

January 2020

# Report to SFI on **BIOS-SCOPE**

**BIOS** 





BIOS-SCOPE, established in 2015, is a multi-institutional microbial oceanographic research program situated in the northwestern Sargasso Sea near the Bermuda Atlantic Time-series Study (BATS) site. BIOS-SCOPE leverages combined expertise in microbial oceanography/dissolved organic matter (DOM) biogeochemistry, marine microbiology, marine chemistry, micro and mesozooplankton ecology, and microbial bioinformatics to evaluate the microbial process, structure, and function on a variety of temporal and spatial scales. In addition, the project continues to benefit from its collaboration with the BATS and Hydrostation 'S' programs and the Mid-Atlantic Glider Initiative and Collaboration (MAGIC) glider program.

In the Year 3 report, we presented the research activity and key findings to date in terms of the temporal scales of variability that take place within the marine microbial ecosystem, ranging from diel (day-to-night) changes to those occurring over several seasons. In this report, we present research progress and findings in higher resolution, drilling down into high-quality data sets that

shed light on how marine microbes control the production, removal, and transformation of dissolved organic matter within a web of ecological interactions.

Supplemental funding from Simons Foundation International (SFI) was utilized to hold the second data workshop from February 22-23 in San Juan, Puerto Rico that coincided with the 2019 Association for the Sciences of Limnology and Oceanography (ASLO) Aquatic Sciences Meeting. A total of 19 BIOS-SCOPE team members attended 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, identified unknowns and new directions to follow up.

It is with the deepest gratitude that we provide the following report to Simons Foundation International on major activities, progress and findings from the 2019-2020 funding period. The Foundation's support in establishing the program and its additional commitments to further enhance the program have made this progress possible.

# BIOS-SCOPE Team Members

The BIOS-SCOPE team includes microbial oceanographers, molecular microbiologists, marine chemists, zooplankton ecologists, and physical oceanographers from BIOS and six other research institutions in the United States and United Kingdom. Each member brings unique expertise and novel technologies to the program.

This year Dr. Ferdinand Hellweger (Technical University Berlin) joined the group as a computational scholar interested in evaluating correlations between genetic distance and fitness differences of microbial populations at BATS.



**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



**Zachary Anderson**, Research Support  
**Leocadio Blanco-Bercial**, Investigator  
**Ruth Curry**, Affiliated SFI Investigator  
**Cordie Goodrich**, Hardware/Software Technician  
**Hannah Gossner**, Research Support  
**Rod Johnson**, Data Processing and Integration  
**Amy Maas**, Investigator  
**Rachel Parsons**, Investigator  
**Kevin Vergin**, Visiting Scholar



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



**Ferdi Hellweger**, Computational Scholar



**Ben Temperton**, Investigator  
**Joanna Warwick-Dugdale**, Doctoral Student



**Hilary Close**, Visiting Scholar



**Elizabeth Harvey**, Visiting Scholar



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



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

# At-Sea Expeditions & Fieldwork

Fieldwork remained a focus of BIOS-SCOPE in Year 4 of the program, with several cruises supporting major BIOS-SCOPE research foci and resulting in robust data sets for further analysis.

**Time-Series Cruises:** In 2018 and 2019 the BATS program again provided monthly collection of BIOS-SCOPE variables, including planktonic DNA, microbial biomass, and DOM composition. In 2019, BIOS-SCOPE expanded the use of the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) to conduct zooplankton tows on a seasonal basis (every 4 months) during Hydrostation 'S' cruises.

**Maas Zooplankton Cruise, May 2019:** Members of the Kujawinski and Close labs were involved with an NSF-sponsored cruise, aimed at investigating the circadian rhythms (24-hour cycles in physiological processes) of zooplankton. They collected measurements relevant to BIOS-SCOPE and conducted shipboard experiments to assess potential linkages between zooplankton diel (day-to-night) physiology, particle production/composition, and microbial community.

**BIOS-SCOPE process cruise, July 2019:** 18 scientists participated in the 6th BIOS-SCOPE process cruise. Round-the-clock hydrographic sampling and plankton tows were used 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 1000 meters. *In situ* sequential filtration pumps collected particles for molecular (Carlson) and isotopic characterization of organic particles (Close) that spanned four biologically-relevant size classes over 12 depths. Numerous shipboard experiments were conducted to evaluate zooplankton and microbial respiration, as well as organic matter transformation by bacterioplankton (free living bacteria).

**Microbial dynamics in Oxygen Minimum Zones (OMZ):** Devil's Hole, located in Harrington Sound, Bermuda, is a model ecosystem to study the development of, and microbial succession within, OMZs because the formation and subsequent overturn of the suboxic layer occurs regularly on an annual basis. Parsons (BIOS) led an effort to assess microbial succession and bioavailability of DOM in this system.



# 2019 Research Progress

Dissolved organic matter (or DOM) consists of materials, including carbon compounds, that result from the biological production and decomposition of organic matter—processes that are governed by phytoplankton, bacteria, and zooplankton. As DOM is produced a portion of this material resists biological degradation and accumulates. Questions about how and why DOM accumulates in the surface layer and its fate after physical removal via mixing to deeper ocean depths are a main focus of the BIOS-SCOPE team. The BIOS-SCOPE project works to identify the components of DOM, as well as their relative concentrations, to help understand the influence of these compounds on both ocean chemistry and the ecology of the marine microbial community.

As the BIOS-SCOPE project progresses, scientists continue to refine the scope of their investigations, moving from broad research into the spatial scales at which marine microbial ecology takes place (2016 and 2017) to temporal scales of variability (2018) to high-resolution observations and measurements of DOM and the organisms responsible for its transformation and cycling in the ocean.

### **Metabolites**

Part of the BIOS-SCOPE mission is to further clarify and quantify the respective roles of bacterioplankton, phytoplankton and zooplankton in the ocean's biological pump. Over the course of a day, zooplankton help regulate phytoplankton by consuming



them. The resulting waste products are recycled by microbes like bacterioplankton and, as a result, influence its community composition. Metabolites, or the molecules resulting from an organism's metabolic activities, are part of the large, chemically diverse DOM pool. Accurate measuring and accounting for the production of nutrients, such as metabolites, helps scientists better estimate the impacts of their compounds on phytoplankton abundance and distribution.

*Improved metabolite resolution:* Many metabolites are small, polar molecules that are highly bioavailable and cycle rapidly, but little is known about the fate of these molecules, largely because of challenges in measuring their concentrations. During this reporting period Brittany Widner (Kujawinski group) developed a novel method for quantifying metabolites in seawater and, during the July BIOS-SCOPE process cruise, measured patterns in metabolite distribution over four depth profiles. Results of her work will be presented at the 2020 American Geophysical Union Ocean Sciences Meeting (OSM) in San Diego, California.

*Temporal variability of metabolites:* In 2018/19, Kujawinski's group continued seasonal metabolite collection at BATS, with increased sampling resolution during the two most recent cruises. Repeated and sustained observations of dissolved metabolites are rare and those collected as part of the BIOS-SCOPE program provide unique and complementary insights to those gained from genomic tools. These measurements have demonstrated that certain short-lived molecules, such as riboflavin and thymidine, are extensively recycled within biologically active regions of the water column. Concentrations of metabolites also appear to vary, both at depth and in the surface layer, on a seasonal basis. These data will be presented at the 2020 OSM.

## Diel and Seasonal Patterns

DOM is produced and transformed on a wide range of time scales—from seconds to days to seasons. Diel patterns of DOM distribution are tightly linked to the timing of vertically migrating zooplankton, such as copepods that vertically migrate hundreds of meters every day. Seasonal patterns of DOM distribution have also been observed: during the winter, strong winds mix the upper portion of the ocean, bringing DOM from the surface waters to depth, while also carrying inorganic nutrients up toward the surface. These winter mixing events set the stage for an annual burst of photosynthetic activity by phytoplankton known as the "spring phytoplankton bloom," which has far-reaching



Craig Carlson, a microbial oceanographer and BIOS-SCOPE program director, has been investigating the role that marine microbes play in governing the ocean's carbon cycle for more than two decades. Photo by Samm Newton

impacts on the ocean's biogeochemical cycles and ecology.

*Diel and seasonal patterns of amino acids and bacterioplankton:* DOM production through food web processes and subsequent microbial oxidation lead to a transformation in its chemical composition. By measuring the total dissolved amino acids in DOM, as well as changes in the ratios of individual amino acids, BIOS-SCOPE researchers can gain insight into how DOM is transformed into bioavailable forms. Work by Dr. Shuting Liu (Carlson group) has indicated that DOM is chemically altered at night, which coincides with the timing of bacterial production maximum also observed at night. On seasonal time scales, concentrations of total dissolved amino acids provide DOM with an easily identifiable

"signature" showing that "fresh" DOM is exported to deeper waters during winter mixing events. These data are currently the focus of a manuscript in preparation and will be presented at the 2020 OSM.

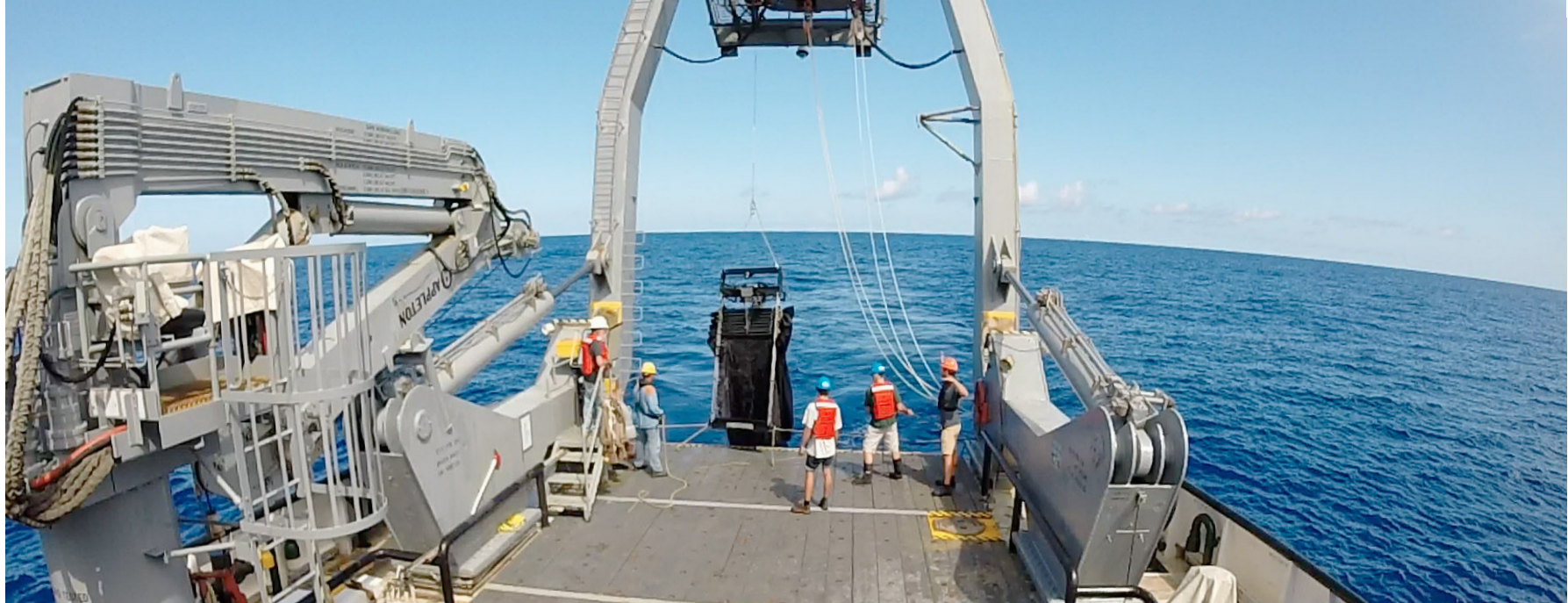
*Biogeochemical implications of diel changes in migratory copepod physiology:* The diel vertical migration of zooplankton over hundreds of meters has consequences for biogeochemical cycling as it moves a substantial portion of surface fixed carbon and nitrogen to depth. However, this contribution remains poorly characterized, largely because daily variations in the metabolic rates of zooplankton are not considered. The Maas and Blanco-Bercial group (BIOS) performed a variety of measurements throughout the daily migratory cycle of a copepod (*Pleuromamma xiphias*) to characterize the impacts of daily physiological rhythms on the organisms' metabolisms. Pairing studies of zooplankton distribution with these metabolic metrics allows for better understanding of how circadian changes in zooplankton physiology potentially impact biogeochemical cycling. These findings will be presented at the 2020 OSM.

*Protist plankton seasonality and community structure:* The composition, functionality and role of protist plankton in the ocean's biogeochemical cycles have been the subject of intense study in the last few decades. Most of these studies are limited to the epipelagic zone of the ocean, which includes waters between 0 and 200 meters deep. As part of the BIOS-SCOPE DNA time series, which collects samples from the surface down to 1000 meters, a specific region of structural RNA found in eukaryotic organisms, including protists, was sequenced (Blanco-Bercial, Parsons and Giovannoni groups). These data show the protist community



Steve Giovannoni, a microbiologist and co-principal investigator on the BIOS-SCOPE project, focuses his research on understanding how dominant marine bacteria function in global biogeochemical cycles. Photo by Samm Newton.





is vertically structured from the epipelagic to the mesopelagic depth at BATS. Strong seasonality in distribution was also observed in the epipelagic, especially at the deep chlorophyll maximum. These data were recently submitted to *Frontiers of Marine Science* and will be presented at the 2020 OSM.

### **Marine Viruses & Bacterioplankton**

Marine viruses are a key part of the ocean's biogeochemical cycles, preying on marine bacteria and consuming approximately 20% of the ocean's microbial biomass on a daily basis. They are also considered reservoirs of genetic diversity, introducing new genetic material into host organisms and driving the evolution of both populations. SAR11 is a group of small, organic carbon-oxidizing bacterioplankton that comprise 25-30% of all bacterioplankton in the ocean, making it the most abundant microbe on the planet. SAR202 is a group of aphotic (residing below 200 meters deep) bacterioplankton and, in some deeper regions of the

ocean can comprise from 5- 40% of the total bacterial community. SAR11 and SAR202 are hosts for a variety of marine viruses, which BIOS-SCOPE scientists are studying to better understand the role that viruses play in marine biogeochemical cycles.

*Novel SAR11 viruses from BATS suggest unusual infection dynamics:* During the July BIOS-SCOPE cruise, Temperton's group isolated 19 new SAR11 viruses. Marine viruses prey on marine bacteria and the current paradigm is that viruses will infect more dense populations until their numbers decline, forcing the viruses to adapt or find new hosts. However, Temperton has found that predation of SAR11 by its viruses seems to have little impact on host abundance. Instead, a sort of equilibrium between host and virus abundance is maintained. Temperton postulates that this could be due to surviving SAR11 efficiently recycling the nutrients released by their fallen comrades. Temperton is working closely with a group of researchers from Woods Hole Oceanographic

Institution, led by marine chemist Elizabeth Kujawinski, to identify if viral infection impacts the organic materials preferentially utilized by SAR11. Preliminary data are expected to be presented at the 2020 BIOS-SCOPE data workshop.

*SAR 202 Genomics and Ecology:* Research continued to focus on SAR202. It has been hypothesized that this group evolved specialized metabolism for the oxidation of organic compounds that are resistant to other microbial degradation pathways. In an analysis of 122 SAR202 genomes that included six subclades, Jimmy Saw (Giovannoni group) observed additional evidence of metabolic specialization. Work by Parsons showed that SAR202 subclades are indigenous to different ocean depths

and geographical regions. Matching genome predictions to DOM chemistry is an ongoing collaborative effort (Kujawinski, Carlson). A manuscript detailing these results is currently in press in *mBIO*.

*Microbial remineralization experiments:* Following the SAR202 genomic study (above) several collaborative remineralization experiments, led by Shuting Liu (Carlson group), were used to determine if specific mesopelagic microbial lineages were capable of breaking down carboxyl-rich alicyclic molecules (CRAM) proxy compounds, for energy and biosynthesis. Results showed different responses of bacterioplankton lineages to CRAM compounds of varying quality, which implies that bacterioplankton have evolved various metabolic strategies and niche specialization to take advantage of limited resources in the seawater. A manuscript describing these results is currently in press in *Limnology & Oceanography*.

*Stable Isotope probing (SIP) experiments:* The Carlson group conducted a series of stable isotope probing experiments in 2018 and again in 2019 to track the incorporation of recalcitrant DOM into microbial oligotrophs such as SAR11, SAR202, and SAR86, thereby increasing our understanding of resource partitioning among bacterioplankton groups in the mesopelagic zone. A manuscript describing this work is currently in preparation for publication.

## Plankton

Equally important to the BIOS-SCOPE mission is further clarifying and quantifying the respective roles of phytoplankton and zooplankton in the biological pump. Organic particles—



Keri Opalk, a seagoing research technician with the BIOS-SCOPE team from the University of California Santa Barbara, collects and analyzes dissolved organic matter in seawater samples. Photo by Samm Newton.

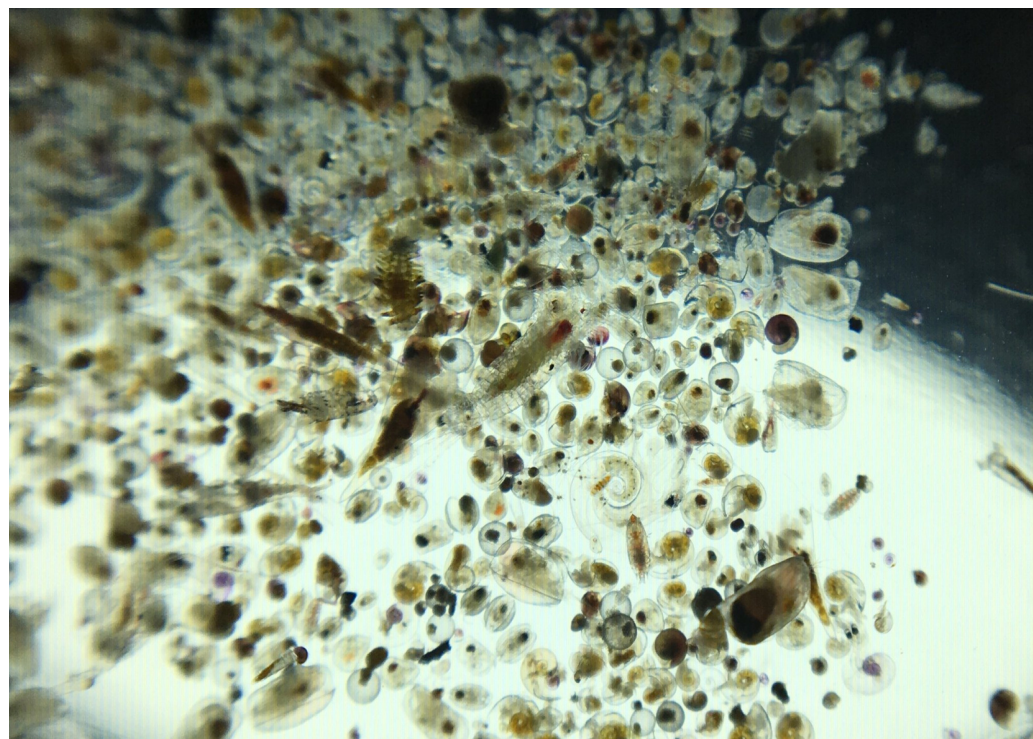


including phytoplankton, waste material from zooplankton, bacteria, and other organic aggregates—are continuously flowing from the surface of the ocean to depth, forming pathways of energy within the water column as they carry carbon along with them. Understanding the source(s) of this organic matter and the fate of these particles will enable BIOS-SCOPE scientists to determine how organic material fluctuates in the ocean.

*Dynamics of particulate organic composition, microbial community, and zooplankton contributions in water column:*

Hilary Close (University of Miami) continued as a BIOS-SCOPE Visiting Scholar using isotopic analysis of amino acids found in organic particles to “fingerprint” them and identify their sources. The data generated to date have allowed for the identification of two major avenues of further exploration: (1) distinct isotopic imprints of microbial and zooplankton consumption of both small (slowly-settling) and large (quickly-sinking) particles, and (2) a pronounced feature (region) in the lower euphotic zone that exhibits signs of photosynthesis, likely linked to low-light autotrophs. Each of these observations has implications for microbial metabolisms and their effects on carbon export to the deep ocean. Preliminary comparison with taxonomic data (Carlson) demonstrates close ties between the general metabolic function of depth-stratified microbial communities and the geochemical imprint of these metabolisms on sinking particles. Further collaboration with Maas’ group aims to identify the geochemical fingerprint of fecal pellets and microbes that can persist in sinking particles. These results were recently presented at the 2019 Goldschmidt Conference in Barcelona, Spain.

*New models to explore microbial succession or co-blooming in plankton.* Hellweger’s group has worked on understanding the fundamental relationship between genome and fitness. Using a meta-analysis of plankton datasets, including the BATS microbial data, they are exploring if there is a correlation between selection coefficient (a measure of difference in fitness) and genetic distance (a measure of genetic divergence). Application of this method to several marine and freshwater datasets revealed a weak but consistently positive correlation between genetic distance and fitness differences. These results will be presented at the 2020 OSM.





## Synergies with SCOPE and New Collaborations

- Previously reported collaborations among the White, Karl, Giovannoni, and Carlson groups resulted in two manuscripts that were accepted for publication in 2019 (White et al. 2019; Foreman et al. 2019)
- A collaboration between the Church and Carlson groups exploring the availability of DOM across a cyclone-anticyclone eddy dipole in the North Pacific has resulted in a manuscript that is currently in review in *Limnology and Oceanography* (Wear et al.)
- Carlson and Ben Van Mooy's group collaborated on a study that used an automated oxygen incubation system (AutoBOD) to resolve bacterial respiration at BATS.

## Scientific Publications

In 2019, nine papers were published or accepted for publication in peer-reviewed scientific journals.

- Foreman, R.K., Karin M. Bjorkman, Craig A. Carlson, Keri Opalk, David M. Karl (2019). Improved ultraviolet photo-oxidation system yields estimates for deep-sea dissolved organic nitrogen and phosphorus. *L&O Methods* 17(4): 277-291.
- Giovannoni, S.J., K. H. Halsey, J. Saw, O. Muslin, C. P. Suffridge, J. Sun, C.-P. Lee, E. R. Moore, B. Temperton and S. E. Noell (2019). A parasitic arsenic cycle that shuttles energy from phytoplankton to heterotrophic bacterioplankton. *mBio* 10(2): e00246-00219.  
Johnson, W.M., K. Longnecker, M.C. Kido Soule, W.A. Arnold, M.P. Bhatia, S.J. Hallam,
- B.A.S. Van Mooy, E.B. Kujawinski (2019). Metabolite composition of sinking particles differs from surface suspended particles across a latitudinal transect in the South Atlantic. *Limnology and Oceanography*. 10.1002/lno.11255.  
Liu, S., Rachel Parsons, Keri Opalk, Nicholas Baetge, Stephen Giovannoni, Luis M.
- Bolanos, Elizabeth B. Kujawinski, Krista Longnecker, YueHan Lu, Elisa Halewood, Craig A. Carlson (in press). Different carboxyl-rich alicyclic molecules (CRAM) proxy compounds select distinct bacterioplankton for oxidation of DOM in the mesopelagic Sargasso Sea. *Limnology and Oceanography*  
McDonald, N., Eric P. Achterberg, Craig A. Carlson, Martha Gledhill, Shuting Liu, Julia
- R. Matheson-Barker, Norm B. Nelson, Rachel J. Parsons (2019). The role of heterotrophic bacteria and archaea in the transformation of terrigenous dissolved organic matter in the open ocean. *Frontiers in Marine Science*:  
DOI:10.3389/fmars.2019.00743
- Saw, J.H.W., Takuro Nunoura, Miho Hirai, Yoshihiro Takaki, Rachel Parsons, Michelle Michelsen, Krista Longnecker, Elizabeth B. Kujawinski, Ramunas Stepanauskas, Zachary Landry, Craig A. Carlson, and Stephen J. Giovannoni (2019). Pangenomics reveal diversification of enzyme families and niche. *mBio*;  
DOI:10.1128/mBio.02975-19





Photos by Samm Newton

- Warwick-Dugdale, J., Natalie Solonenko, Karen Moore, Lauren Chittick, Ann C. Gregory, Michael J. Allen, Matthew B. Sullivan, and Ben Temperton (2019). Long-read viral metagenomics captures abundant and microdiverse viral populations and their niche-defining genomic islands. *PeerJ* 7:e6800 <https://doi.org/10.7717/peerj.68>
- Warwick-Dugdale, J., Buchholz, H.H., Allen, M.J. et al. Host-hijacking and planktonic piracy: how phages command the microbial high seas. *Virology* 16, 15 (2019) doi:10.1186/s12985-019-1120-1
- White, A.E., Stephen Giovannoni, Yanlin Zhao, Kevin Vergin, Craig A. Carlson (2019). Elemental content and stoichiometry of SAR11 chemoheterotrophic marine bacteria. *Limnology and Oceanography Letters* 4(2): 44-51.-

## Scientific Presentations

One presentation was given at the Ocean, Carbon and Biogeochemistry Meeting held June 24-27, 2019 in Woods Hole, MA.

- Blanco-Bercial, L. (poster). Zooplankton Community response to seasonality at BATS by metabarcoding.

**BIOS** 

[www.bios.edu](http://www.bios.edu)  
[scope.bios.edu](http://scope.bios.edu)