Bermuda Institute of Ocean Sciences

Report to SFI on
BIOS-SCOPE

May 2023

The BIOS-SCOPE program, now in the **third year of a five-year renewal**, is a multi-institutional oceanographic research program aimed at evaluating the microbial and zooplankton processes, structures, and functions in the context of biogeochemical patterns of the northwestern Sargasso Sea. The program uses a collaborative, cross-disciplinary approach and leverages a broad suite of oceanographic, genomic, chemical, and ecological approaches in its investigations.

The international team combines expertise in microbial oceanography/dissolved organic matter (DOM) biogeochemistry, marine microbiology, marine chemistry, organic isotope geochemistry, phytoplankton biodiversity, viral ecology/microbial bioinformatics, and quantitative modeling. This project continues to benefit from its collaboration with the Bermuda Atlantic Time-series Study (BATS) and Hydrostation 'S' programs, as well as the Mid-Atlantic Glider Initiative and Collaboration (MAGIC) glider program.

Despite ongoing challenges presented by COVID in the initial part of this funding period, **monthly cruises to BATS** continued uninterrupted. In addition, the **8th and 9th BIOS-SCOPE process cruises** were completed in November 2021 and July 2022, respectively.

From May 4 to 5, 2022, approximately **forty team members** from **five countries** assembled for an in-person data workshop in Cambridge, MA (USA). The format included a series of talks, poster presentations, and breakout discussions, during which the BIOS-SCOPE team further evaluated the data as a group, targeted and outlined manuscripts, and set new directions to follow up. BIOS-SCOPE researchers gave more than **25 presentations** at national/international conferences and meetings during this reporting period, and the BIOS-SCOPE team published 1**4 peer-reviewed articles**, with another **five manuscripts** in various stages of peer review.

It is with deepest gratitude that we provide the following report to the Simons Foundation International (SFI), Ltd. on major activities, progress, and findings from the **Nov 1, 2021-Oct 2022** funding period. These achievements would not be possible without the Foundation's continued support of the program's goals.

BIOS-SCOPE Leadership

The BIOS-SCOPE team comprises microbial oceanographers, molecular microbiologists, marine chemists, zooplankton ecologists, computational modelers, and physical oceanographers from BIOS and eight other research institutions in the United States, United Kingdom, and Germany. Each member brings unique expertise and novel technologies to the program. (see complete list at https://scope.bios.edu/people/)

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 that the research carried out is effective in its cross-disciplinary and integrative approach.

BIOSSCOPE
Focusing research on the ocean's smallest life forms

BIOS-SCOPE Team Members

Bermuda Institute of Ocean Sciences and Arizona State University

Leocadio Blanco-Bercial, Investigator,
Ruth Curry, Investigator,
Jessica Godfrey, Research Support,
Hannah Gossner, Research Support
Ali Hochberg, Scientific Writing, Technician
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

Oregon State University

Libby Brennan, Graduate Student
Holger Buchholz, Postdoctoral Fellowy
Stephen Giovannoni, Co-Principal Investigator
Chih-Ping Lee, Postdoctoral Fellow
Chris Suffridge, Postdoctoral Scholar

University of California Santa Barbara

Craig Carlson, Co-Principal Investigator
Jacqui Comstock, Graduate Student
Chance English, Research Support
Elisa Halewood, Research Support and Data Management
Keri Opalk, Research Suppor
Rachel Sandquist, Graduate Student

Kean University (University of California Santa Barbara affiliate)

Shuting Liu, Postdoctoral Fellow

GEOMAR Helmholtz Centre for Ocean Research Kiel

Kristin Bergauer, Postdoctoral Researcher
Fabian Wittmers, Doctoral Student
Alexandra Z. Worden, Investigator

University of Exeter

Luis Bolaños, Postdoctoral Research Fellow
Michelle Michelsen, Research Support
Ben Temperton, Investigator
Joanna Warwick-Dugdale, Doctoral Student

Rosenstiel School of Marine, Atmospheric, and Earth Science, University of Miami

Hilary Close, Visiting Scholar
Lillian Henderson, Graduate Student

Woods Hole Oceanographic Institution (WHOI)

Herman Garcia, Postdoctoral Fellow
Noah Germolus, Graduate Student
Elizabeth Kujawinski, Investigator
Krista Longnecker, Research Support
Paloma Lopez, Research Support
Matt McIlvin, Research Support
Erin McParland, Postdoctoral Fellow
Annaliese Meyer, Graduate Student
Mak Saito, Investigator
Melissa Soule, Research Support
Gretchen Swarr, Research Support
Yuting Zhu, Postdoctoral Scholar

Technical University Berlin

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

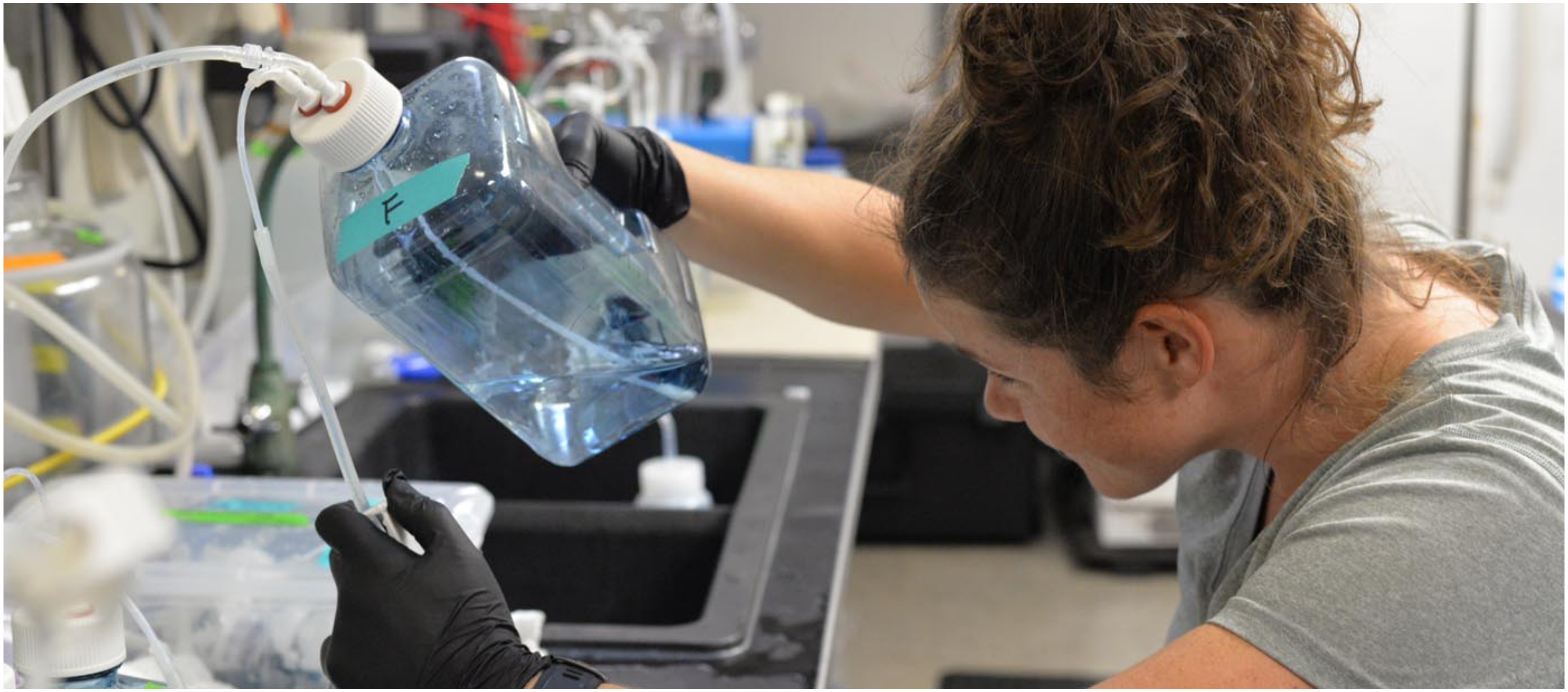
Laboratory, At-Sea Expeditions and Fieldwork

Archive DNA sequencing effort:

For over three decades, the *Giovannoni and Carlson groups* have generated a multi-depth DNA archive from a nearly uninterrupted monthly sampling effort at BATS. Following the data workshop in May, the *Carlson, Giovannoni, Temperton, and Worden groups* met at UCSB and OSU to prepare and submit the archived DNA sample set for metabarcoding sequence analyses. Once complete, the "BATS archive amplicon data" will allow the BIOS-SCOPE team to evaluate if long-term trends in the microbial community structure have occurred in response to increasing warming and stability of the water column at the BATS site.

Time-Series Cruises:

The monthly BATS time-series cruises continued uninterrupted. Sampling included planktonic DNA, microbial biomass, metabolite dissolved organic matter (DOM) composition, zooplankton distribution, and the occasional sediment trap over the surface 500 m. This provides valuable context to evaluate emerging patterns of microbial-DOM-zooplankton interactions on a seasonal time scale.



BIOS-SCOPE Process Cruises:

The BIOS-SCOPE team completed two dedicated process cruises in Nov. 2021 and July 2022. Diel (24-hour) hydrographic sampling helped resolve the temporal and vertical variability of organic and inorganic nutrients, vitamins, metabolites, microbial biomass and production, bacterial and viral DNA, and zooplankton biomass over the surface 500 m. In-situ McLane pumps were used to collect particles for molecular and isotopic characterization of organic particles that spanned four biologically relevant size classes over nine depths collected during the day and night on both the autumn and summer cruises. Additional shipboard experiments were conducted to assess the microbial availability of Sargassum-derived DOM; field test new methods to separate and identify dissolved metabolites; and conduct metagenomic and metatranscriptomic sampling.

Workshops, Synergies and Collaborations

Following on the success of virtual meetings that started in autumn 2020, the team continued to hold bi-weekly zoom meetings throughout the academic year to share data, discuss data synthesis and plan collaborative efforts. All zoom meeting notes and recordings are archived and available upon request.

After a forced hiatus in 2021, the fourth in-person data workshop was held in May 2022, bringing together BIOS-SCOPE investigators, postdoctoral scholars, research support, and technicians. Over two days the team gathered in Cambridge, MA for a series of targeted science talks, poster presentations, breakout sessions, and discussion groups. Topics ranged from the physics and biogeochemical dynamics in the northwestern Sargasso Sea; to types of analyses; to modeling microbial processes.

Research Progress and Key Findings

During the first phase of BIOS-SCOPE, research activities focused primarily on filling knowledge gaps related to the biogeochemical processes that occur in the Sargasso Sea on a variety of scales, ranging from organism-compound and organism-organism interactions to large patterns on the ecosystem scale. As the program progressed through this initial five years of funding, its focus expanded to include the temporal scales of variability that take place within the marine microbial ecosystem, ranging from diel (day-to-night) to seasonal to those occurring over several seasons.

This report focuses on the second year of a five-year renewal, during which BIOS-SCOPE investigators developed and utilized a variety of new data sets, models, and quantification methods. This work served to enhance their understanding of the diverse organisms—including bacteria, coccolithophores, ad viruses—that comprise the microbial community at BATS. In addition, these efforts further elucidated how each group of organisms contributes to the transport and transformation of DOM through the water column, with some playing significant roles in key nutrient cycles.

Metabolites and DOM Chemistry

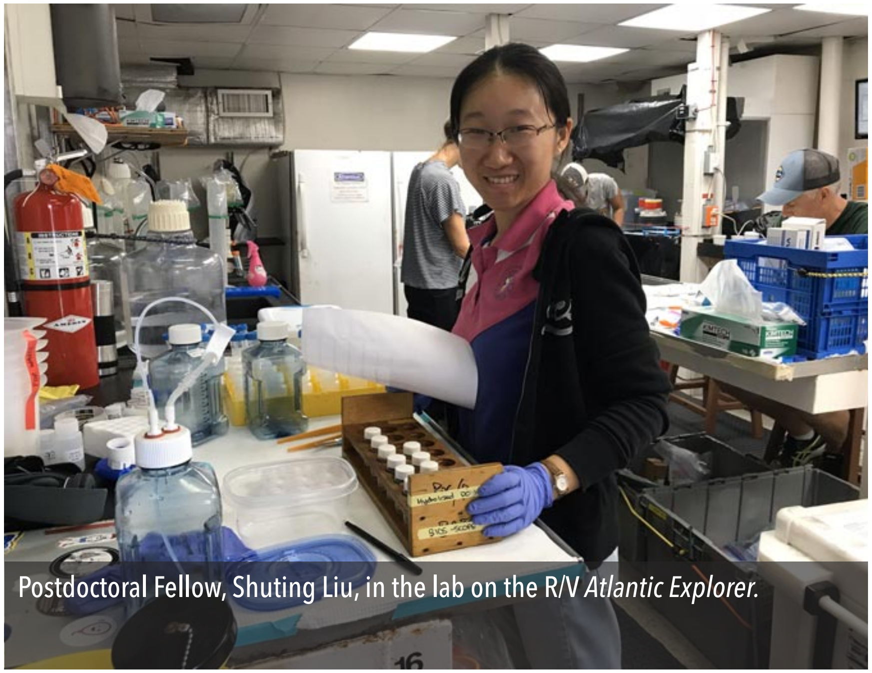
Metabolites are small organic molecules central to cellular metabolism that are produced and consumed within the microbial food web. They are the set of compounds that comprise dissolved organic carbon (DOC), including vitamin B complexes (vitamins B2 and B5) and free amino acids (such as leucine and phenylalanine), among other organic molecules.

Decades of data have revealed the Sargasso Sea experiences predictable seasonal changes. Winter storms mix the water column down to depths of 1000 feet (300 meters), followed by a spring phytoplankton bloom and a stratification of the water column that begins in April and persists throughout the summer.

A data workshop held in May 2022, brought together BIOS-SCOPE investigators, postdoctoral scholars, research support, and technicians.

This seasonal variability is reflected in physical and biogeochemical processes, nutrient cycles, oxygen levels, as well as the distribution of viruses, microorganisms, and zooplankton. There was good reason to believe that metabolites would follow a similar seasonal pattern.

New quantitative methods link dissolved metabolites to organisms and their metabolic function –The *Kujawinski group* developed new methods that improve quantification of metabolites produced by microbes, zooplankton, and macroalgae like *Sargassum*. A collaboration with the *Worden and Temperton groups* reported that select metabolites exhibit seasonal patterns at BATS, while the microorganisms that produce or consume them vary annually. Their analyses suggest that the metabolic functions responsible for the observed metabolites are stable across 20 years of existing metagenomic data collected at BATS. This finding supports the hypothesis that microbial diversity provides a buffering capacity within the microbial food web to perform metabolic functions, resulting in the annual cycling of the same vital metabolites.



Postdoctoral Fellow, Shuting Liu, in the lab on the R/V *Atlantic Explorer.*

Seasonal patterns of DOM export, dissolved metabolites, and microbial community structure at BATS –The predictable pattern of winter mixing in the Sargasso Sea is an important export pathway of the biological carbon pump and provides BIOS-SCOPE researchers in the Carlson Group with a unique opportunity to study DOM export, as well as how DOM is subsequently transformed by microbial oxidation processes. Liu et al. (2022) presents the first data set that examines changes in specific components of DOM, such as amino acids, vitamins, and benzoic acids, on a seasonal scale. The study also revealed an increase in production among bacterial lineages in the SAR11, SAR202, SAR86, Acidimicrobiales, and Flavobacteria clades following the deep mixing events.

Plankton & Systems Ecology

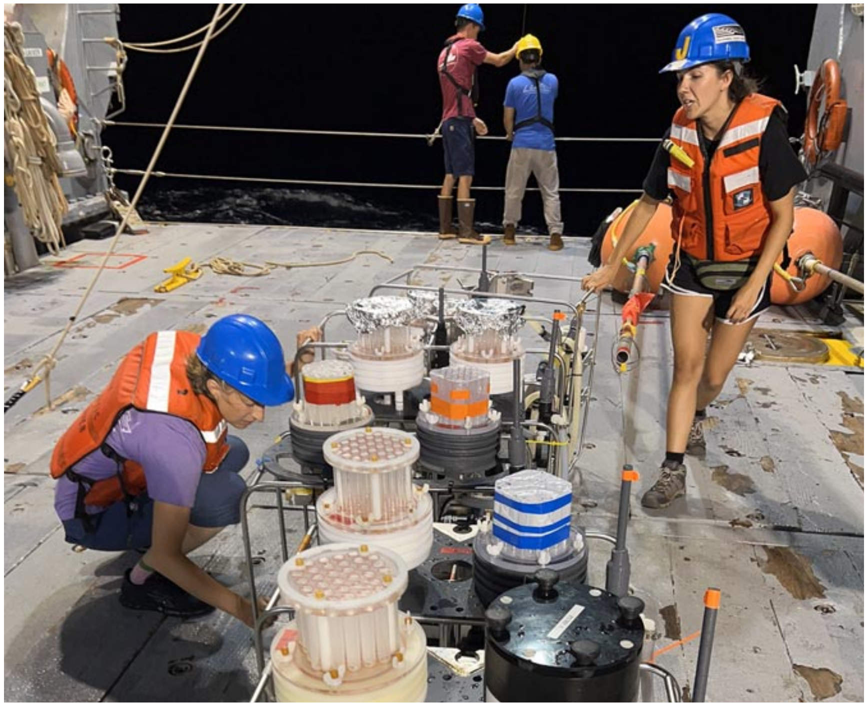
BIOS-SCOPE's investigators are working to unravel how marine microbes–such as plankton, bacteria, and viruses–control the production, removal and transformation of DOM within a web of ecological interactions in the open ocean. The project's overarching questions include: what is the fate of organic matter in the water column, what organisms or mechanisms affect its quality (transformation), and which organisms or mechanisms are responsible for recycling it or moving it up the food web?

Variable carbon isotope fractionation of photosynthetic communities over depth – Natural carbon is composed of two stable isotopes, ^{13}C and ^{12}C. The ratio between the abundance of ^{13}C to ^{12}C in the marine environment is affected by a variety of processes carried out by microbes and zooplankton, including photosynthesis and subsequent degradation. The degree to which the isotopic ratio decreases by depth from the standard phytoplankton isotopic signature is used to assess whether the particle is relatively fresh phytoplankton material or if it has been recently transformed by animals or microbes. Doctoral candidate Lillian Henderson (*Close group*) identified distinctly lower carbon isotope signatures of the phytoplankton biomarker phytol for communities in the deeper, low-light region of the photic zone at BATS. This study reveals that the decreasing carbon isotopic ratio of particles can be driven by a low light-adapted phytoplankton community, as well as by transformation via microbes and zooplankton. Results were presented at a 2022 Gordon Research Conference and are the subject of a recently drafted manuscript.

Seasonal transitions in green algae expose niche differentiation in the Atlantic Ocean – Phytoplankton dynamics and contributions to primary production have been studied at BATS for decades, but with methods that missed several phytoplankton groups. The *Worden group* found that one of these groups–a tiny eukaryotic phytoplankton called the prasinophyte–is a significant contributor during the phytoplankton bloom period. Analysis of open ocean prasinophytes over several seasonal cycles also revealed niche partitioning in the prasinophyte community. *Manuscript in prep*.

Discovery of Coccolithophore biodiversity – The *Blanco-Bercial and Maas Laboratories* discovered over 40 species and one new genus of phytoplankton, called coccolithophores, at BATS. This group of calcifying phytoplankton is particularly important to the carbon cycle because their dense calcium carbonate shells cause them to sink at the end of their life cycle, carrying carbon with them to the bottom of the ocean floor.

Carbon and Arsenic Cycling at BATS – Arsenic and phosphorus are biochemically very similar; in phosphate-limiting environments, phytoplankton will take up arsenic (arsenate), which is toxic to their energy metabolism, instead of phosphorus (phosphate), an essential nutrient. The Sargasso Sea ecosystem is a phosphate-limiting environment, and BIOS-SCOPE postdoctoral researcher Dr. Chih-Ping Lee (*Giovannoni group*) is aiming to establish the contribution of arsenate cycling to the plankton energy budget within this system. Using samples collected from BATS cruises, he completed a one-year time-series of arsenic compounds over 200 m depth and discovered that members of the OM43 bacterial clade are capable of demethylating arsenic compounds. *Manuscript in prep*.



Marine Microbiology & Microbial Ecology

Protists in the marine microbiome – With support from SFI's BIOS-SCOPE program, Dr. Charles Bachy (Worden Group) led a review of marine protists, their evolutionary histories, diversity, ecological roles, and lifestyles within the ocean. Protists were the first microbes observed by microscopy, yet it took the advent of molecular techniques to begin to resolve their complex and reticulate evolutionary history. Photosynthetic marine protists are appreciated for their activities as primary producers, rivaling land plant contributions in the global carbon cycle. Predatory protists are known for consuming prokaryotes and other protists,

From Bermuda Program intern to research intern, Marcus Rewan, processes samples in the Microbial Ecology Laboratory.

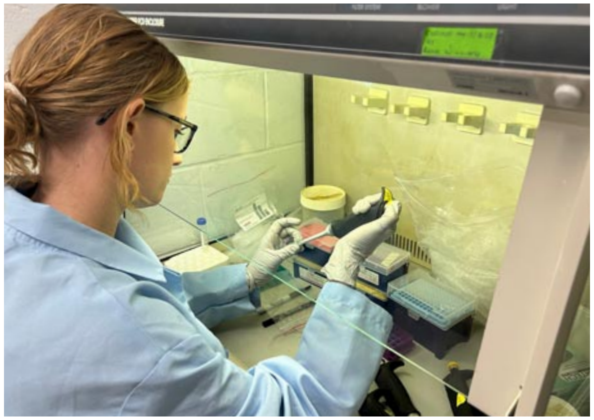
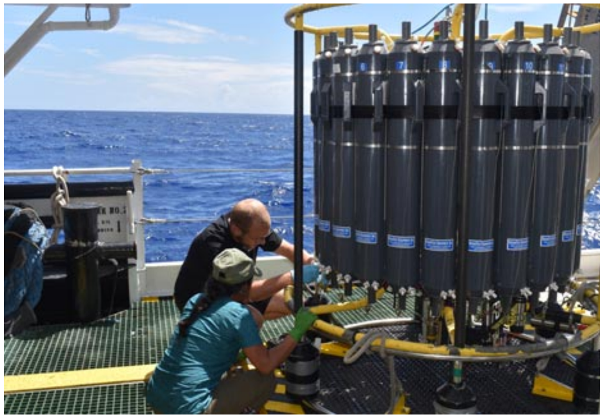
with some combining metabolisms (predatory and photosynthetic) into a mixotrophic lifestyle. Details are described in Bachy et al. (2022).

Development of the PatchModel – The *Hellweger group* initiated and completed the development of a microscale microbial ecology model (PatchModel) and is presently applying it to the BATS surface mixed layer. The PatchModel predicts novel and exciting patterns for the microbiome of phytoplankters. This is one of the first models that simulates microbes at ecologically relevant time and space scales. *Draft manuscript complete*.

Marine Viruses & Viral Ecology

Streamlining of SAR92 marine bacteria – The *Giovannoni group* discovered a remarkable example of genomic streamlining selection within the SAR92 clade of planktonic marine bacteria. They have tied SAR92 speciation to widespread changes in SAR92 genomes and tracked these changes to specific niches in the water column at BATS. This research advances our understanding of how carbon-oxidizing planktonic cells adapt to the expanding environment of nutrient-depleted ocean gyres.

Long read sequencing reveals counterintuitive finding about viral infection – Current estimates suggest that phages, i.e., viruses that infect bacteria, account for ~50% of cellular mortality in bacterioplankton communities. In a study of viromes collected from the BATS site, postdoc Dr. Joanna Warwick-Dugdale (*Temperton group*) found little evidence of active viral infection of the dominant members of the microbial community. They hypothesize that the limited lytic infection may be due to low levels of available phosphate that phages need to replicate, and that replicating viruses come from rarer but faster-growing host bacterioplankton taxa. The study identified 2,301 Sargasso Sea viral phage populations (~species-level taxonomy) across 186 genera, but also revealed that approximately 50% of viral "taxa" at BATS are absent from other global marine viromes. This new finding suggests that many viral taxa may be unique (i.e., endemic) to this geographic region or below detection limits in other ocean regions. Details are described in *Warwick-Dugdale (2022)*.


General Audience Publications

- "A Meeting of Minds, About Microbes," June 2022, https://bios.edu/currents/a-meeting-of-minds-about-microbes/
- "BATS, Big Data, and the Base of the Marine Food Web," November 2022, https://bios.edu/currents/bats-big-data-and-the-base-of-the-marine-food-web/

BIOS-SCOPE Team Awards, Honors, and Recognitions

- Craig Carlson: Promoted to Distinguished Professor of Marine Science at UCSB
- Hilary Close: Named as an Alfred P. Sloan Research Fellow for 2022-2024
- Elizabeth Kujawinski: Awarded the Stanley W. Watson Chair for Excellence in Oceanography from WHOI
- Shuting Liu: Appointed as Assistant Professor of Marine Science. Kean University. Liu et al.,2020, featuring BIOS-SCOPE research received Wiley's 2020-2021 top cited article certificate.
- Ben Temperton: Promoted to Associate Prof. of Microbiology at the University of Exeter
- Alexandra Worden: Elected as a member of the German Academy of Sciences Leopoldina

Peer reviewed publications that were partially or fully supported by SFI in 2021-2022 reporting period

Bachy C., F. Wittmers, J. Muschiol, M.Hamilton, B. Henrissat, A.Z. Worden (2022) The Land–Sea Connection: Insights Into the Plant Lineage from a Green Algal Perspective. *Annual Review of Plant Biology*; doi: 10.1146/annurev-arplant-071921-100530

Bachy, C., E. Hehenberger, Y.-C. Ling, D.M. Needham, J. Strauss, S. Wilken, A.Z. Worden (2022) Marine Protists: A Hitchhiker's Guide to their Role in the Marine Microbiome. *The Marine Microbiome*; doi: 10.1007/978-3-030-90383-1_4

Baetge, N., L.M. Bolaños, A.D. Penna, P. Gaube, S. Liu, K. Opalk, J.R. Graff, S. J. Giovannoni, M.J. Behrenfeld, C.A. Carlson. 2022. Bacterioplankton response to physical stratification following deep convection. *Elementa* doi.org/10.1525/elementa.2021.00078

Bayer, B., K. McBeain, C. A. Carlson and A. E. Santoro. (2022). "Carbon content, carbon fixation yield and dissolved organic carbon release from diverse marine nitrifiers." bioRxiv; *Limnology and Oceanography* 68 (1), 84-96.

Blanco-Bercial, L., R. Parsons, L.M. Bolaños, R. Johnson, G. Giovannoni, R. Curry (2022) The protist community traces seasonality and mesoscale hydrographic features in the oligotrophic Sargasso Sea. *Frontiers in Marine Sciences*, 9:897140.

Bolaños LM, Tait K, Somerfield PJ, Parsons RJ, Giovannoni SJ, Smyth T, Temperton B. (2022). Influence of short and long term processes on SAR11 communities in open ocean and coastal systems. *ISME COMMUN.* 2, 116 (2022). https://doi.org/10.1038/s43705-022-00198-1

Buchholz HH, Bolaños LM, Bell AG, Michelsen ML, Allen MJ, Temperton B. (2022). A Novel and Ubiquitous Marine Methylophage Provides Insights into Viral-Host Coevolution and Possible Host-Range Expansion in Streamlined Marine Heterotrophic Bacteria. *Appl. Env. Micro.* 88:e0025522.

Comstock, J., C. E. Nelson, A. James, E. Wear, N. Baetge, K. Remple, A. Juknavorian and C. A. Carlson. (2022) "Bacterioplankton communities reveal horizontal and vertical influence of an Island Mass Effect." *Environmental Microbiology* 24(9): 4193-4208. https://doi.org/10.1111/1462-2920.16092

Halewood, E., Opalk, K., Custals, L., Carey, M., Hansell, D.A., and Carlson, C.A. (2022) GO-SHIP Repeat Hydrography: Determination of dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) in seawater using High Temperature Combustion Analysis. *Ocean Best Practices* http://dx.doi.org/10.25607/OBP-1745.

Johnson, W. M., M. C. Kido Soule, K. Longnecker, M. P. Bhatia, S. J. Hallam, M. W. Lomas and E. B. Kujawinski (2022). Insights into the controls on metabolite distributions along a latitudinal transect of the western Atlantic Ocean. *Limnology and Oceanography* https://doi.org/10.1002/lno.12275

Kim, S., I. Kang , J.W. Lee, C.O. Jeon, S.J. Giovannoni , and J.C. Cho. 2021. Heme auxotrophy in abundant aquatic microbial lineages. *Proc. Natl. Acad. Sci. U.S.A.* DOI: 10.1073/pnas.2102750118

Liu, S., K. Longnecker, E.B. Kujawinski, K.Vergin, L.M. Bolaños, S.J. Giovannoni, R. Parsons, K. Opalk, E. Halewood, D.A. Hansell, R. Johnson, R. Curry and C.A. Carlson. 2022. Linkages Among Dissolved Organic Matter Export, Dissolved Metabolites, and Associated Microbial Community Structure Response in the Northwestern Sargasso Sea on a Seasonal Scale. *Frontiers in Microbiol*. doi.org/10.3389/fmicb.2022.833252

Moore, E.R., A. J. Weaver, E.W. Davis, S. J. Giovannoni, and K. H. Halsey. 2021. Metabolism of key atmospheric volatile organic compounds by the marine heterotrophic bacterium Pelagibacter HTCC1062 (SAR11). *Environ. Microbiol.* DOI: 10.1111/1462-2920.15837

Wittmers, F., D. M. Needham, E. Hehenberger, S. J. Giovannoni, A.Z. Worden. 2021. Genomes from Uncultivated Pelagiphages Reveal Multiple Phylogenetic Clades Exhibiting Extensive Auxiliary Metabolic Genes and Cross-Family Multigene Transfers. *mSystems* https://doi.org/10.1128/msystems.01522-21

BIOS-SCOPE submitted manuscripts in various stages of peer review during the 2021-2022 funding period

Buchholz HH, Bolaños LM, Bell AG, Michelsen ML, Allen MJ, Temperton B. (2022). Pelagibacter phage Skadi - An abundant polar specialist that exemplifies ecotypic niche specificity among the most abundant viruses on Earth. *bioRxiv*:2022.08.10.503363. DOI: 10.1101/2022.08.10.503363.

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. *bioRxiv* preprint doi: https://doi.org/10.1101/2022.07.21.501054. *In Review*

Warwick-Dugdale JL, Tian F, Michelsen ML, Cronin DR, Moore K, Farbos A, Chittick L, Bell A, Buchholz HH, Parsons RJ, Zayed AA, Allen MJ, Sullivan MB, Temperton B. (2022). Long-read powered viral metagenomics in the oligotrophic Sargasso Sea. *bioRxiv*:2022.09.19.508504. DOI: 10.1101/2022.09.19.508504.

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*.

Villiot, N., A.E. Maas, A. Poulton, L. Blanco-Bercial. Organic and inorganic nutrients modulate taxonomic diversity and trophic strategies of small eukaryotes in oligotrophic oceans. *In Review*.

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