

Report to SFI on BIOS-SCOPE

March 2022



Bermuda Institute of Ocean Sciences



BIOS-SCOPE researchers collect *Sargassum* samples. Photo by Hilary Close

BIOS-SCOPE's **five-year renewal** continues its multi-institutional, cross-disciplinary research program to study microbial oceanography in the northwestern Sargasso Sea. BIOS-SCOPE leverages combined expertise in microbial oceanography/dissolved organic matter (DOM) biogeochemistry, marine microbiology and bioinformatics, marine chemistry, micro- and mesozooplankton ecology, viral ecology, and agent-based modeling to evaluate the microbial processes, structures, and functions and how their associated interactions with organic matter vary over a range of temporal and spatial scales in the open sea. BIOS-SCOPE continues to benefit from collaborations with the Bermuda Atlantic Time-series Study (BATS), Hydrostation 'S,' and MAGIC glider programs at BIOS. Here we report on the program's major activities, progress, and findings from Year 1 (Nov 1, 2020-Oct 2021) of the renewal.

While the ongoing COVID-19 pandemic impacted planned field and laboratory-based activities, investigators remained highly productive. The shutdown provided the team with a unique opportunity to organize and synthesize existing data into new manuscripts and data sets. After a delay in field operations, the **7th BIOS-SCOPE**

process cruise was successfully completed in August 2021, with **thirteen** scientists from **four** countries participating.

The annual BIOS-SCOPE in-person data workshop was not held this year due to COVID; however, the team transitioned to bi-weekly virtual zoom meetings to share data and discuss product synthesis. BIOS-SCOPE researchers gave **ten** presentations at international workshops and conferences, including the 2021 Aquatic Sciences Meeting, the 2021 Ocean Carbon and Biogeochemistry Meeting, and the 2021 Goldschmidt Meeting. A total of **sixteen** papers with full or partial support from SFI were published or were in peer-review during this funding period. **Two** master's thesis projects were conducted in collaboration with BIOS-SCOPE researchers.

It is with deepest gratitude that we provide the following report to the **Simons Foundation International, Ltd.** on major activities, progress, and findings from the 2020-2021 funding period. The Foundation's support in establishing the program and its additional commitments to further enhancing the program have made this progress possible.

BIOSCOPE Team Members

Focusing research on the ocean's smallest life forms

The BIOS-SCOPE renewal allowed for the expansion of research expertise to include PI groups focused on quantitative modeling (F. Hellweger; Technical University of Berlin), organic isotope geochemistry (H. Close; University of Miami), and phytoplankton diversity (A. Worden; GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany). These new research directions complement the existing combined expertise in microbial oceanography/dissolved organic matter (DOM) biogeochemistry (C. Carlson, University of California at Santa Barbara; R. Parsons, Bermuda Institute of Ocean Sciences), marine microbiology (S. Giovannoni, Oregon State University), marine chemistry (L. Kujawinski, Woods Hole Oceanographic Institution), protistan and mesozooplankton ecology (A. Maas & L. Blanco-Bercial, BIOS), and viral ecology/microbial bioinformatics (B. Temperton, University of Exeter).



Bill Curry
Program Leader

Curry is the President & CEO of BIOS and leads the multi-institutional BIOS-SCOPE program.



Craig Carlson
Program Director and
Co-Principal Investigator

Carlson is a Professor at the University of California Santa Barbara (UCSB) in the Department of Ecology, Evolution and Marine Biology and is a member of UCSB's Marine Science Institute. He is also a member of BIOS's Adjunct Faculty. As the Program Director of BIOS-SCOPE, Carlson oversees the overall science plan to ensure the research carried out is effective in its cross-disciplinary and integrative approach.

BIOS-SCOPE Team Members



Leocadio Blanco-Bercial, Investigator
Ruth Curry, Affiliated SFI Investigator
Hannah Gossner, Research Support
Ali Hochberg, Scientific Communications
Rod Johnson, Data Processing and Integration
Amy Maas, Investigator
Claire Medley, At-sea Support
Rachel Parsons, Investigator
Dom Smith, At-sea Support
Kevin Vergin, Visiting Scholar
Kevin Yongblah, Research Support



Stephen Giovannoni, Co-Principal Investigator
Chih-Ping Lee, Postdoctoral Fellow



Craig Carlson, Co-Principal Investigator
Chance English, Research Support
Elisa Halewood, Research Support
Shuting Liu, Postdoctoral Fellow
Keri Opalk, Research Support



Alexandra Worden, Visiting Scholar
Fabian Wittmers, Doctoral Student



Elizabeth Harvey, Visiting Scholar



Ben Temperton, Investigator
Holger Buchholz, Graduate Student
Michelle Michelsen, Research Support
Joanna Warwick-Dugdale, Doctoral Student



Hilary Close, Visiting Scholar
Shannon Doherty, Graduate Student
Lillian Henderson, Graduate Student



Elizabeth Kujawinski, Investigator
Krista Longnecker, Research Support
Brittany Widner, Postdoctoral Scholar
Erin McParland, Postdoctoral Fellow
Craig McLean, Graduate Student
Gretchen Swarr, Research Support



Ferdi Hellweger, Computational Scholar
Falk Eigemann, Postdoctoral Scholar
Jutta Hoffman, Graduate Student



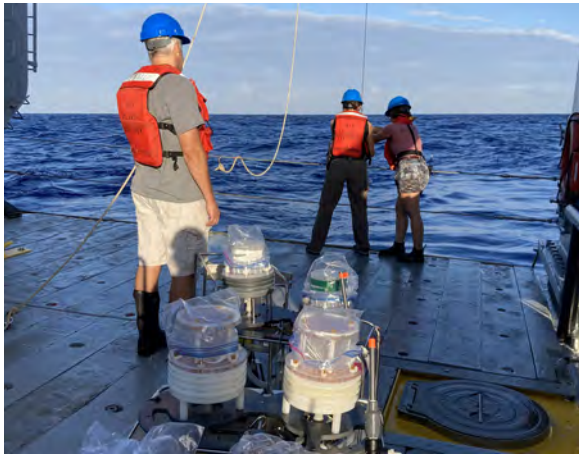
At-Sea Expeditions & Fieldwork

As previously mentioned, the COVID-19 pandemic impacted planned BIOS-SCOPE laboratory and fieldwork; however, all was not lost. Investigators used the pause in field activities to accomplish a significant amount of data organization and synthesis, resulting in the publication of several manuscripts. By the end of the funding period, fieldwork had resumed, supporting a variety of BIOS-SCOPE research foci with new data sets for future analyses.

Time-Series Cruises: BATS cruises were reinstated in July 2020 after a four-month hiatus due to COVID-19. As a result, monthly collection of BIOS-SCOPE variables, i.e., planktonic DNA, microbial biomass, and DOM composition over 1000 m, continued uninterrupted during the reporting period.

BIOS-SCOPE Process Cruise: After a long delay in field operations, the 7th BIOS-SCOPE process cruise was success-

fully completed in August 2021, with thirteen scientists from four countries participating. Round-the-clock water sampling and plankton tows were conducted to assess the temporal and vertical variability of organic and inorganic nutrients, vitamins, metabolites, microbial biomass and production, bacterial and viral DNA, and zooplankton biomass at depths over 500 m. In situ sequential filtration pumps collected particles during the day and night to allow for molecular and isotopic characterization of organic particles that spanned four biologically relevant size classes over nine depths. Numerous shipboard experiments were conducted to evaluate zooplankton and microbial respiration and organic matter transformation by bacterioplankton. In addition, the unusually high abundance of the macroalgal species *Sargassum* provided a unique opportunity for at-sea experiments to quantify how much DOM the algae releases and what types of microbial organisms consume it.



Left: Craig Carlson, BIOS-SCOPE Program Director and oceanographer at UCSB, readies a series of water samplers. Middle: Fabian Wittmers uses the CTD to sample water—and phytoplankton—from various depths. Right: Researchers collect Sargassum seaweed during the 7th BIOS-SCOPE process cruise.

Workshops, Synergies, Collaborations

Although the pandemic restricted our ability to hold an in-person data workshop in 2021, the BIOS-SCOPE team transitioned to bi-weekly virtual zoom meetings as a means to share data and discuss product synthesis. Since December 2020, these meeting formats alternated every two weeks (except during August) between *all-hands meetings* and *breakout discussions*. The all-hands meeting served as a platform for scientific presentations and project planning.

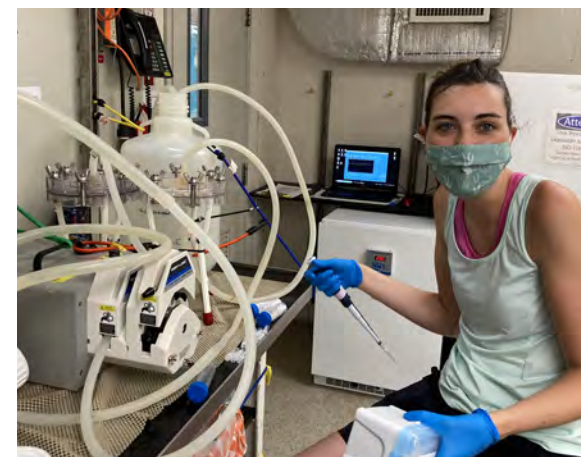
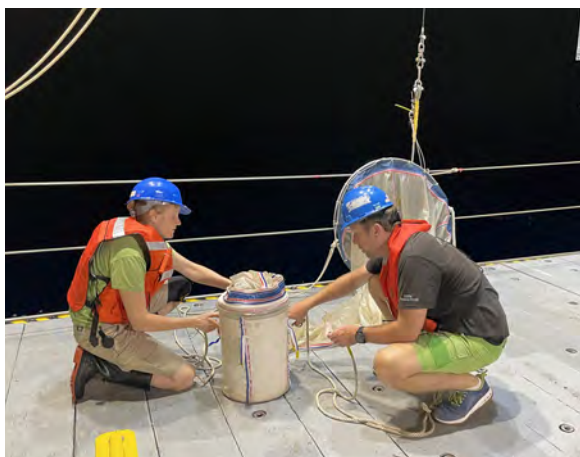


Research Progress

Photo by Fabian Wittmers

With funding renewed for another five years, the BIOS-SCOPE team is poised to continue to advance our understanding of the sources, sinks, and transformations of organic matter in the Sargasso Sea. In its second phase, BIOS-SCOPE researchers plan to explore links between the ocean's biological, geological, and chemical cycles (or biogeochemical cycles, such as nitrogen), the structure of the phytoplankton community, and how this affects the quality, quantity, and cycling of particulate and dissolved organic matter (DOM).

In addition, new technological approaches that involve the recovery of genetic material directly from the environment, called metagenomics, will be used to look at the ecology of marine viruses and how they impact the microbial community and biogeochemical cycles. Researchers will continue to explore the fate of DOM and how it is transformed by zooplankton and other microbial communities to learn more about how these transformation processes are driven and what they can tell us about the water column.



Left: Amy Maas, BIOS Associate Scientist and BIOS-SCOPE Investigator, removes zooplankton from a net after it was towed down to 330 feet (100 meters). Middle: BIOS-SCOPE researchers deploy a high-volume water sampling pump. Right: Michelle Michelsen, Research Support from the University of Exeter, filters large volumes of seawater for metagenomics sampling.

Metabolites and DOM Chemistry

DOM consists of materials, including carbon compounds called metabolites, that result from the biological production and decomposition of organic matter (algae, microbes and animals) in the ocean. In the Sargasso Sea, where nutrients are limited due to high temperature, low mixing, weak currents, and calm winds, DOM is tightly recycled throughout the ecosystem. Linking DOM dynamics with microbial activity is key to understanding factors controlling carbon fluxes across the food web. In addition, assessing this linkage over the course of a day provides insights into the rapid turnover of labile (easily broken-down) DOM components, such as total dissolved amino acids (TDAA) and other organic metabolites.

Daily patterns of DOM and microbial dynamics: Carlson's group analyzed biogeochemical and microbial data over two summers to assess the fate and transformation of DOM by microbes on daily time scales. Results show that rapid microbial uptake occurs at night, corresponding with maximum bacterial production. DOM shifts from a "fresher" daytime signature to a more degraded signature at night, and the relative abundance of certain bacterial lineages also corresponds to daily patterns of light.

Metabolite method improvement: Metabolites are actively produced and consumed by plankton; however, some are too small or too polar to be captured by standard methods. A new technique described by the Kujawinski Group (Widener et al., 2021) expands the metabolites that can be detected with standard methods by 50%, but with much smaller volume requirements.



Ella Cedarholm, marine technician on the *Atlantic Explorerer*, directs the deployment of the MOCNESS.

Another method that targets small acids at the heart of carbon metabolism in all microbes is currently under development. The Kujawinski Group has also generated the first marine time-series of thousands of dissolved metabolites. Metabolites and the microbial communities that interact with them are stratified by depth and exhibit unique temporal signatures on either hourly or monthly timescales.

Plankton & Systems Ecology

Phytoplankton constitute a significant source of DOM and phytoplankton species can affect both the quality of DOM released and the heterotrophic community that responds to it. In addition,

migratory zooplankton, which transport organic compounds created at the surface to depth on a daily basis, may act as important sources of nutrients for deep-dwelling microbial communities. BIOS-SCOPE researchers continue to investigate specific mechanisms of DOM incorporation, oxidation, and transformation by zooplankton and distinct microbial communities at BATS.

Phytoplankton derived DOM and Stable Isotopic Probing (SIP) experiment: The Carlson Group conducted a series of stable isotope probing (SIP) experiments to assess the bacterioplankton response to DOM derived from three phytoplankton species: diatom *Thalassiosira weissflogii*, and the cyanobacteria *Synechococcus* and *Prochlorococcus*. Results showed the

bacterioplankton grew slower after being exposed to DOM with altered quality, and were incorporated by a diverse and variable group of fast-growing and slow-growing bacterioplankton.

Image analyses of Zooplankton: The Blanco-Bercial and Maas Laboratories advanced the semiautomated application of image and size-based measurements of zooplankton for the biogeochemical assessments of carbon flux. They are working collaboratively to develop novel methods that directly quantify the impact of zooplankton on midwater carbon and microbial ecosystems.

Marine Microbiology & Microbial Physiology

Isotopic measurements as particle biomarkers: The Close Group introduced two new tools for understanding carbon sources and cycling in the water column. Through these, researchers can account for the proportion of the three particulate components that contribute to vertical carbon flux versus microbial recycling: phytoplankton-derived materials, zooplankton-transformed organic matter, and microbial-transformed organic matter. The second tool is a chemical marker in fecal pellets that indicates the relative efficiency of zooplankton digestion. New data suggest that zooplankton collected at the BIOS-SCOPE site in the low-productivity summer period had high digestive efficiency. These results are consistent with existing carbon flux efficiency models and were recently published in Doherty et al., 2021.

Linking isotopic signature with microbial activity: Lillian Henderson, a graduate student in the Close Group, found a specific car-

bon isotopic signature that is a product of low-light photosynthetic organisms inhabiting depths within the sunlit photic zone. These are among the first field data indicating that sunlight intensity is a significant control on the isotopic signature of organic carbon. The Close Group aims to separate and identify the components that comprise the mixture of degraded and freshly-produced material which serve as substrates for microbial activity. Upcoming work with the Carlson Group will relate the available substrates to the specific taxa of microbes using them.

Microbial activity in response to oxygen: By analyzing the metadata of ocean systems, the Giovannoni Group made a new report on a fundamental property of marine enzymes that may be important to understanding oxygen minimum zones. Results showed that enzymes that degrade organic matter are 20 times less sensitive to oxygen than the enzymes cells use to respire across the tree of life. They predict this impacts the degradation rates of different forms of organic matter during oxygen declines (Giovannoni et al., 2021).

Application of the FluxNet mechanistic microbial ecosystem model: The FluxNet (Mayerhofer et al., 2021) application to the Helgoland time-series enabled, for the first time, the prediction of quantitative carbon fluxes between numerous phytoplankton and bacterial species during a phytoplankton bloom. It confirmed a strong correlation between the abundance of bacteria taxa and carbon flux during blooms. As expected, copiotrophs were relatively more important than oligotrophs in terms of carbon fluxes; however, oligotrophs, like SAR11, were unexpectedly high carbon processors for weeks into blooms due to their higher biomass.



2021 BIOS-SCOPE at-sea expedition team onboard the research vessel *Atlantic Explorer*. Photo by Noah Germolus.

Marine Viruses & Viral Ecology

Streamlining of SAR92 marine bacteria: While studying the SAR92 marine bacteria, the Giovannoni Group encountered a clear example of an evolutionary shift from a normal to a minimized (streamlined) cell type, in which the cells divide with minimal resources (nitrogen and phosphorus). These new data show no loss in the genes involved in the repair of DNA mutations, which runs contrary to long-held ideas in cell biology regarding the “streamlining” process. The streamlined versions of SAR92 are important organisms in the surface ocean at BATS.

Bacteriophages at BATS: In their analysis of samples collected at BATS, the Temperton Group showed that bacteriophages—viruses that infect and replicate within bacteria—predicted to infect SAR11 were absent from the 50 most abundant viral populations (Zablocki, et al., 2021). This finding indicates that, despite high global abundance,

phages infecting SAR11 are low in abundance in the Sargasso Sea and are likely secondary to other processes in shaping SAR11 populations (Bucholtz, et al., 2021a). In addition to viruses infecting bacteria, the Temperton Group isolated a phage of methylotroph OM43 from BATS, despite the absence of a suitable host in that environment. Further analysis of the genome of this phage provided strong evidence of host-switching between SAR11 and OM43 in a recent ancestor.

Discovering novel algae lineages and viruses: Prasinophytes are a group of unicellular green algae that were often considered unimportant in the open ocean due to sampling bias that led to missed dynamics and associated productivity. Using BIOS-SCOPE data, the Worden Group discovered an uncultured lineage of prasinophytes with relatively high abundance at the BATS site (Eckmann, et al. in prep). In addition, the discovery of three novel viruses that infect the prasinophyte *Bathycoccus* was also reported from the BATS site (Bachy, et al., 2021).



Photo by Hilary Close

Synergies with Simons Marine Collaborations

The research efforts of the BIOS-SCOPE program are both complementary and synergistic with the SCOPE program at Station ALOHA. The Carlson and Van Mooy Labs continue to collaborate on a study that uses an automated oxygen incubation system (AutoBOD) to resolve bacterial respiration at BATS. A collaboration with the Temperton, Levine lab (PriME Project), and Thrash lab (both at USC) is ongoing to determine if dormancy acts as a means of defense against viruses, reducing active infections. Carlson was invited to present results from BIOS-SCOPE to the UH's oceanography departmental seminar in October 2021.

General Audience Publications

In an effort to share the importance of BIOS-SCOPE with the general public, two articles were published during the funding period in BIOS's online newsletter Currents:

- "BIOS-SCOPE Funding Renewed," November 2020, www.bios.edu/currents/bios-scope-funding-renewed/
- "The Synergies of Sargassum Seaweed," August 2021, www.bios.edu/currents/the-synergies-of-sargassum-seaweed

Awards, Honors, and Recognitions

- Kujawinski is the director of the new, NSF-funded, Science and Technology Center: Center for the Chemical Currencies of a Microbial Planet
- Maas selected as Associated Editor for AGU's journal Global Biogeochemical Cycles
- McParland was named a 2020 Simons Foundation Postdoctoral Fellowship in Marine Microbial Ecology
- Worden was named a Fellow of the Max Planck Institute for Evolutionary Biology
- Worden was named a Harvard Radcliffe Institute for Advanced Studies Fellow

Publications

Peer Reviewed publications that were partially or fully supported by SFI in 2020-2021 reporting period.

- Bachy, C. & Yung, C-M., D.M. Needham, C. Gazitua, S. Roux, A.J. Limardo, C.J. Choi, M.B. Sullivan, A.Z. Worden (2021). Viruses infecting a warm water picoeukaryote shed light on spatial co-occurrence dynamics of marine viruses and their hosts. *The ISME Journal*. doi.org/10.1038/s41396-021-00989-9.
- Buchholz, H.H., Michelsen, M.L., Bolaños, L.M. et al. Efficient dilution-to-extinction isolation of novel virus-host model systems for fastidious heterotrophic bacteria. *ISME J* 15, 1585–1598 (2021). <https://doi.org/10.1038/s41396-020-00872-z>
- Buchholz, H. H., L. M. Bolaños, A. G. Bell, M. L. Michelsen, M. J. Allen and B. Temperton (2021). Genomic evidence for inter-class host transition between abundant streamlined heterotrophs by a novel and ubiquitous marine Methylophage. bioRxiv: 2021.2008.2024.457595.10.1101/2021.08.24.457595
- Buchholz HH, Michelsen M, Parsons RJ, Bates NR, Temperton B. 2021b. Draft genome sequences of pelagimyophage Mosig EXVC030M and pelagipodophage Lederberg EXVC029P, isolated from Devil’s Hole, Bermuda. *Microbiol Resour Announc* 10: e01325-20. <https://doi.org/10.1128/MRA.01325-20>.
- Cox, D. A., Parsons, R. J., Van Mooy, B. A. S. and Valentine, D. L. (Submitted). “Methylphosphonate is utilized by macroalgal holobionts in low nutrient environments”. *Geophysical Research Letters*.
- Doherty, S.C., A.E. Maas, D.K. Steinberg, B.N. Popp, H.G. Close (2021) Distinguishing fecal pellets as a component of the biological pump using compound-specific isotope analysis of amino acids. *Limnology and Oceanography*, 66, 2827-2841.
- Giovannoni S, Chan F, Davis E, II, Deutsch C, Wolf S. 2021. Biochemical barriers on the path to ocean anoxia? 12:e01332-21. <https://doi.org/10.1128/mBio.01332-21>.
- Johnson, W. M., M. C. Kido Soule, K. Longnecker, M. P. Bhatia, S. J. Hallam, M. W. Lomas and E. B. Kujawinski (submitted March 2021, in revision as of August 2021). Insights into the controls on metabolite distributions along a latitudinal transect of the western Atlantic Ocean. *Limnology and Oceanography*. DOI: 10.1101/2021.03.09.434501
- Lee, C.P. , L.P. Collart, K. H. Halsey and S. J. Giovannoni. Quantitative seawater arsenic speciation by proton-transfer-reaction mass spectrometry. In Review.
- Liu, S., K. Longnecker, E.B. Kujawinski, K. Vergin, L.M. Bolaños, S. Giovannoni, R. Parsons, K. Opalk, E. Halewood, D.A. Hansell, R. Johnson, R. Curry, C.A. Carlson. Linkage between dissolved organic matter export, dissolved metabolites and associated microbial community structure in the northwestern Sargasso Sea. *Frontiers in Marine Science*. (Submitted).

Publications continued

- Mayerhofer, M.M., Eigemann, F., Lackner, C. et al. Dynamic carbon flux network of a diverse marine microbial community. *ISME COMMUN.* 1, 50 (2021). <https://doi.org/10.1038/s43705-021-00055-7>
- Moore, E.R., A. J. Weaver, E.W. Davis, S. J. Giovannoni, and K. H. Halsey. Metabolism of key atmospheric volatile organic compounds by the marine heterotrophic bacterium *Pelagibacter HTCC1062* (SAR11). *Environ. Microbiol.* In Review
- Noell SE, Barrell GE, Suffridge C, Morr e, J, Gable KP, Graff JR, VerWey BJ, Hellweger FL, Giovannoni SJ. 2021. SAR11 cells rely on enzyme multifunctionality to metabolize a range of polyamine compounds. *mBio* 12:e01091-21. <https://doi.org/10.1128/mBio.01091-21>.
- Noell, S.E., E.W. Davis II, F.L. Hellweger, and S.J. Giovannoni. Differences in regulatory strategies in marine oligotrophs and copiotrophs reflect differences in motility. In Review
- Widner, B., M. C. Kido Soule, F. Ferrer-Gonz lez, M. A. Moran and E. B. Kujawinski (2021). Quantification of amine- and alcohol-containing metabolites in saline samples using pre-extraction benzoyl chloride derivatization and ultra-high performance liquid chromatography tandem mass spectrometry (UHPLC MS/MS). *Analytical Chemistry* 93: 4809-4817. DOI: 10.1021/acs.analchem.0c03769.
- Zablocki O, Michelsen M, Burris M, Solonenko N, Warwick-Dugdale J, Ghosh R, Pett-Ridge J, Sullivan MB, Temperton B. 2021. VirION2: a short- and long-read sequencing and informatics workflow to study the genomic diversity of viruses in nature. *PeerJ* 9:e11088 <https://doi.org/10.7717/peerj.11088>



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