP program during the last five years on cruises to the Atlantic, Indian and Pacific Oceans (Larkin et al., 2021). One example is the Atlantic Meridional Transect (AMT), which is a repeat transect spanning the Atlantic Ocean (Robins and Aiken, 1996). The AMT Program has incorporated routine measurements of biological EOVs since its inception in 1995 and serves as a model for integrating biological data collection into repeat surveys. These efforts span genomics to identify ecosystem functions and biodiversity patterns, the elemental stoichiometry of marine ecosystems, and the biogeography of the biological pump. Common to all these efforts are the clear linkages and integration between physical, chemical, and biological observations (Figure 1).

GO-SHIP transects incorporating biology have allowed for a systematic analysis of large-scale gradients in plankton genomic diversity. The most abundant marine phytoplankton, *Prochlorococcus*, has been shown to adapt to nutrient availability through gene gains and losses (Coleman and Chisholm, 2010). This biological feature was applied as a living 'biosensor' for the elemental type and severity of nutrient stress (Ustick et al., 2021). This analysis is supported by past nutrient-amendment bottle experiments and models (Moore et al., 2013), but also has uncovered many previously unrecognized regions of nutrient stress, suggesting that nutrient stress biogeography might be tied to shifts in vertical mixing and the aeolian supply of iron (Martiny et al., 2019). Genomic data has also been used to infer variations in C cycling strategies between ocean regions (Raes et al., 2021). Finally, plankton biodiversity patterns significantly diverged from current theoretical predictions suggesting that we lack a fundamental understanding of the drivers of planktonic biodiversity (Raes et al., 2018).

The elemental stoichiometry of ocean ecosystems is of fundamental importance to many biogeochemical processes such as the biological pump, nitrogen fixation, and the transfer of elements to higher trophic levels. Measurements of particulate organic matter on GO-SHIP transects demonstrated a clear latitudinal gradient in C:N:P (Lee et al., 2021; Garcia et al., 2018). Detailed hydrographic measurements from sections showed that ecosystems with a deep nutricline had elevated C:N and C:P ratios. Furthermore, it was shown that shifts in genomic markers captured the impact of cellular nutrient limitation on C:N:P (Garcia et al., 2020). Finally, samples from GO-SHIP provided the first large-scale estimate of the carbon-to-oxygen remineralization ratio (Moreno et al., 2020).

3 TECHNOLOGICAL ADVANCES FOR SUSTAINED GLOBAL BIOLOGICAL OBSERVATIONS

Detailed observations of the biological components of marine planktonic ecosystems have historically been restricted to targeted process studies of limited duration and spatial extent, such as NAAMES (Penna and Gaube, 2019; Behrenfeld et al., 2019) and EXPORTS (Siegel et al., 2016), or long term ocean time series including the Hawaii Ocean Timeseries (HOT; Karl and Church, 2014), the Bermuda Atlantic Time Series (BATS; Michaels and Knap, 1996), the CARIACO Ocean Time-Series Program (Muller-Karger et al., 2019), and the Continuous Plankton Recorder Survey (Batten et al., 2019). Barriers to global-scale extended studies include the expense and labor involved with collecting, processing, and analyzing biological samples and associated properties. However, over the last two decades, many biological observational technologies have matured, been ground-tested and broadly applied, and are now capable of affordable and high-throughput sampling, making it feasible to mount a global biological sampling program in conjunction with existing repeat hydrographic survey programs. For the first time, these observational tools (and analytical pipelines) make routine global repeat sections of biological and ecosystem EOVs a reality (Bojinski et al., 2014; Miloslavich et al., 2018).

3.1 Scaling up the measurement of biological and ecosystem EOVs

Within the changing ocean environment, a baseline of sustained, consistent measurements is central to our ability to study, characterize, and monitor patterns in biodiversity and the downstream impacts of that diversity on ecosystem and biogeochemical processes. The GO-SHIP program currently includes the routine sampling of several biogeochemical EOVs, including dissolved oxygen, nutrients, dissolved organic carbon, and pCO_2 (Sloyan et al., 2019). Here we provide a brief overview of the technologies and sampling strategies that will be included in the Bio-GO-SHIP program to study planktonic ecosystems, with a focus on biological EOVs central to pelagic ecosystems: specifically microbial, phytoplankton, zooplankton, and fish biomass and diversity (Miloslavich et al., 2018). By combining multiple optical, 'omic, and particulate sampling strategies, we plan to measure these variables in overlapping and complementary ways (Figure 2).

Microbial communities (comprised of prokaryotic and eukaryotic microbes and viruses) are centrally important to the functioning of the ocean. Using a combination of particulate, omic, and optical measures, we will be able to track their (relative) biomass and taxonomic composition. Flow cytometry will be used to target the smallest class of cells (0.5 - 10 μm), from which we can quantify cell numbers and extrapolate biomass, as well as coarse taxonomic composition. 'Omics are a well-developed and broadly used set of approaches to assess the diversity and function of microbial communities (Gilbert and Dupont, 2011; Ustick et al., 2021; Sunagawa et al., 2015). Metabarcoding, targeting conserved genes such as 16S or 18S, and shotgun metagenomics, which randomly samples DNA from the environment, shed light on the taxonomic composition of the microbial communities. Metatranscriptomics, which randomly samples the

141 RNA from the environment, both provide information on the taxonomic and functional potential and a
142 proxy for activity of the community.

143 Phytoplankton form the base of the marine food web and account for roughly half of global primary
144 productivity (Field et al., 1998). Their diversity, biomass and physiology will be assessed using a
145 combination of 'omic, optical, and particulate measures. Phytoplankton span a wide range of size classes
146 from $< 1\mu m$ to $> 2000\mu m$ (Finkel et al., 2009), necessitating the combination of multiple optical tools
147 (flow cytometry, imaging flow cytometry, video imaging) to fully sample and estimate their contribution
148 to biomass and cell size distribution (Lombard et al., 2019). By integrating bio-optical measures of
149 fluorescence, absorption and backscatter at multiple wavelengths (e.g., SeaBird flbb, AC-S, and bb3) and
150 Fast Repetition Rate Fluorometry (FRRF), we can also get information on the taxonomic composition of
151 the community and their photo-physiological status (Organelli et al., 2017; Vaillancourt, 2004; Suggett
152 et al., 2009). Moreover, these measures can facilitate the calibration, validation and interpretation of remote
153 sensing data products for phytoplankton functional types (PFTs) and particle size distributions (PSDs). As
154 with the heterotrophic microbial communities, 'omics provide a window into the fine-scale taxonomic and
155 functional diversity of the eukaryotic plankton. In particular, 18S amplicon data has been successfully used
156 to delineate protistan diversity within communities (de Vargas et al., 2015), while metatranscriptomics
157 can reveal community function, activity and metabolism (Marchetti et al., 2012; Alexander et al., 2015;
158 Carradec et al., 2018).

159 Pelagic consumers, fish and zooplankton, are central to supporting higher trophic levels, including
160 humans. Given the increasing patchiness with organism size within the pelagic environment, sampling
161 includes extended trawling or net-based collections (e.g. MOCNESS). Such tools require a significant
162 time investment and may not always be feasible on GO-SHIP or similar survey efforts. Rather, there are
163 a variety of techniques that can be applied to derive proxies for abundance and taxonomic composition
164 including imaging (e.g. Underwater Video Profiler, UVP), acoustics, and environmental DNA (eDNA).
165 Active acoustics can be used to assess the abundance and community composition of large zooplankton
166 and small fish (Howe et al., 2019). eDNA metabarcoding, a method which has become more commonly
167 used in the conservation and ecological fields, amplifies marker genes to assess and estimate the presence
168 and relative abundance of larger organisms (read: animals and multi-cellular plants) based on sloughed
169 cells (Thomsen et al., 2012; Suter et al., 2020).

170 **3.2 Synergy between diverse data types**

171 Each of the tools detailed above provides information on a particular property of the pelagic ecosystem
172 that can be used to answer specific questions in oceanography: e.g. metabarcoding quantifies the species
173 composition, and flow cytometry can illuminate shifts in community size structure over space and time.
174 More so, it is in the combination and integration of multiple tools and approaches (and resulting combined
175 datasets) that a more coherent understanding of the functioning of the ocean ecosystem can be built.
176 As can be seen from the list above, these distinct sampling approaches and technologies often result
177 in overlap for quantities of interest (Figure 2). For instance, particle size data produced by multiple
178 approaches or instruments (e.g. Laser In-Situ Scattering and Transmissometry (LISST), Flow Cytometry
179 (FCM), Imaging Flow Cytobot (IFCB)) overlap across a portion of their datasets and provide a plankton
180 size distribution ranging from microbes to large phytoplankton that could not be achieved from a single
181 instrument (Lombard et al., 2019). Multiple methods might be used to assess the taxonomic diversity of a
182 community, with metabarcoding and metagenomics describing presence, metatranscriptomics highlighting
183 active organisms, and high-throughput imaging identifying the morphology. Similarly, omics targeting
184 of nutrient-related genes with either metagenomics or metatranscriptomics can be combined with fast

repetition rate fluorometry (FRRF) and particulate C:N:P to assess the dominant nutritional state of a community. Using complimentary techniques will provide a more accurate and comprehensive assessments of each EOY.

3.3 Keeping up with advances in biological oceanographic sampling

Advances in ocean technologies drive new discoveries but maintaining pace with these advances is challenging and requires the attention of the community. This race to keep pace with evolving technologies is particularly evident within the area of 'omics, as sequencing platforms rapidly shift and improve overall sequencing yield and potential contiguous read length (Levy and Myers, 2016). Looking only 10 years into the future, it is difficult to imagine what our potential capabilities might be within this sphere. As such, it is of paramount importance that we consider ways to ensure that the sequencing data we collect now is forward compatible with data collected 10 years from now. To ensure that this is possible, we must consider the best practices for intercalibration of these types of datasets. Additionally, there are great benefits to "biobanking" samples and "databanking" images for future analysis with the improved technology (Jarman et al., 2018). The curation of samples in this way will be key to being able detect future changes in the ocean ecosystem.

Ship-based observations remain the "gold standard" in oceanographic exploration. However, these efforts are costly, and much effort has been put into developing autonomous observation technologies. Moored arrays and autonomous robotic instrumentation (e.g. Argo floats, gliders, and drifters) have enabled continuous remote observation of several physical oceanographic parameters (e.g. temperature, salinity, currents) and show great promise for the collection of chemical and biological data. Profiling Biogeochemical-Argo floats instrumented with sensors that collect up to six biogeochemically relevant measures (chlorophyll a, oxygen, nitrate, pH, backscatter, and PAR) as part of the SOCCOM and GO-BGC programs, and whose data is comparable to those collected via shipboard observation, is a good example of the use of these technologies for biological investigations (Claustre et al., 2020). There is potential for developing remote and automated technologies to facilitate the collection of the biological data we list above ('omics, imaging, FCM, etc.). In particular, autonomous ecogenomic samplers, like the Environmental Sample Processor (ESP) (Scholin et al., 2017), have already demonstrated the possibility to sample DNA or RNA remotely (Ottesen et al., 2013). Additionally, new platforms that facilitate the fine-scale sampling of dissolved and particulate seawater biochemistry along vertical profiles, such as *Clio* (Breier et al., 2020), stand to expand the potential of automated collection of these parameters and decrease required ship time. Rigorous calibration and validation of such autonomous biological observing platforms will be key in their successful development and deployment. GO-SHIP cruises are currently used as a platform not only for the deployment of BGC-Argo profiling floats, but also provide key data for subsequent validation of the data provided by the on-board biogeochemical sensors and sampling (Bittig et al., 2019). We envision that Bio-GO-SHIP will provide a similar synergies for deploying new biological sensors and, thus, accelerate the development and adoption of remote biological observational strategies.

4 CHALLENGES AND OPPORTUNITIES FOR DATA MANAGEMENT AND INTEGRATION

Developing guidelines for the use of and consistent analysis of data produced by the technologies described above has been the focus of several working groups in recent years. This includes a SCOR working group ("Integration of Plankton-Observing Sensor Systems to Existing Global Sampling Programs"; Boss et al. (2019, 2020)), an OCB-sponsored small working group on Phytoplankton Taxonomy ("Data Standards and Practices for Taxon-Resolved Phytoplankton Observations" (Neeley et al., 2021), and an

OCB-sponsored working group on Ocean Nucleic Acids 'Omics Intercalibration². Although invaluable in building understanding, individual data types provide only a limited view of the whole system. Here, we outline an integrated approach to synthesizing physical and chemical oceanographic data (temperature, salinity, density, velocity, vertical profiles) with continuously (e.g. optics) or discrete (e.g. omics, FCM, particulate nutrients) biological measures. Beginning to holistically integrate these different data types may help us address fundamental questions in biological oceanography, and facilitate the development of integrated analyses (including machine learning and AI applications) to examine feedbacks between ocean physics, chemistry and biology.

4.1 Data management and sharing to enhance data-driven discovery across the community

Data sharing and dissemination is a challenging aspect of large-scale programs, like Bio-GO-SHIP, that collect high volumes of diverse data types. A first order issue is ensuring that all the data generated through the Bio-GO-SHIP program will align with FAIR (Findable, Accessible, Interoperable, and Reusable) data management practices (Wilkinson et al., 2016). There is also a need to align this data with existing conventions in ocean and biological sciences (e.g. EOVs, ECVs, taxonomy). More so, ensuring that integrated, linked metadata with consistent vocabularies is present will be crucial. Additionally, as the program grows and develops, samples will be taken by many different individuals, so methodological documentation, data quality control, and intercalibration will be important.

There are many good models of data management and data sharing within the oceanographic community (e.g. Bowie and Tagliabue, 2018; Acinas et al., 2019). In particular, Tara Oceans implemented a highly successful system for data management and accessibility through a combination of robust collection of linked metadata and user-focused curated final data products made available alongside the raw data products (Villar et al., 2018). GO-SHIP's success in facilitating new scientific discoveries has been largely supported by a clear, consistent and well-documented set of data requirements and data submission timelines and policies³. Bio-GO-SHIP will employ data management strategies used by these groups and integrate data-platforms to conform to the current best practices in data management and data requirements within the oceanographic community. Given the wide range of data types that will be produced by the Bio-GO-SHIP program, the data will inevitably be curated within several data repositories (e.g. GenBank, BCO-DMO, CCHDO, NASA SeaBASS). However, a Bio-GO-SHIP website will provide a central repository that describes all of the data, lists its locations and DOIs and ensures redundancy for data discovery and access.

5 WHERE DOES BIO-GO-SHIP FIT INTO THE GLOBAL OCEAN OBSERVING SYSTEM?

A mechanistic and coherent understanding of ocean ecosystems and the capacity for marine organisms to evolve is crucial in light of climate change. While there are many well-developed physical-chemical ocean observing campaigns (e.g., GO-SHIP, GeoTraces, OSNAP, RAPID), few programs have incorporated the systematic collection of biological data across the global ocean. Tara Oceans, Malaspina, and the Global Ocean Survey represent a proof of concept and showcase the potential of global scale biological data collection. Still, a routine biological component of the global ocean observing system has yet to be established. The importance of biological measures at a global scale is undeniable and recognised as such by the Global Ocean Observing System (GOOS) EOVs. Until now we have not been able

² <https://www.us-ocb.org/ocean-nucleic-acids-omics-workshop/>

³ <https://www.go-ship.org/DatReq.html>

264 to systematically and simultaneously make repeated observations due to technological and sampling
265 constraints and methodological differences between programs.

266 Ultimately, we envision that Bio-GO-SHIP will not be unique or operate in isolation and the
267 more frequently these types of biological observations are incorporated into global-scale studies (e.g.
268 BioGeoTraces (Biller et al., 2018)) the better. The scientific community studying these highly complex and
269 dynamic systems will benefit from greater volumes of consistent, high-quality data. More measurements,
270 regardless of the program name, will ultimately accelerate discovery. A key component of the Bio-GO-
271 SHIP program, as with GO-SHIP, will be rapid data sharing and open data access. Open data democratizes
272 the scientific process and allows for greater participation in oceanography within and beyond the scientific
273 community.

274 Bio-GO-SHIP will augment the exiting GO-SHIP program by collecting core biological measurements
275 in a globally consistent and integrated program. Building on preceding biological survey programs, Bio-
276 GO-SHIP will generate data at a global scale at high spatial resolution (Larkin et al., 2021). The program
277 is being developed in a highly interdisciplinary environment, working directly with physical and chemical
278 oceanographers to scale up the biological observational strategies generally reserved for targeted process
279 studies to global scale repeat sections. The technologies now exist to expand the core measurements
280 of global hydrographic programs to build our understanding of interacting physical-chemical-biological
281 processes and feedbacks that control and mediate the global biogeochemical cycles and link surface and
282 deep ocean ecosystems.

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283 AM, SC, HA, NP and JRG contributed to conception of the manuscript. SC and HA drafted the manuscript.
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REFERENCES

- 289 Acinas, S. G., P. Sánchez, G. Salazar, F. M. Cornejo-Castillo, M. Sebastián, R. Logares, S. Sunagawa,
290 P. Hingamp, H. Ogata, G. Lima-Mendez, S. Roux, J. M. González, J. M. Arrieta, I. S. Alam, A. Kamau,
291 C. Bowler, J. Raes, S. Pesant, P. Bork, S. Agustí, T. Gojobori, V. Bajic, D. Vaqué, M. B. Sullivan,
292 C. Pedrós-Alió, R. Massana, C. M. Duarte, and J. M. Gasol (2019, may). Metabolic architecture of the
293 deep ocean microbiome.
- 294 Acinas, S. G., P. Sánchez, G. Salazar, F. M. Cornejo-Castillo, M. Sebastián, R. Logares, S. Sunagawa,
295 P. Hingamp, H. Ogata, G. Lima-Mendez, S. Roux, J. M. González, J. M. Arrieta, I. S. Alam, A. Kamau,
296 C. Bowler, J. Raes, S. Pesant, P. Bork, S. Agustí, T. Gojobori, V. Bajic, D. Vaqué, M. B. Sullivan,
297 C. Pedrós-Alió, R. Massana, C. M. Duarte, and J. M. Gasol (2019). Metabolic architecture of the deep
298 ocean microbiome. *bioRxiv*.

- Alexander, H., M. Rouco, S. T. Haley, S. T. Wilson, D. M. Karl, and S. T. Dyhrman (2015, nov). Functional group-specific traits drive phytoplankton dynamics in the oligotrophic ocean. *Proceedings of the National Academy of Sciences* 112(44), E5972–E5979.
- Batten, S. D., R. Abu-Alhaija, S. Chiba, M. Edwards, G. Graham, R. Jyothibabu, J. A. Kitchener, P. Koubbi, A. McQuatters-Gollop, E. Muxagata, et al. (2019). A global plankton diversity monitoring program. *Frontiers in Marine Science* 6, 321.
- Behrenfeld, M. J., R. H. Moore, C. A. Hostetler, J. Graff, P. Gaube, L. M. Russell, G. Chen, S. C. Doney, S. Giovannoni, H. Liu, C. Proctor, L. M. Bolaños, N. Baetge, C. Davie-Martin, T. K. Westberry, T. S. Bates, T. G. Bell, K. D. Bidle, E. S. Boss, S. D. Brooks, B. Cairns, C. Carlson, K. Halsey, E. L. Harvey, C. Hu, L. Karp-Boss, M. Kleb, S. Menden-Deuer, F. Morison, P. K. Quinn, A. J. Scarino, B. Anderson, J. Chowdhary, E. Crosbie, R. Ferrare, J. W. Hair, Y. Hu, S. Janz, J. Redemann, E. Saltzman, M. Shook, D. A. Siegel, A. Wisthaler, M. Y. Martin, and L. Ziemba (2019, mar). The north atlantic aerosol and marine ecosystem study (NAAMES): Science motive and mission overview. 6.
- Biller, S. J., P. M. Berube, K. Dooley, M. Williams, B. M. Satinsky, T. Hackl, S. L. Hogle, A. Coe, K. Bergauer, H. A. Bouman, T. J. Browning, D. De Corte, C. Hassler, D. Hulston, J. E. Jacquot, E. W. Maas, T. Reinthaler, E. Sintes, T. Yokokawa, and S. W. Chisholm (2018). Data descriptor: Marine microbial metagenomes sampled across space and time. *Scientific Data*.
- Bittig, H. C., T. L. Maurer, J. N. Plant, C. Schmechtig, A. P. Wong, H. Claustre, T. W. Trull, T. Udaya Bhaskar, E. Boss, G. Dall’Olmo, et al. (2019). A bgc-argo guide: Planning, deployment, data handling and usage. *Frontiers in Marine Science* 6, 502.
- Bojinski, S., M. Verstraete, T. C. Peterson, C. Richter, A. Simmons, and M. Zemp (2014, sep). The concept of essential climate variables in support of climate research, applications, and policy. *Bulletin of the American Meteorological Society* 95(9), 1431–1443.
- Boss, E., N. Haëntjens, S. G. Ackleson, B. Balch, A. Chase, G. Dall’Olmo, S. Freeman, Y. Liu, J. Loftin, W. Neary, et al. (2019). Ioccg ocean optics and biogeochemistry protocols for satellite ocean colour sensor validation inherent optical property measurements and protocols: Best practices for the collection and processing of ship-based underway flow-through optical data (v4. 0).
- Boss, E., A. M. Waite, J. Uitz, S. G. Acinas, H. M. Sosik, K. Fennel, I. Berman-Frank, M. Cornejo, S. Thomalla, H. Yamazaki, et al. (2020). Recommendations for plankton measurements on the go-ship program with relevance to other sea-going expeditions. scor working group 154 go-ship report.
- Bowie, A. and A. Tagliabue (2018). Geotraces data products: standardising and linking ocean trace element and isotope data at a global scale. *Elements: An International Magazine of Mineralogy, Geochemistry, and Petrology* 14(6), 436–437.
- Breier, J. A., M. V. Jakuba, M. A. Saito, G. J. Dick, S. L. Grim, E. W. Chan, M. R. McIlvin, D. M. Moran, B. A. Alanis, A. E. Allen, C. L. Dupont, and R. Johnson (2020, nov). Revealing ocean-scale biochemical structure with a deep-diving vertical profiling autonomous vehicle. *Sci. Robot.* 5(48), eabc7104.
- Carradec, Q., E. Pelletier, C. Da Silva, A. Alberti, Y. Seeleuthner, R. Blanc-Mathieu, G. Lima-Mendez, F. Rocha, L. Tirichine, K. Labadie, A. Kirilovsky, A. Bertrand, S. Engelen, M.-A. Madoui, R. Méheust, J. Poulain, S. Romac, D. J. Richter, G. Yoshikawa, C. Dimier, S. Kandels-Lewis, M. Picheral, S. Searson, S. G. Acinas, E. Boss, M. Follows, G. Gorsky, N. Grimsley, L. Karp-Boss, U. Krzic, S. Pesant, E. G. Reynaud, C. Sardet, M. Sieracki, S. Speich, L. Stemmann, D. Velayoudon, J. Weissenbach, O. Jaillon, J.-M. Aury, E. Karsenti, M. B. Sullivan, S. Sunagawa, P. Bork, F. Not, P. Hingamp, J. Raes, L. Guidi, H. Ogata, C. de Vargas, D. Iudicone, C. Bowler, and P. Wincker (2018). A global ocean atlas of eukaryotic genes. *Nature Communications* 9(1), 373.

- 343 Claustre, H., K. S. Johnson, and Y. Takeshita (2020). Observing the global ocean with biogeochemical-argo.
 344 *Annual review of marine science* 12, 23–48.
- 345 Coleman, M. L. and S. W. Chisholm (2010, oct). Ecosystem-specific selection pressures revealed through
 346 comparative population genomics. *107*(43), 18634–18639.
- 347 de Vargas, C., S. Audic, N. Henry, J. Decelle, F. Mahe, R. Logares, E. Lara, C. Berney, N. L. Bescot,
 348 I. Probert, M. Carmichael, J. Poulain, S. Romac, S. Colin, J.-M. Aury, L. Bittner, S. Chaffron,
 349 M. Dunthorn, S. Engelen, O. Flegontova, L. Guidi, A. Horak, O. Jaillon, G. Lima-Mendez, J. Luke,
 350 S. Malviya, R. Morard, M. Mullet, E. Scalco, R. Siano, F. Vincent, A. Zingone, C. Dimier, M. Picheral,
 351 S. Searson, S. Kandels-Lewis, S. G. Acinas, P. Bork, C. Bowler, G. Gorsky, N. Grimsley, P. Hingamp,
 352 D. Iudicone, F. Not, H. Ogata, S. Pesant, J. Raes, M. E. Sieracki, S. Speich, L. Stemmann, S. Sunagawa,
 353 J. Weissenbach, P. Wincker, E. Karsenti, E. Boss, M. Follows, L. Karp-Boss, U. Krzic, E. G. Reynaud,
 354 C. Sardet, M. B. Sullivan, and D. V. and (2015, may). Eukaryotic plankton diversity in the sunlit ocean.
 355 *Science* 348(6237), 1261605–1261605.
- 356 Fasham, M. J., B. M. Balino, M. C. Bowles, R. Anderson, D. Archer, U. Bathmann, P. Boyd, K. Buesseler,
 357 P. Burkil, A. Bychkov, et al. (2001). A new vision of ocean biogeochemistry after a decade of the joint
 358 global ocean flux study (jgofs). *AMBIO: A Journal of the Human Environment* 2001(Sp. No. 10), 4–31.
- 359 Feely, R. A., C. L. Sabine, K. Lee, W. Berelson, J. Kleypas, V. J. Fabry, and F. J. Millero (2004). Impact of
 360 anthropogenic co₂ on the caco₃ system in the oceans. *Science* 305(5682), 362–366.
- 361 Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski (1998). Primary production of the
 362 biosphere: integrating terrestrial and oceanic components. *science* 281(5374), 237–240.
- 363 Finkel, Z. V., J. Beardall, K. J. Flynn, A. Quigg, T. A. V. Rees, and J. A. Raven (2009, oct). Phytoplankton
 364 in a changing world: cell size and elemental stoichiometry. *Journal of Plankton Research* 32(1), 119–137.
- 365 Garcia, C. A., S. E. Baer, N. S. Garcia, S. Rauschenberg, B. S. Twining, M. W. Lomas, and A. C. Martiny
 366 (2018). Nutrient supply controls particulate elemental concentrations and ratios in the low latitude
 367 eastern indian ocean. *Nature communications* 9(1), 1–10.
- 368 Garcia, C. A., G. I. Hagstrom, A. A. Larkin, L. J. Ustick, S. A. Levin, M. W. Lomas, and A. C. Martiny
 369 (2020). Linking regional shifts in microbial genome adaptation with surface ocean biogeochemistry.
 370 *Philosophical Transactions of the Royal Society B* 375(1798), 20190254.
- 371 Gilbert, J. A. and C. L. Dupont (2011, jan). Microbial metagenomics: Beyond the genome. *Annu. Rev.*
 372 *Mar. Sci.* 3(1), 347–371.
- 373 Gruber, N., D. Clement, B. R. Carter, R. A. Feely, S. Van Heuven, M. Hoppema, M. Ishii, R. M. Key,
 374 A. Kozyr, S. K. Lauvset, et al. (2019). The oceanic sink for anthropogenic co₂ from 1994 to 2007.
 375 *Science* 363(6432), 1193–1199.
- 376 Howe, B. M., J. Miksis-Olds, E. Rehm, H. Sagen, P. F. Worcester, and G. Haralabus (2019). Observing the
 377 oceans acoustically. *Frontiers in Marine Science* 6, 426.
- 378 Jarman, S. N., O. Berry, and M. Bunce (2018, jul). The value of environmental DNA biobanking for
 379 long-term biomonitoring. *Nat Ecol Evol* 2(8), 1192–1193.
- 380 Karl, D. M. and M. J. Church (2014, aug). Microbial oceanography and the hawaii ocean time-series
 381 programme. *Nat Rev Microbiol* 12(10), 699–713.
- 382 Larkin, A. A., C. A. Garcia, N. Garcia, M. L. Brock, J. A. Lee, L. J. Ustick, L. Barbero, B. R. Carter,
 383 R. E. Sonnerup, L. D. Talley, et al. (2021). High spatial resolution global ocean metagenomes from
 384 bio-go-ship repeat hydrography transects. *Scientific Data* 8(1), 1–6.
- 385 Lee, J. A., C. A. Garcia, A. A. Larkin, B. R. Carter, and A. C. Martiny (2021, may). Linking a latitudinal
 386 gradient in ocean hydrography and elemental stoichiometry in the eastern pacific ocean. 35(5).

- 387 Levy, S. E. and R. M. Myers (2016, aug). Advancements in next-generation sequencing. *Annu. Rev. Genom.*
388 *Hum. Genet.* 17(1), 95–115.
- 389 Lombard, F., E. Boss, A. M. Waite, J. Uitz, L. Stemann, H. M. Sosik, J. Schulz, J. B. Romagnan,
390 M. Picheral, J. Pearlman, M. D. Ohman, B. Niehoff, K. O. Möller, P. Miloslavich, A. Lara-Lopez,
391 R. M. Kudela, R. M. Lopes, L. Karp-Boss, R. Kiko, J. S. Jaffe, M. H. Iversen, J. O. Irisson, H. Hauss,
392 L. Guidi, G. Gorsky, S. L. C. Giering, P. Gaube, S. Gallager, G. Dubelaar, R. K. Cowen, F. Carlotti,
393 C. Briseño-Avena, L. Berline, K. J. Benoit-Bird, N. J. Bax, S. D. Batten, S. D. Ayata, and W. Appeltans
394 (2019). Globally consistent quantitative observations of planktonic ecosystems. *Frontiers in Marine*
395 *Science*.
- 396 Marchetti, A., D. M. Schruth, C. A. Durkin, M. S. Parker, R. B. Kodner, C. T. Berthiaume, R. Morales,
397 A. E. Allen, and V. E. Armbrust (2012, 2). Comparative metatranscriptomics identifies molecular bases
398 for the physiological responses of phytoplankton to varying iron availability. *Proceedings of the National*
399 *Academy of Sciences* 109(6), E317–E325.
- 400 Martiny, A. C., M. W. Lomas, W. Fu, P. W. Boyd, Y. I. L. Chen, G. A. Cutter, M. J. Ellwood, K. Furuya,
401 F. Hashihama, J. Kanda, D. M. Karl, T. Kodama, Q. P. Li, J. Ma, T. Moutin, E. M. S. Woodward, and
402 J. K. Moore (2019). Biogeochemical controls of surface ocean phosphate. *Science Advances*.
- 403 McClain, C. R. (2009). A decade of satellite ocean color observations. *Annual Review of Marine Science* 1,
404 19–42.
- 405 Michaels, A. F. and A. H. Knap (1996). Overview of the us jgofs bermuda atlantic time-series study and the
406 hydrostation s program. *Deep Sea Research Part II: Topical Studies in Oceanography* 43(2-3), 157–198.
- 407 Mieszkowska, N., H. Sugden, L. B. Firth, and S. J. Hawkins (2014, sep). The role of sustained observations
408 in tracking impacts of environmental change on marine biodiversity and ecosystems. 372(2025),
409 20130339.
- 410 Miloslavich, P., N. J. Bax, S. E. Simmons, E. Klein, W. Appeltans, O. Aburto-Oropeza, M. Andersen Garcia,
411 S. D. Batten, L. Benedetti-Cecchi, D. M. Checkley, S. Chiba, J. E. Duffy, D. C. Dunn, A. Fischer,
412 J. Gunn, R. Kudela, F. Marsac, F. E. Muller-Karger, D. Obura, and Y. J. Shin (2018). Essential ocean
413 variables for global sustained observations of biodiversity and ecosystem changes. *Global Change*
414 *Biology*.
- 415 Moore, C. M., M. M. Mills, K. R. Arrigo, I. Berman-Frank, L. Bopp, P. W. Boyd, E. D. Galbraith, R. J.
416 Geider, C. Guieu, S. L. Jaccard, T. D. Jickells, J. L. Roche, T. M. Lenton, N. M. Mahowald, E. Marañón,
417 I. Marinov, J. K. Moore, T. Nakatsuka, A. Oschlies, M. A. Saito, T. F. Thingstad, A. Tsuda, and O. Ulloa
418 (2013, mar). Processes and patterns of oceanic nutrient limitation. 6(9), 701–710.
- 419 Moore, W. S. (1984). Review of the geosecs project. *Nuclear Instruments and Methods in Physics*
420 *Research* 223(2-3), 459–465.
- 421 Moreno, A. R., C. A. Garcia, A. A. Larkin, J. A. Lee, W.-L. Wang, J. K. Moore, F. W. Primeau, and A. C.
422 Martiny (2020). Latitudinal gradient in the respiration quotient and the implications for ocean oxygen
423 availability. *Proceedings of the National Academy of Sciences* 117(37), 22866–22872.
- 424 Muller-Karger, F. E., Y. M. Astor, C. R. Benitez-Nelson, K. N. Buck, K. A. Fanning, L. Lorenzoni,
425 E. Montes, D. T. Rueda-Roa, M. I. Scranton, E. Tappa, et al. (2019). The scientific legacy of the cariacco
426 ocean time-series program. *Annual review of marine science* 11, 413–437.
- 427 Neeley, A., S. Beaulieu, C. Proctor, I. Cetinić, J. Futrelle, I. Ramos-Santos, H. Sosik, E. Devred, L. Karp-
428 Boss, M. Picheral, N. Poulton, C. Roesler, and A. Shepherd (2021). Standards and practices for reporting
429 plankton and other particle observations from images (in press). XX.
- 430 Organelli, E., C. Nuccio, L. Lazzara, J. Uitz, A. Bricaud, and L. Massi (2017, may). On the discrimination
431 of multiple phytoplankton groups from light absorption spectra of assemblages with mixed taxonomic

- composition and variable light conditions. *56*(14), 3952.
- Ottesen, E. A., C. R. Young, J. M. Eppley, J. P. Ryan, F. P. Chavez, C. A. Scholin, and E. F. DeLong (2013, jan). Pattern and synchrony of gene expression among sympatric marine microbial populations. *Proceedings of the National Academy of Sciences* *110*(6), E488–E497.
- Penna, A. D. and P. Gaube (2019, jul). Overview of (sub)mesoscale ocean dynamics for the NAAMES field program. *Front. Mar. Sci.* *6*.
- Purkey, S. G. and G. C. Johnson (2010). Antarctic bottom water warming between the 1990s and the 2000s: Contributions to global heat and sea level rise budgets. *J. Clim* *23*, 6336–6351.
- Raes, E. J., L. Bodrossy, J. Van De Kamp, A. Bissett, M. Ostrowski, M. V. Brown, S. L. Sow, B. Sloyan, and A. M. Waite (2018). Oceanographic boundaries constrain microbial diversity gradients in the south pacific ocean. *Proceedings of the National Academy of Sciences* *115*(35), E8266–E8275.
- Raes, E. J., K. Karsh, S. L. Sow, M. Ostrowski, M. V. Brown, J. van de Kamp, R. M. Franco-Santos, L. Bodrossy, and A. M. Waite (2021). Metabolic pathways inferred from a bacterial marker gene illuminate ecological changes across south pacific frontal boundaries. *Nature communications* *12*(1), 1–12.
- Robins, D. and J. Aiken (1996). The atlantic meridional transect: An oceanographic research programme to investigate physical, chemical, biological and optical variables of the atlantic ocean. *Underwater Technology* *21*(4), 8–14.
- Roemmich, D., J. Gilson, R. Davies, P. Sutton, S. Wijffels, and S. Riser (2007). Decadal spin up of the deep subtropical gyre in the south pacific. *J. Phys. Oceanogr* *37*, 162–173.
- Rusch, D. B., A. L. Halpern, G. Sutton, K. B. Heidelberg, S. Williamson, S. Yooseph, D. Wu, J. A. Eisen, J. M. Hoffman, K. Remington, K. Beeson, B. Tran, H. Smith, H. Baden-Tillson, C. Stewart, J. Thorpe, J. Freeman, C. Andrews-Pfannkoch, J. E. Venter, K. Li, S. Kravitz, J. F. Heidelberg, T. Utterback, Y. H. Rogers, L. I. Falcon, V. Souza, G. Bonilla-Rosso, L. E. Eguiarte, D. M. Karl, S. Sathyendranath, T. Platt, E. Bermingham, V. Gallardo, G. Tamayo-Castillo, M. R. Ferrari, R. L. Strausberg, K. Nealson, R. Friedman, M. Frazier, and J. C. Venter (2007). The sorcerer ii global ocean sampling expedition: Northwest atlantic through eastern tropical pacific. *PLoS Biology* *5*(3), e77. Journal article.
- Salazar, G., F. M. Cornejo-Castillo, V. Benítez-Barrios, E. Fraile-Nuez, X. A. Álvarez-Salgado, C. M. Duarte, J. M. Gasol, and S. G. Acinas (2015, aug). Global diversity and biogeography of deep-sea pelagic prokaryotes. *ISME J Journal* *10*(3), 596–608.
- Schmidtko, S., L. Stramma, and M. Visbeck (2017). Decline in global oceanic oxygen content during the past five decades. *Nature* *542*(7641), 335–339.
- Scholin, C., J. Birch, S. Jensen, R. M. III, E. Massion, D. Pargett, C. Preston, B. Roman, and W. U. III (2017, dec). The quest to develop ecogenomic sensors: A 25-year history of the environmental sample processor (ESP) as a case study. *Oceanog* *30*(4), 100–113.
- Siegel, D., M. J. Behrenfeld, S. Maritorena, C. R. McClain, D. Antoine, S. W. Bailey, P. S. Bontempi, E. S. Boss, H. M. Dierssen, S. C. Doney, et al. (2013). Regional to global assessments of phytoplankton dynamics from the seawifs mission. *Remote Sensing of Environment* *135*, 77–91.
- Siegel, D. A., K. O. Buesseler, M. J. Behrenfeld, C. R. Benitez-Nelson, E. Boss, M. A. Brzezinski, A. Burd, C. A. Carlson, E. A. D'Asaro, S. C. Doney, M. J. Perry, R. H. R. Stanley, and D. K. Steinberg (2016, mar). Prediction of the export and fate of global ocean net primary production: The EXPORTS science plan. *Front. Mar. Sci.* *3*.
- Sloyan, B. M., R. Wanninkhof, M. Kramp, G. C. Johnson, L. D. Talley, T. Tanhua, E. McDonagh, C. Cusack, E. O'Rourke, E. McGovern, K. Katsumata, S. Diggs, J. Hummon, M. Ishii, K. Azetsu-Scott, E. Boss, I. Ansorge, F. F. Perez, H. Mercier, M. J. M. Williams, L. Anderson, J. H. Lee, A. Murata, S. Kouketsu,

- 477 E. Jeansson, M. Hoppema, and E. Campos (2019, aug). The global ocean ship-based hydrographic
478 investigations program (GO-SHIP): A platform for integrated multidisciplinary ocean science. *Front.*
479 *Mar. Sci.* 6.
- 480 Suggett, D., C. Moore, A. Hickman, and R. Geider (2009, feb). Interpretation of fast repetition rate (FRR)
481 fluorescence: signatures of phytoplankton community structure versus physiological state. 376, 1–19.
- 482 Sunagawa, S., L. P. Coelho, S. Chaffron, J. R. Kulima, K. Labadie, G. Salazar, B. Djahanschiri, G. Zeller,
483 D. R. Mende, A. Alberti, F. M. Cornejo-Castillo, P. I. Costea, C. Cruaud, F. d'Ovidio, S. Engelen,
484 I. Ferrera, J. M. Gasol, L. Guidi, F. Hildebrand, F. Kokoszka, C. Lepoivre, G. Lima-Mendez, J. Poulain,
485 B. T. Poulos, M. Royo-Llonch, H. Sarmiento, S. Vieira-Silva, C. Dimier, M. Picheral, S. Searson,
486 S. Kandels-Lewis, C. Bowler, C. de Vargas, G. Gorsky, N. Grimsley, P. Hingamp, D. Iudicone, O. Jaillon,
487 F. Not, H. Ogata, S. Pesant, S. Speich, L. Stemann, M. B. Sullivan, J. Weissenbach, P. Wincker,
488 E. Karsenti, J. Raes, S. G. Acinas, P. Bork, E. Boss, C. Bowler, M. Follows, L. Karp-Boss, U. Krzic,
489 E. G. Reynaud, C. Sardet, M. Sieracki, and D. V. and (2015, may). Structure and function of the global
490 ocean microbiome. *Science* 348(6237), 1261359–1261359.
- 491 Suter, L., A. M. Polanowski, L. J. Clarke, J. A. Kitchener, and B. E. Deagle (2020). Capturing open
492 ocean biodiversity: Comparing environmental dna metabarcoding to the continuous plankton recorder.
493 *Molecular Ecology*.
- 494 Thomsen, P. F., J. Kielgast, L. L. Iversen, P. R. Møller, M. Rasmussen, and E. Willerslev (2012). Detection
495 of a diverse marine fish fauna using environmental dna from seawater samples. *PLoS one* 7(8), e41732.
- 496 Ustick, L. J., A. A. Larkin, C. A. Garcia, N. S. Garcia, M. L. Brock, J. A. Lee, N. A. Wiseman, J. K. Moore,
497 and A. C. Martiny (2021, apr). Metagenomic analysis reveals global-scale patterns of ocean nutrient
498 limitation. *Science* 372(6539), 287–291.
- 499 Vaillancourt, R. D. (2004, feb). Light backscattering properties of marine phytoplankton: relationships to
500 cell size, chemical composition and taxonomy. 26(2), 191–212.
- 501 Villar, E., T. Vannier, C. Vernet, M. Lescot, M. Cuenca, A. Alexandre, P. Bachelier, T. Rosnet, E. Pelletier,
502 S. Sunagawa, and P. Hingamp (2018, may). The ocean gene atlas: exploring the biogeography of plankton
503 genes online. *Nucleic Acids Research* 46(W1), W289–W295.
- 504 Waugh, D. W., F. Primeau, T. DeVries, and M. Holzer (2013). Recent changes in the ventilation of the
505 southern oceans. *science* 339(6119), 568–570.
- 506 Wilkinson, M. D., M. Dumontier, I. J. Aalbersberg, G. Appleton, M. Axton, A. Baak, N. Blomberg,
507 J.-W. Boiten, L. B. da Silva Santos, P. E. Bourne, J. Bouwman, A. J. Brookes, T. Clark, M. Crosas,
508 I. Dillo, O. Dumon, S. Edmunds, C. T. Evelo, R. Finkers, A. Gonzalez-Beltran, A. J. Gray, P. Groth,
509 C. Goble, J. S. Grethe, J. Heringa, P. A. 't Hoen, R. Hooft, T. Kuhn, R. Kok, J. Kok, S. J. Lusher, M. E.
510 Martone, A. Mons, A. L. Packer, B. Persson, P. Rocca-Serra, M. Roos, R. van Schaik, S.-A. Sansone,
511 E. Schultes, T. Sengstag, T. Slater, G. Strawn, M. A. Swertz, M. Thompson, J. van der Lei, E. van
512 Mulligen, J. Velterop, A. Waagmeester, P. Wittenburg, K. Wolstencroft, J. Zhao, and B. Mons (2016,
513 mar). The FAIR guiding principles for scientific data management and stewardship. *Sci Data* 3(1).
- 514 Woods, J. D. (1985). The world ocean circulation experiment. *Nature* 314(6011), 501–511.

6 FIGURES

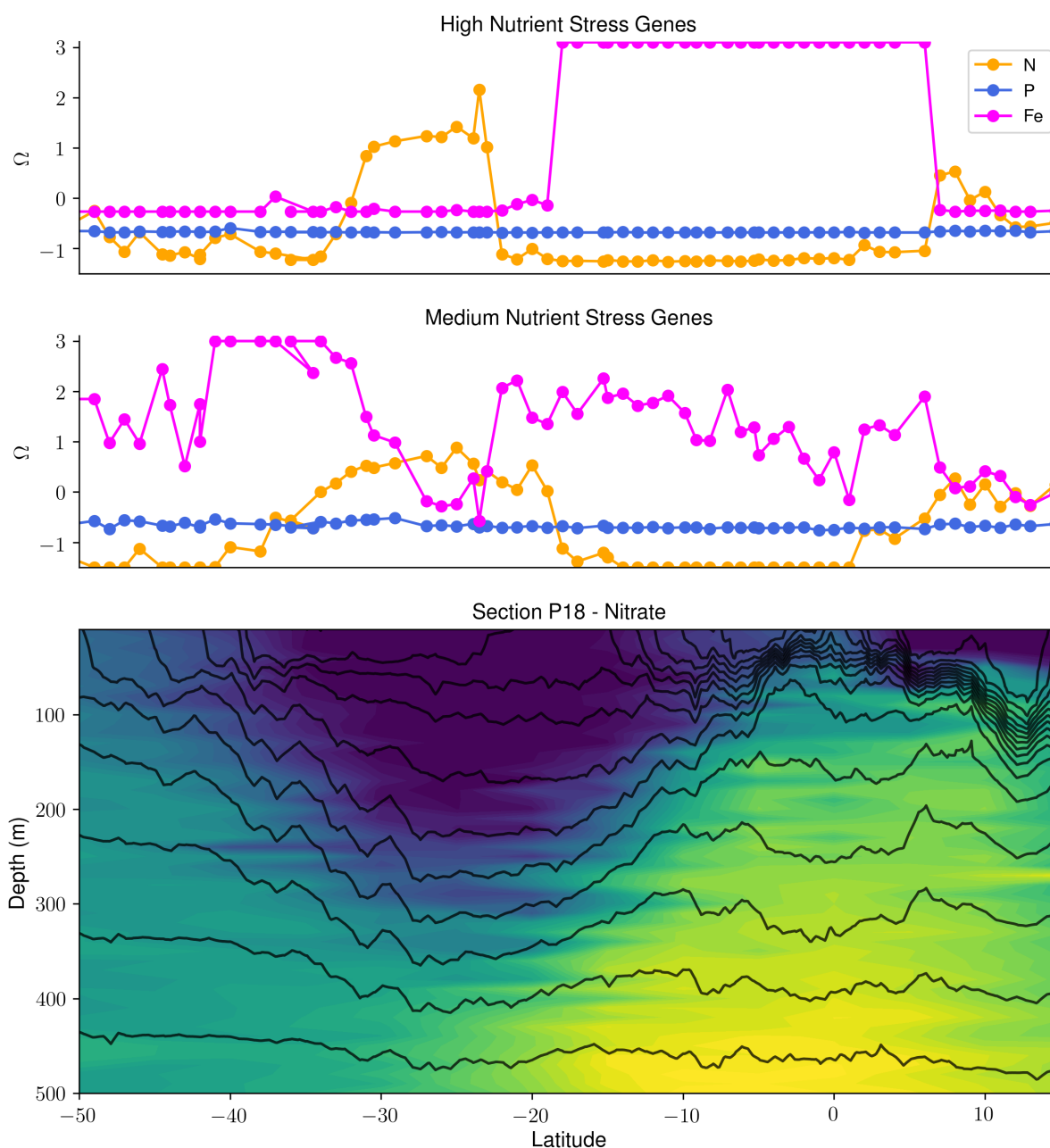


Figure 1. Synergy of biological, hydrographic and chemical data collected during the GO-SHIP P18 repeat section uncovers patterns and drivers of nutrient stress in *Prochlorococcus*. The upper two panels show the high and medium stress composite metrics (Ω) for N, Fe and P (taken from Ustick et al., 2021). The bottom panel shows the nitrate distribution in the upper 500m along the P18 transect with density contours (black contour lines). There is a clear relationship between the severity of N stress in *Prochlorococcus* and the depth of the nitracline. The P18 section is highlighted in red in Figure 2.

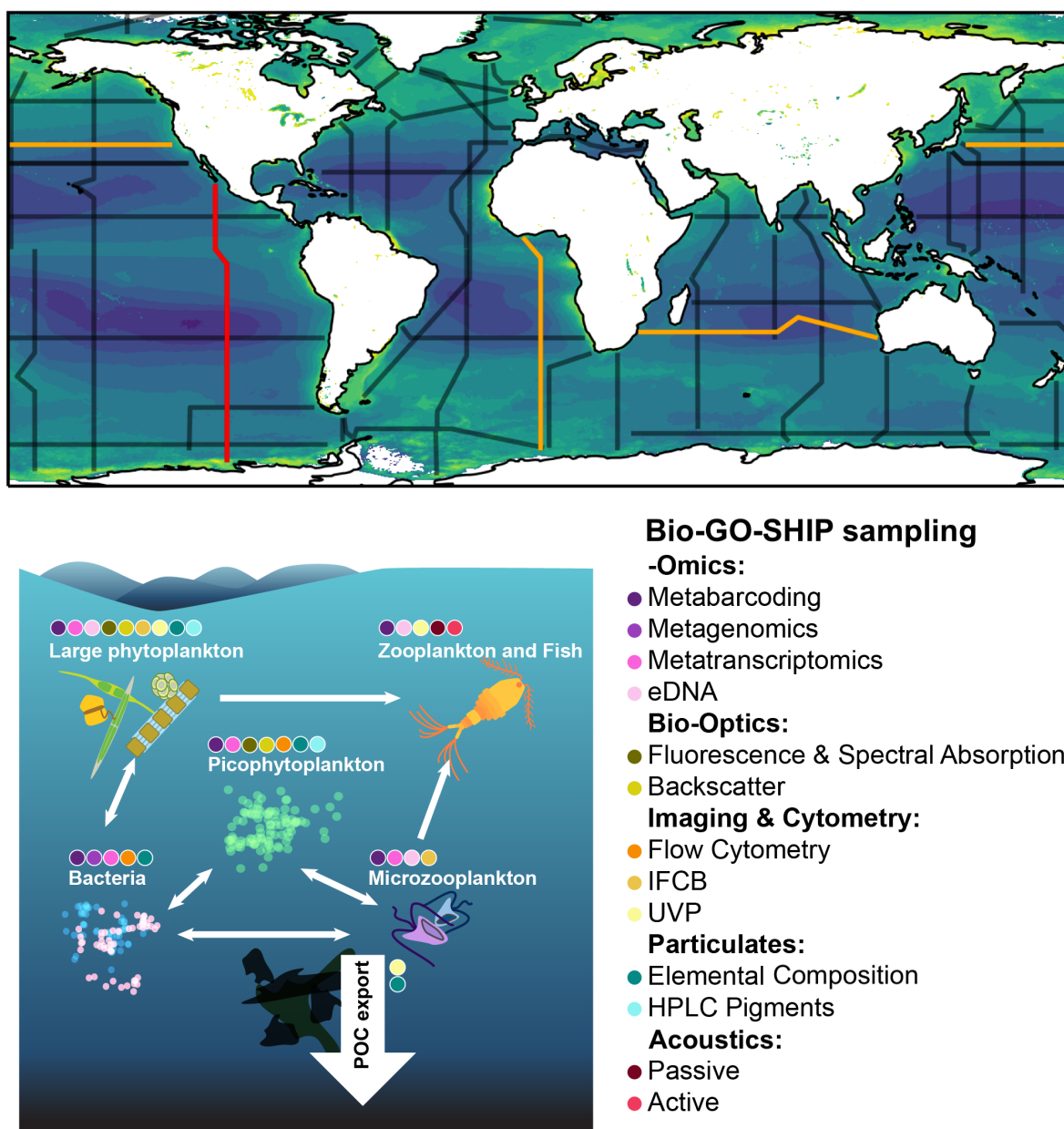


Figure 2. Biological sampling to be incorporated into GO-SHIP. The upper panel shows the GO-SHIP repeat sections overlain on global mean Chlorophyll obtained from MODIS. Section P18 from which the data in Figure 1 was collected is highlighted in red. Highlighted in orange are sections I05, P02 and A13.5, which will be the first sections fully sampled as part of the Bio-GO-SHIP program in 2021-2022. The lower panel summarizes the range of different measurement types that will be incorporated as part of the Bio-GO-SHIP program, and how they relate to biological and ecosystem EOVs that are targeted as part of the Bio-GO-SHIP program.