Prochlorococcusfest
2008

Celebrating 20 years of research on Prochlorococcus, the smallest and most abundant photosynthetic cell on Earth

Co-convened by:
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MIT

Held at:
Massachusetts Institute of Technology
Cambridge, MA 02139

May 30-31, 2008
**Prochlorococcus 20th Anniversary Colloquium**

Over the last 20 years, *Prochlorococcus* has emerged from being a newly-discovered group of cyanobacteria to become a well-studied model marine microbe that is of global importance. What began as an observation of a novel group of small marine phytoplankton, *Prochlorococcus* is now recognized as a genetically and physiologically diverse cluster of marine cyanobacteria that represents a key component in marine ecology and global biogeochemical cycles.

We organized this colloquium to mark the 20 year anniversary of the first formal description of *Prochlorococcus*, review what has been learned, and envision future trajectories of research on this valuable model system for marine microbiology.

We wish to extend our deep appreciation to the following sponsors:

The Gordon and Betty Moore Foundation  
The Agouron Institute  
The Chesonis Foundation  
The MIT Earth System Initiative  
The MIT Energy Initiative  
NSF-STC Center for Marine Oceanography Research and Education (C-MORE)

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Zackary Johnson  
University of Hawaii

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Sallie W. Chisholm  
MIT
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# Program

## Saturday, May 31st

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<td>Wolfgang Hess Regulatory RNA in cyanobacteria</td>
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Massachusetts Institute of Technology

#2 ESTIMATING THE SUPRA GENOME OF MARINE PICOCYANOBACTERIA
Baumdicker, Franz and Wolfgang R. Hess
University of Freiburg, Experimental Bioinformatics

#3 REGULATION OF GROWTH RATE AND ABUNDANCE IN *PROCHLOROCOCCUS* AND *SYNECHOCOCCUS* POPULATIONS IN THE SARGASSO SEA
Binder, Brian
University of Georgia

#4 A CRITICAL ANALYSIS OF THE CELL CYCLE METHOD FOR CALCULATING IN-SITU GROWTH RATES IN *PROCHLOROCOCCUS* POPULATIONS
Blythe, Brad and Brian Binder
University of Georgia

#5 MODELING SELECTIVE PRESSURES ON PICOCYANOBACTERIAL NITROGEN USE ABILITIES IN THE GLOBAL OCEAN
Bragg, Jason B., Stephanie Dutkiewicz, Michael J. Follows and Sallie W. Chisholm
Massachusetts Institute of Technology

#6 *PROCHLOROCOCCUS* ECOTYPE ABUNDANCES OF THE WESTERN PACIFIC OCEAN ELUCIDATED BY QUANTITATIVE PCR METHODS
University of Tennessee

#7 INTRODUCING THE MINI-ILLUMINATOR: CULTURING PHOTOSYNTHETIC MICROBES ON A SMALL SCALE WITH HIGH THROUGHPUT
Coe, Allison, David Otten and Sallie Chisholm
Massachusetts Institute of Technology

#8 A DATABASE PORTAL FOR *PROCHLOROCOCCUS*
Huang, Katherine and Sallie W. Chisholm
Massachusetts Institute of Technology

#9 IMPACT OF GENE CONTENT ON *PROCHLOROCOCCUS* ENATL ADAPTATION: BEYOND HIGH LIGHT AND LOW LIGHT
Kettler, Greg
Massachusetts Institute of Technology
PRIMARY PRODUCTIVITY AND THE CONTRIBUTION BY A “PROCHLOROCOCCUS SIZE-FRACTION” IN THE WESTERN PACIFIC
Lance, Veronica P.¹,², Johnson, Z.I.², Ritchie, A.E³, Barber, R.T.¹
¹NSEES, Duke University;  
²now at Lamont-Doherty Earth Observatory at Columbia University;  
³SOEST, University of Hawaii.

CONVERSATIONAL PIECES: PROCHLOROCOCCUS RESPONSES TO ARSENIC TOXICITY AND IRON LIMITATION
Mann, Elizabeth. L., J. Fox, C. Wakeham, J. G. Sanders and G. F. Riedel
Skidaway Institute of Oceanography

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University of Southern Maine

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University of Tennessee

THE EFFECTS OF UV RADIATION ON PROCHLOROCOCCUS ECOTYPES
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Massachusetts Institute of Technology

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J. Craig Venter Institute

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Ritchie, Anna
University of Hawaii

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Rivers, Adam R. and Eric A. Webb
Massachusetts Institute of Technology / Woods Hole Oceanographic Institution

SINGLE-CELL GENOMICS OF PROCHLOROCOCCUS
Rodrigue, Sébastien, Rex Malmstrom, Matthew Henn, Kun Zhang, Adam Martiny, George Church and Sallie W. Chisholm
Massachusetts Institute of Technology

A MARINE HETEROTROPHIC BACTERIUM THAT INHIBITS THE GROWTH OF PROCHLOROCOCCUS IN CO-CULTURE
Sher, Daniel, Laura R. Croal and Sallie W. Chisholm
Massachusetts Institute of Technology
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Sosik, Heidi M. and Robert J. Olson
Woods Hole Oceanographic Institution

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Tai, Vera, Qinghu Ren, Ian T. Paulsen, Brian Palenik
University of California, San Diego

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Thompson, Anne, Mak Saito, and Sallie W. Chisholm
Massachusetts Institute of Technology

#23 TRANSALDOLASE IN VIRUSES INFECTING PROCHLOROCOCCUS: HIJACKING HOST CARBON METABOLISM WITH A NON-CYANOBACTERIAL ENZYME
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Massachusetts Institute of Technology

#24 BIOCHEMICAL STOICHIOMETRY OF PROCHLOROCOCCUS CELLS
Waldbauer, Jacob R., Jason G. Bragg and Sallie W. Chisholm
Massachusetts Institute of Technology

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Welsh Rory M., M.L. Cuvelier and A.Z. Worden
Monterey Bay Aquarium Research Institute
Abstracts

Ahlgren, Nathan and Gabrielle Rocap
University of Washington

CHANGES IN PICOCYANOBACTERIAL COMMUNITY STRUCTURE ACROSS TRANSITIONS FROM Oligotrophic TO UPWELLING REGIONS OF COSTA RICA
Marine cyanobacteria provide a model system for exploring how multiple, closely-related microbial populations coexist and partition environmental niche-space. A wealth of previous studies demonstrates that *Prochlorococcus* populations are comprised of distinct populations (ecotypes) that partition the marine habitat both with depth through the euphotic zone and at larger scales across whole ocean basins. While light, temperature, and macronutrients are thought to be primary drivers of ecotype adaptation in *Prochlorococcus*, availability of trace metals also likely plays an important role in differentiation of cyanobacteria. To explore the impact of trace metals on ecotype adaptation and distribution, we applied real-time PCR assays to map both *Prochlorococcus* and *Synechococcus* (the sister taxa of *Prochlorococcus*) ecotype abundances in adjacent water masses that possess different trace metal signatures. Samples were taken off the Pacific coast of Costa Rica along a transect cutting through oligotrophic waters and two neighboring upwelling zones—the Costa Rica upwelling Dome (CRD) and the Equatorial upwelling zone. *Prochlorococcus* were most abundant in the CRD, in contrast to the paradigm that *Prochlorococcus* are usually restricted from more eutrophic waters. In the CRD, *Synechococcus* cell concentrations also peaked, reaching densities of up to 1*10^6* cells/ml and outnumbering *Prochlorococcus*. It is hypothesized that a distinct combination of trace metals in this upwelling feature produces this unusual picocyanobacterial community structure. Mapping of ecotype distribution reveals distinct communities for each of the three regions. By analyzing correlations of ecotype distributions to nutrient and trace metal concentrations, we assess the impact of trace metals on cyanobacterial community structure.

Bagby, Sarah C. and Sallie W. Chisholm
Massachusetts Institute of Technology

CHARACTERIZATION OF PROChLOROCoccus CARBON DIOXIDE AND OXYGEN PHYSIOLOGY
Goericke et al. (2000)[1] observed that *Prochlorococcus* is a uniquely successful phototroph in low-light suboxic waters, but the reason for *Prochlorococcus*’ dominance in these waters remains unknown. Structural biology predicts that the partial pressure of oxygen will affect the efficiency of carbon fixation: Rubisco discriminates only poorly between carbon dioxide and molecular oxygen, leading to high rates of photorespiration when Rubisco is exposed to low CO2:O2 ratios. The goal of this project is to assess the whole-genome transcriptional response and the metabolic response of high- and low-light *Prochlorococcus* ecotypes to acute changes in gas conditions, and ask whether these ecotypes’ sensitivity to carbon starvation depends on oxygen partial pressure. In addition, we ask how different steady-state CO2 and O2 conditions affect the growth, oxygen evolution, and respiration rates of high- and low-light *Prochlorococcus* strains, and whether differences in these ecotypes’ gas optima in culture can explain any of the observed variation in ecotype abundances in the ocean.

Baumdicker, Franz and Wolfgang R. Hess  
University of Freiburg

ESTIMATING THE SUPRA GENOME OF MARINE PICOCYANOBACTERIA  
Analyses of 22 total genome sequences of closely related marine picocyanobacteria have shown an unprecedented number of differences in their genome size, the number of annotated protein-coding genes and GC content. These cyanobacteria belong to only two genera, Prochlorococcus and Synechococcus. Homologs of cyanobacterial genes have also been found in the genomes of cyanophages, possibly important players in mediating efficient horizontal gene flow within and among populations of marine picocyanobacteria. The population size of marine unicellular cyanobacteria has been estimated at >1027 and their genes contribute to a significant share in marine metagenome projects. Thus the question arises how many genes would constitute the Prochlorococcus/Synechococcus gene pool and how many additional genomes would need to be analyzed to obtain a realistic picture of its composition.

There are two models for inferring this information based on analyzed genomes. The pan genome model assumes a bascially open genome and consists of all genes in the core and the dispensable genome parts. A large amount of intraspecies genic variation has also been observed for many other bacteria. The distributed-genome hypothesis states that for some bacteria the full complement of genes exists in a “supragenome” pool, one that each member of a population of strains contributes to and gains genes from, resulting in a high degree of genic diversity in investigated genome sequences. Using mathematical modelling, here we have determined the Prochlorococcus/Synechococcus average number of genes belonging to the core genome at 1201 - 1206 and the average number of new genes expected to be found in any new genome sequence at 182 - 195. Using the same data in the finite-supragenome model we have obtained predictions that (i) the Prochlorococcus/Synechococcus supragenome contains more than 35,000 orthologous clusters and (ii) 1489 representative genomes needed to be sequenced to identify all orthologous clusters that are represented in the Prochlorococcus/Synechococcus population at frequencies of >=0.1.

Binder, Brian  
University of Georgia

REGULATION OF GROWTH RATE AND ABUNDANCE IN PROCHLOROCOCCUS AND SYNECHOCOCCUS POPULATIONS IN THE SARGASSO SEA  
The contrasting seasonal patterns of Prochlorococcus and Synechococcus abundance in the Sargasso Sea are well-documented, but the factors shaping these patterns are poorly understood. In order to learn more about the regulation of Prochlorococcus and Synechococcus populations in the Sargasso, growth rates of these populations were measured in the spring and fall using
dilution incubations. Over both seasons, Prochlorococcus and Synechococcus absolute growth rates were well-correlated with each other. Together, growth rates of these two groups were significantly correlated with integrated light exposure (though not with depth) within each season, though the slope of the relationship differed between seasons. These data, combined with the fact that N and P additions did not stimulate growth in our experiments, suggest that the proximal limiting factor for both Prochlorococcus and Synechococcus growth rate in this environment is light. At the same time, the growth vs. light relationship is apparently influenced by nutrients or other seasonally-varying factors. The relationship between relative growth rate and abundance for these two groups also varied with season: in the spring, relative growth rate was positively correlated with relative abundance, whereas in the fall, the correlation was negative (though not significant). Taken together, these results suggest that differences in growth physiology alone are insufficient to explain the contrasting seasonal cycles of Prochlorococcus and Synechococcus abundance in the Sargasso Sea.

Blythe, Brad and Brian Binder
University of Georgia

A CRITICAL ANALYSIS OF THE CELL CYCLE METHOD FOR CALCULATING IN-SITU GROWTH RATES IN PROCHLOROCOCCUS POPULATIONS

Diel patterns in cell cycle phase-fractions can be used to estimate growth rate for natural Prochlorococcus populations. We compared two approaches for making such estimates: the traditional “manual” approach, which uses the raw (discontinuous) cell cycle phase-fraction data, and a “curve-fit” approach that uses periodic functions fit to the raw data. Although the curve-fit approach has been shown theoretically to improve growth rate estimates, it has not been widely applied to Prochlorococcus. Flow cytometrically-measured DNA frequency distributions were obtained from diel time series (both in situ and in on-deck incubations) in the Sargasso Sea over the course of five research cruises, and analyzed using both approaches. Growth rates calculated by these two approaches were not well-correlated. Overall, the curve-fit approach resulted in less variable growth rate estimates than did the manual approach. These findings suggest that the curve-fit approach for estimating in situ Prochlorococcus growth rates is preferable, and point to a need for caution when interpreting previously published growth rates calculated by the manual approach.

Bragg, Jason G., Stephanie Dutkiewicz, Michael J. Follows and Sallie W. Chisholm
Massachusetts Institute of Technology

MODELING SELECTIVE PRESSURES ON PICOCYANOBACTERIAL NITROGEN USE ABILITIES IN THE GLOBAL OCEAN

The distribution and physiology of marine microbes are shaped by processes of ocean physics and biogeochemistry, as well as ecology and evolutionary genetics. Here we incorporate these processes into a model that examines the selective pressures on marine picophytoplankton in different ocean regions to use nitrite and nitrate. The model predicts that losing the ability to use
Chandler have weaker selective consequences in tropical oligotrophic regions, relative to higher latitudes. This is consistent with the observation that non-nitrate using Prochlorococcus picocyanobacteria are often numerically dominant in the most oligotrophic ocean regions, whereas nitrate using Synechococcus reach greater abundances at slightly higher latitudes. These analyses help us understand specialization by Prochlorococcus on ammonium as a source of nitrogen, and introduce an approach that may be valuable for studying evolutionary pressures on the distribution of genes more broadly.

Chandler, Jeremy W., Eric R. Zinser, Zachary I. Johnson
University of Tennessee

PROCHLOROCOCCUS ECOTYPE ABUNDANCES OF THE WESTERN PACIFIC OCEAN ELUCIDATED BY QUANTITATIVE PCR METHODS
Prochlorococcus is an open ocean cyanobacterium, thought to be globally significant in nutrient cycling. Several genetically distinct populations of Prochlorococcus called “ecotypes” coexist throughout the world’s subtropical and tropical oceans. These ecotypic distributions result in an intriguing phenomenon because of their highly variable distributions and ability to survive and thrive in a plethora of environmental gradients, which range from the extreme limits of the euphotic zone to the surface. Quantitative PCR methods were employed to ascertain this ecotypic diversity across a transect spanning the Pacific Ocean from 20°N to 37°S latitude. The transect incorporated the Western Pacific Warm Pool (WPWP), a large area of extremely warm ocean water (30°C+), where environmental pressures are thought to be elevated. This transect offers insight into the dominant ecotypic players of the western Pacific. eMED4 and eMIT9312 (high light associated) ecotypes were found to dominate the transect, with eMIT9312 dominating the waters of the WPWP. eNATL2A and eMIT9313 (low light associated) played a smaller, yet significant component in total Prochlorococcus populations. Results of the transect align with similar population dynamics discovered in a transect of the North Atlantic Ocean. Study of the WPWP may also provide a glimpse at which populations might thrive in the future oceans, as a consequence of global warming.

Chisholm, Penny (et al.)
Massachusetts Institute of Technology

EMERGING FROM THE NOISE: THE PROCHLOROCOCCUS STORY
Eclipsed for a decade by its orange-fluorescing cousin, Prochlorococcus finally made itself known to us a little over 20 years ago. Since then we have learned that it is (so far) the smallest and most abundant photosynthetic cell on the planet. With a mere 2000 genes, it can create organic matter from sunlight and inorganic compounds. As we learn more and more about this group, it has become clear that Prochlorococcus, the collective, is an extraordinarily useful model system for advancing our understanding of nature and evolution of microbial systems.
**Coe, Allison, David Otten, and Sallie Chisholm**
Massachusetts Institute of Technology

**INTRODUCING THE MINI-ILLUMINATOR: CULTURING PHOTOSYNTHETIC MICROBES ON A SMALL SCALE WITH HIGH THROUGHPUT**
As the number of microbial genomes grows dramatically, one of the challenges in our field is connecting differential fitness of closely related genomic variants with differences in genetic composition. To do this one must be able to measure growth rates of strains under tightly controlled environmental conditions with great reproducibility. We have designed a culturing system for *Prochlorococcus* that will help us achieve this goal. It uses 96 well plates as the culture vessel, and blue light-emitting diodes (LEDs) as the light source. The light level of each LED or row or column is programmable with one minute resolution over a 24 hour period. Light levels can range from 0 µE m-2 sec-1 to 200 µ m-2 sec-1. The temperature of the plate is controlled by a Peltier device over a temperature range of 15°C-30°C. The temperature is also programmable with one minute resolution over a 24 hour period. Condensation on the plate lid is eliminated with the use of a heated lid. The design is small enough to use on a benchtop and is very “user friendly”. We have examined the difference between growing in a Percival incubator and growing in the mini illuminator by monitoring daily fluorescence via a BioTek Synergy2 plate reader and find the growth rates to be comparable.

**Coleman, Maureen L. and Sallie W. Chisholm**
Massachusetts Institute of Technology

**PROCHLOROCOCCUS POPULATION GENOMICS IN THE SUBTROPICAL PACIFIC**
Metagenomics offers an approach for studying natural microbial communities, but its power is dramatically magnified when combined with knowledge from cultured isolates. The marine cyanobacterium *Prochlorococcus* represents one of the best model systems for linking culture-based and metagenomics approaches. As one of the most abundant taxa in the open oceans, it is highly represented in marine metagenomics datasets, and physiological and genome diversity have been characterized for numerous isolates. We examined the diversity and population structure of *Prochlorococcus* from three depths at Station ALOHA near Hawaii. Principal aspects of *Prochlorococcus* diversity observed in cultured isolates, including the presence of core and flexible genomes and ecotypic variation in gene content, were also apparent in the population metagenome. Although cells belonging to the high-light adapted ecotype eMIT9312 are most abundant at all three depths, the genome content of these cells is not uniform; eMIT9312 cells found towards the base of the euphotic zone are distinct from those near the surface. A set of genes showing differential abundance along the depth profile also implicate *Prochlorococcus* in an active water column cycle of thiamin. Finally, we detected signals of intragenic recombination in several key metabolic genes, suggesting that recombination plays a far more important role in *Prochlorococcus* genome evolution than previously thought. From complex community metagenomics data, patterns emerge that can be interpreted in the context of the *Prochlorococcus* model system, and this combination promises to rapidly advance our understanding of ocean ecosystems.
MODELING PROCHLOROCOCCUS ECOTYPES: FROM GENOME TO BIOMES

The identification and mapping of genetically and physiologically distinct ecotypes of *Prochlorococcus* led us to explore a new, self-organizing approach to modeling marine ecosystems. We show how potentially viable model-analogs of *Prochlorococcus* are selected to occupy realistic habitats when seeded in a "Darwinian" ocean circulation, biogeochemistry and ecosystem model. The unparalleled genomic, physiological and biogeographical knowledge of *Prochlorococcus* make it, at present, a unique "model" organism for testing ecological models. The detailed understanding of *Prochlorococcus* also inspires a new generation of marine ecosystem models, spanning from genomic and cellular scale characterizations, through the physiological sensitivities of cultured populations, to the global-scale biogeochemistry of marine phytoplankton. We will describe ongoing activities which attempt to bring this vision to life.

COMPETITION EXPERIMENTS WITH GENETICALLY ENGINEERED VIRUSES AND ECOSYSTEM-SCALE GENE KNOCKOUT EXPERIMENTS TO UNDERSTAND HOW PHOTOSYNTHESIS GENES AFFECT THE ECOLOGICAL FITNESS OF VIRUSES? (A SYSTEMS BIOECOLOGY MODELING ANALYSIS)

Viruses infecting the marine cyanobacterium *Prochlorococcus* have photosynthesis genes (psbA, hli) that are expressed and yield proteins (D1, HLIP) that help maintain photosynthesis during the latent period. This speeds up virion production, which is good (reduced latent period), but it also increases the genome size, which is bad (smaller burst size). The complexity of the system makes understanding the ecological fitness advantage of this trait difficult, and to investigate it, a combined systems biology/ecology approach is used here. A new model with a mechanistic photosynthesis model that explicitly considers genes and proteins is presented. The agent-based model explicitly simulates cyanobacteria cells and phage virions, each with their own dynamic genome and protein levels. The model is calibrated against data from the literature, including observed photosynthesis and growth vs. irradiance of high- and low-light adapted ecotypes (MED4, MIT9313), diel patterns of cell division, size and fractions of the population in S and G2+M phases, and cell-virus interaction in a laboratory experiment including gene expression. To understand the effect of photosynthesis genes on the ecological fitness of viruses, we perform a number of numerical (in silico) experiments. This includes competition experiments with wild-type (e.g. P-SSP7) and genetically engineered viruses containing various combinations of photosynthesis genes, and ecosystem scale gene knockout experiments in a Sargasso Sea water column.
**REGULATORY RNA IN CYANOBACTERIA**

Regulatory RNA molecules have been discovered in all three domains of life. Without detailed information about the numbers and functions of these regulators it is not possible to understand the intracellular regulatory network in all its complexity. In cyanobacteria, only a small number of potentially trans-acting non-coding RNAs (ncRNAs) has been described(1,2) and three instances of antisense RNAs(3-5). IsrA, an antisense RNA to the isiA gene of *Synechocystis* PCC 6803 regulates the expression of isiA under iron and redox stress(3). However, for the vast majority of ncRNAs functions are still unknown.

We have used comparative genome analysis for the identification of ncRNAs(1,2,6). *Synechococcus* WH7803 is a model picocyanobacterium abundant in the mesotrophic areas of the ocean. For this and several closely related strains of marine *Synechococcus* about 150 RNA elements (non-coding RNAs, riboswitches and highly structured UTRs) were predicted (RNAz support value >0.4). In addition, a custom-made tiling microarray was developed for the WH7803 strain targeting exclusively the “empty” intergenic and non protein-coding regions of the genome. RNA was isolated from cyanobacteria cultivated under standard growth conditions or following environmentally relevant stress conditions and was directly fluorescence-labeled without cDNA synthesis.

Using this array we have identified several known as well as novel ncRNAs. Among them is the small RNA Yfr1, the 6S RNA, RNAs partially overlapping important functional genes coding for photosynthetic or circadian clock-related proteins. We found two ncRNAs responding specifically to cold stress. These are the first candidates for regulatory RNAs in marine *Synechococcus* potentially involved in adaptation to colder temperatures.

**References:**


**Huang, Katherine** and Penny Chisholm

Massachusetts Institute of Technology

**A DATABASE PORTAL FOR PROCHLOROCOCCUS**

One of the goals of the Chisholm Lab is to develop *Prochlorococcus*, and its phage, as a model system for Integrative Systems Biology. Advances in sequencing and high-throughput
technologies have begun to generate massive databases of microbial genes and transcriptomes in the oceans, and we are fortunate that Prochlorococcus genes are well represented in these data bases. In addition, genomes of cultured isolates of Prochlorococcus, and the phage that infect them, are growing in number, as are microarray experiments to examine gene expression. In order to fully exploit this growing database a well designed, user friendly, thought out and robust data management system is necessary. To this end, we are gathering all available Prochlorococcus data and centralizing them using MySQL, a relational database, which not only stores data but also describes the complex relationships between data types. This significantly broadens the accessibility of the data, and the flexibility of data mining. The database will include all sequenced genomes, metagenomes, metatranscriptomes, microarray experiments and the Prochlorococcus "bibliome" which we have been building for some time.

A public website will serve as a graphic user interface for the database. Power users will have direct access to the database for high-throughput data analysis that is beyond the scope of the website

Johnson, Zackary  
University of Hawaii

PROCHLOROCOCUS: UNDISCOVERED
Over the last 20 years, Prochlorococcus has emerged from being a newly-discovered group of cyanobacteria to become a well-studied model marine microbe that is of global importance. What began as an observation of a novel group of small marine phytoplankton, Prochlorococcus is now recognized as a genetically and physiologically diverse cluster of marine cyanobacteria that represents a key component in marine ecology and global biogeochemical cycles. In spite of this remarkable progress, there exists much that remains undiscovered. In this presentation I review some of the major unknowns and explore pathways for their elucidation.

Kettler, Gregory  
Massachusetts Institute of Technology

IMPACT OF GENE CONTENT ON PROCHLOROCOCUS ENATL ADAPTATION: BEYOND HIGH LIGHT AND LOW LIGHT
With twelve Prochlorococcus isolates' genomes now fully sequenced, we now know that the gene contents vary greatly both between and within the different ecotypes. We are interested in identifying the adaptive consequences of these differences. The high light- and low light-adapted phenotypes are well established, but the genomes suggest additional specialization within those groups. The NATL1A and NATL2A isolates are identified as low-light both experimentally and phylogenetically. And yet, they each possess more copies of the high light inducible (hli) gene family than any other Prochlorococcus isolate, even the high light-adapted. My aim is to test whether these genes confer a resistance to short-term high light exposures. In parallel, I am
mining metagenomic data to determine the prevalence the prevalence of hli genes in the natural population.

Kirchman, David L., V. Michelou, and M. Lomas
University of Delaware

PHOTOHETEROTROPHY BY PROCHLOROCOCCUS AND SYNECHOCOCCUS IN THE NORTH ATLANTIC OCEAN
The contribution of coccoid cyanobacteria (Prochlorococcus and Synechococcus) to phytoplankton biomass and primary production in the oceans is well known, but their role in using dissolved organic material (DOM) is less well understood. This presentation will summarize what is currently known about the uptake of organic C, N, and P by Prochlorococcus and other presumptive photoheterotrophic microbes in the North Atlantic Ocean. Recent work indicates that Prochlorococcus is responsible for a large fraction of light-stimulated bacterial production (leucine incorporation), but this microbe can also assimilate other amino acids, P33-DNA and P33-DNA at low concentrations in surface waters of various North Atlantic regimes. Synechococcus can also assimilate these compounds, although its contribution and that of other presumptive photoheterotrophs to bacterial production is often low. In addition to being the most abundant photoautotroph, Prochlorococcus may also be the most abundant photoheterotroph in the world’s ocean.

Lance, Veronica P.1,2, Johnson, Z.I.3, Ritchie, A.E.3, Barber, R.T.1
1NSEES, Duke University;
2now at Lamont-Doherty Earth Observatory at Columbia University;
3SOEST, University of Hawaii.

PRIMARY PRODUCTIVITY AND THE CONTRIBUTION BY A “PROCHLOROCOCCUS SIZE-FRACTION” IN THE WESTERN PACIFIC
During Jan-Feb 2007, near the end of the moderate 2006-2007 El Niño, the Western Pacific Warm Pool study sampled along a diagonal transect from Hawaii, crossing the equator at the dateline, then on to the Tasman Sea. Surface chlorophyll concentrations ranged from 0.03 to 0.17 mg chl m-3, mean areal primary productivity (PPEU; in units of mmol C m-2 d-1) was ~26 in the warm pool, ~10 in the Northern subequatorial region, ~17 south of the equator and ~40 in the Tasman Sea. A “Prochlorococcus size-fraction” (>0.2 to 0.8 µm) was responsible for ~78% of total PPEU in the north subequatorial region decreasing to ~30% south of the equator. This evidence suggests that Prochlorococcus can contribute a much higher fraction of the total primary in oligotrophic oceans than previously thought. As the oceans become warmer and more stratified with global climate change, the global contribution of Prochlorococcus to marine primary productivity may increase significantly.
**Lindell, Debbie, Maureen L. Coleman, Jacob D. Jaffe, Matthias E. Futschik, Trent Rector, Gazalah Sabehi, Claudia Steglich, Matthew B. Sullivan, Zackary I. Johnson, Erik R. Zinser, Robert Steen, George M. Church, Sallie W. Chisholm**  
Israel Institute of Technology

**CYANOBACTERIA-CYANOPHAGE INTERACTIONS: IMPACTS ON GENOME EVOLUTION AND GENOME EXPRESSION**

Viruses (phages) are an important component of ocean ecosystems, influencing population dynamics, diversity and evolution of their hosts. Here we present evidence for the impact of host-phage interactions on genome evolution and genome expression during infection. Using the cyanobacterium *Prochlorococcus* MED4 and the T7-like podovirus P-SSP7 as a model system we investigated whole-genome expression of both host and phage during infection. Phage genome expression progressed from left to right of the genetic map with time after infection (for the most part) with three distinct expression clusters being discerned. The DNA replication expression cluster included four ‘bacterial-like’ genes (psbA, hli, nrd, taIC) which we hypothesize are required for the acquisition of energy and deoxynucleotides for phage replication. Transcript levels of the vast majority of host genes, including psbA and most hli genes, declined during infection. Conversely, transcription of ca 40 host genes was induced with 2 distinct expression profiles being discerned. Upregulated genes included host stress response (including 5 hli genes), RNA degradation and protein turnover genes. Intriguingly, many of these up-regulated host genes are located in hypervariable regions thought to be laterally transferred by phages and homologues are found in cyanophage genomes. We therefore propose that the expression of these genes during infection may constitute the initial stage in the co-evolutionary process of gene exchange between host and phage.

**Mann, Elizabeth L., J. Fox, C. Wakeham, J. G. Sanders and G. F. Riedel**  
Skidaway Institute of Oceanography

**CONVERSATIONAL PIECES: *PROCHLOROCOCCUS* RESPONSES TO ARSENIC TOXICITY AND IRON LIMITATION**

Instead of a traditional poster, selected data describing *Prochlorococcus* responses to arsenic toxicity and iron limitation will be presented in the hope of sparking discussion. Two vignettes follow: A) Arsenic is toxic to phytoplankton in part because arsenate is an analog of phosphate. As a result, arsenic toxicity is most evident under conditions of phosphate limitation. The high light adapted stain Med4 is less affected by the addition of arsenate than the low light 9313 isolate. One explanation is that Med4 avoids importing arsenate by utilizing organic sources of phosphate, an ability that 9313 does not possess. B) Chlorophyll content and the number of photosynthetic units increase under low irradiance, which increases the demand for iron. Therefore, *Prochlorococcus* in deep chlorophyll maxima (DCM) may be iron limited, even in areas which are not considered typical HNLC regions. Preliminary data indicate that cell division rates increased slightly when iron was added to a DCM population in the eastern tropical North Pacific.
Milo, Ron
Harvard University

ENERGY OPTIMIZATION AND THE DESIGN OF PHOTOSYNTHESIS
The sun’s spectrum harvested through photosynthesis is the primary source of energy for life on earth. Plants, green algae and cyanobacteria – the major primary producers on earth - utilize reaction centers that operate at wavelengths of 680 and 700 nm. Why were these wavelengths “chosen” in evolution? We analyze the efficiency of light conversion into chemical energy as a function of hypothetical reaction center absorption wavelengths given the sun’s spectrum and the thermodynamic and kinetic cost associated with charge separation. We find that when taking into account the empirical charge separation cost the range 680-720 nm maximizes the efficiency. This finding suggests that the wavelengths of photosystem I and II are optimized for the utilization of the sun’s spectrum.

Moore, Lisa R., K. Krumhardt, L. Jackson, G. Rocap, K. Roache-Johnson, D. Robinson, D. Hardy
University of Southern Maine

PHYSIOLOGICAL RESPONSE OF PROCHLOROCOCCUS IN P-LIMITED CHEMOSTATS AND ON-DECK NUTRIENT ENRICHMENT EXPERIMENTS
In some regions of the world’s oceans where marine cyanobacterium Prochlorococcus dominate, phosphorus (P)-limitation is a regular occurrence. It is not clear, however, whether Prochlorococcus populations (or some ecotypes) are P-limited or have a competitive advantage under P limitation. Studies on P-stress response of various Prochlorococcus ecotypes revealed differences in their ability to utilize organic P sources and in alkaline phosphatase activity (APA), and these differences are reflected in genome content. This raises the question of what differentiates the P physiology of Prochlorococcus ecotypes and whether natural populations experience P limitation. To begin exploring these questions, P-limited chemostats of Prochlorococcus MED4 (HLI) were established and uptake kinetic experiments carried out. These results indicate that MED4 has a rapid uptake rate for P when grown under P-limiting conditions but is not more efficient at P uptake than other marine picophytoplankton. Also, increased P-uptake rates do not occur at the same time as increases in APA. On-deck nutrient enrichment studies in oligotrophic western Pacific indicate that Prochlorococcus populations grew and increased their APA in response to ATP but not inorganic P additions.

Morris, J. Jeffrey, Robin Kirkegaard, Anna Ritchie, Zackary I. Johnson, Leo Poorvin, Martin Szul, and Erik R. Zinser
University of Tennessee

HETEROTROPHIC BACTERIA “HELP” PROCHLOROCOCCUS SURVIVE OXIDATIVE STRESS
Prochlorococcus, a unicellular cyanobacterium, is the numerically dominant primary producer in the oligotrophic ocean, reaching maximum concentrations of ~105 cells/mL. However, axenic cultures of Prochlorococcus do not grow well at similar concentrations, and not at all at lower
concentrations. We report the ability of a phylogenetically diverse group of heterotrophic bacteria to “help” Prochlorococcus survive at low concentrations in liquid culture. These bacteria also allow Prochlorococcus to form colonies on semisolid media with high plating efficiency. On the other hand, catalase-deficient mutants of some of these bacteria were not able to “help,” while the addition of purified catalase to agar plates allowed colony formation without added heterotrophs. Taken together, these observations suggest that the “helping” phenotype involves the scavenging of hydrogen peroxide from the culture media. Finally, we present preliminary field evidence that the “helping” phenomenon is not a laboratory artifact but rather represents an interaction that is important for the survival of Prochlorococcus in the ocean.

Osbourne, Marcia S., Brianne M. Holmbeck, Jorge Frias-Lopez, Sallie W. Chisholm
Massachusetts Institute of Technology

THE EFFECTS OF UV RADIATION ON PROCHLOROCOCCUS ECOTYPES

Exposure to high solar radiation, especially in the UV-B range (280-320nm) causes high mortality in natural communities of pico-phytoplankton, including Prochlorococcus, both at the surface and down to a depth of at least 30 m (Llabres´ and S. Agust&#305;´, Limnol. Oceanogr. 51, 21–29, 2006, Agusti´ and Llabres´, Photochemistry and Photobiology 83: 793-801, 2007). DNA damage is a primary cause of death, mainly due to the formation of cyclobutane pyrimidine dimers, which are often lethal if not repaired.

In the process of developing a UV mutagenesis protocol for Prochlorococcus we isolated a UV-resistant strain of high-light adapted Prochlorococcus MED4. Initial characterization of the mutant showed it to be significantly more resistant to both UV-C (254 nm) and UV-B (302 nm) radiation than the WT parent. Furthermore, both the mutant and WT strains of MED4 were more resistant to UV than the low-light strain MIT9313. No differences were seen among the 3 strains following irradiation with UV-A (365 nm), which does not cause pyrimidine dimer formation, suggesting that UV resistance is related to the ability to repair pyrimidine dimers. Expression array analysis of the mutant relative to the wild type showed constitutive upregulation of 3 genes: phrB (photolyase), mutT (nudix hydrolase), and a small protein containing a putative spectrin repeat. Photolyase breaks pyrimidine dimers caused by UV exposure and is found in all high-light adapted and the low-light NATL Prochlorococcus strains, but is absent from other low-light strains. Nudix hydrolase, found in all ecotypes, also repairs DNA by hydrolyzing 8-oxo-dGTP resulting from oxidizing radiation. phrB and mutT appear to form an operon in MED4. Interestingly, these repair enzymes are not error prone and their activity is therefore non-mutagenic, in contrast to SOS (dark repair), which allows survival at the cost of mutagenesis.

qRT-PCR time-course analysis of the expression of 5 genes (phrB, mutT, spectin, recA, and radA) following UV treatment at 254 nm confirmed the elevated expression of photolyase and nudix hydrolase in the UV-resistant mutant. We also observed significant upregulation of recA expression in both the WT and mutant strains by 30-60 minutes after UV irradiation. Analysis of gene expression following UV-B irradiation is ongoing. In addition, whole genome sequencing of the UV-resistant mutant is under way, and results should help to unravel the number of
mutations involved and whether structural and/or regulatory genes are altered. We have also recently isolated a UV-resistant mutant of MIT9313 and are beginning its characterization.

These studies should help to elucidate differences in the mechanisms by which low-light strains such as MIT9313, that inhabit depths with very little UV exposure and that lack photolyase, and high-light strains such as MED4, that dominate the surface waters and are subjected to high doses of potentially mutagenizing radiation, have evolved to cope with DNA damage.

**Dufresne A, Ostrowski M, Scanlan DJ, Garczarek L, Six C, Hess WR and Partensky, Frederic**

Station Biologique

**MARINE SYNECHOCOCUS ADAPT TO NEW LIGHT NICHES BY LATERAL TRANSFER OF PHYCOBILISOME ROD GENE CLUSTERS**

Comparative genome analysis of 11 marine *Synechococcus* isolates, representing 10 distinct lineages and seven different pigment types or subtypes, enabled us to better understand the evolutionary processes driving genome divergence and niche adaptation in this group. The plasticity of *Synechococcus* genome sizes (2.22-2.86 Mbp) mainly results from a highly variable number of unique genes. Many of these are located in very dynamic regions or ‘islands’. Genes encoding the light-harvesting phycobilisome rod proteins are clustered in one of these islands, suggesting that *Synechococcus* cells can modify their light absorption properties via lateral gene transfer.

This is confirmed by phylogenetic analyses based on concatenated phycocyanin and phycoerythrin protein sequences which match the *Synechococcus* pigment types, but are incongruent with the core genome phylogeny. In contrast, phylogenetic trees based on concatenated allophycocyanin protein sequences are consistent with the latter. This suggests that light energy transport from the PBS core to photosystem II is an evolutionarily ancient and conservative mechanism that has not allowed much phenotypic variability during the course of evolution. Thus, it is more the diversity of the rod composition and the possibility of rod gene exchange between *Synechococcus* lineages which explains the adaptation of this genus to a variety of light niches.

**Post, Anton F., Chernichovsky M., Kamennaia N., Lindell D., Penno, S., Zandbank K.**

Marine Biology Laboratory, Hebrew University

**NITROGEN STRESS RESPONSES IN THE MARINE CYANOBACTERIA SYNECHOCOCUS AND PROCHLOROCOCUS SPP.**

Nitrogen is an essential nutrient, which is often limiting in marine waters, especially in oligotrophic, (sub)tropical seas where the unicellular cyanobacteria *Prochlorococcus* and *Synechococcus* are most abundant. These cyanobacteria are capable of acquiring different inorganic and organic nitrogen sources with each having a distinct spatial and temporal distribution. Nitrogen acquisition in these organisms is solely controlled via transcription of genes and operons controlled by NtcA, a transcriptional activator specific to N-stress responses. By
respectively studying ntcA nucleotide sequences, transcript levels and NtcA-targets across genome regions, we characterized genotypic diversity, stress response and adaptive potential of natural populations of *Synechococcus* and *Prochlorococcus* in the northern Red Sea. The northern Red Sea is abundantly populated with HLIi *Prochlorococcus* and 6-8 different *Synechococcus* clades, four of which had not been identified earlier by means of 16S, ITS or rpoC based PCR protocols. There was a distinct seasonal succession of the more mesotrophic clade II ecotypes that thrive during the spring bloom to oligotrophic clade III ecotypes during summer stratification. Interestingly, ntcA expression indicated that the latter were ammonium sufficient even though ambient concentrations were only 7-70 nM. However, clade II ecotypes expressed ntcA during the spring bloom, presumably to facilitate nitrate utilization. Genome analyses have permitted the identification and characterization of the NtcA target genes and their binding sites. The bulk of nitrogen acquisition genes were found to be localized to a 60 kb genomic region. This region showed a large degree of variation among the different *Prochlorococcus* and *Synechococcus* genomes, which enabled identification of novel nitrogen niches in ocean environment and better define terms of co-existence for these abundant marine cyanobacteria.

**Ritchie, Anna and Zackary Johnson**
University of Hawaii

**PROCHLOROCOCCUS ABUNDANCES IN THE WESTERN TROPICAL PACIFIC**

Numerous meridional transects in the Atlantic Ocean have revealed dynamic populations of *Prochlorococcus* that are most abundant from about 40N to 40S. Much of this variability tracks along isotherms, suggesting that temperature may be a driving environmental variable. Nevertheless, vertically integrated concentrations of *Prochlorococcus* remain relatively constant along the transects, pointing to the importance of other processes. Recently, we completed two major samplings efforts in the Western Pacific Ocean, one a zonal sampling along the equator from 140W to 160E and the other a meridional sampling from Hawaii to the Tasman Sea. Like in the Atlantic Ocean, we find that the variability of *Prochlorococcus* concentrations closely tracks isotherms along the meridional transect. However, we also find significant variability along the equator that is unrelated to temperature variability. Like in the Atlantic, the depth-integrated concentrations of *Prochlorococcus* are relatively conserved across the vast regions of the ocean sampled by the two transects, in spite of significant depth variability. These results suggest that in spite of significant variability in local concentrations, which are further divided by different ecotypes, fundamental mechanisms exist which constrain the variability of depth-integrated *Prochlorococcus* biomass over vast ocean regions.
**Rivers, Adam R., and Eric A. Webb**  
Massachusetts Institute of Technology / Woods Hole Oceanographic Institution

**IRON STRESS GENES IN MARINE SYNECHOCOCUS AND THE DEVELOPMENT OF A FLOW CYTOMETRIC IRON STRESS ASSAY**

Marine *Synechococcus* are frequently found in environments where iron (Fe) is a limiting nutrient. To understand their capacity to respond to Fe stress, we screened picoplankton genomes and the Global Ocean Survey (GOS) metagenome for known Fe stress genes. Many open-ocean strains of *Synechococcus* lack known genes for Fe stress, while coastal and upwelling strains contain many, suggesting that maintaining multiple Fe-limitation compensation strategies is not a selective advantage in the open ocean. All genomes contained iron deficiency-induced protein A (IdiA) and its complementary Fe\(^{3+}\) transport proteins. The ubiquity of IdiA was exploited to develop an *in situ* Fe stress bioassay based on immunolabeling and flow cytometry. As a test of field applicability, we used the assay on natural *Synechococcus* populations from one station in the Costa Rica Upwelling Dome (CRD) where the phytoplankton were speculated to experience Fe stress. The bioassay supported the Fe stress hypothesis, finding IdiA labeling in more than one third of the *Synechococcus* population present. Based on our findings, we believe that this assay can reveal environmental and clade-specific differences in the response of *Synechococcus* to Fe stress.

**Rodrigue, Sébastien, Rex Malmstrom, Matthew Henn, Kun Zhang, Adam Martiny, George Church and Sallie W. Chisholm**  
Massachusetts Institute of Technology

**SINGLE-CELL GENOMICS OF PROCHLOROCoccus**

Complete genome sequencing of individual microbes is rapidly becoming a reality through the combination of randomly-primed whole genome amplification and next generation sequencing platforms. One of the critical requirements in developing robust single-cell genomics pipelines is the elimination of background DNA from the sample before amplifying the genome of the single cell. This is particularly challenging when trying to study single microbial cells from the wild, such as the ubiquitous marine cyanobacterium *Prochlorococcus*. To overcome this challenge, we are developing a flow-cytometry based approach to remove single *Prochlorococcus* cells from the high concentrations of free-DNA normally found in the seawater. Our high throughput approach entails sorting individual cells into separate wells of a 96-well plate, amplifying extracted DNA with phi29 polymerase, and PCR screening of amplified genomic material using diagnostic primer sets. This pipeline not only provides products for whole genome sequencing of selected cells, but also enables multi-locus sequence analysis of natural populations without the need for isolation of different strains. To validate the method, we first sorted individual cells of the cultured *Prochlorococcus* strain MED4, and prepped them for sequencing using the Illumina Genetic Analyzer and Roche 454 platforms. In spite of a substantial unevenness in the amplified DNA, we have been able to cover an important fraction of the *Prochlorococcus* MED4 genome with this strategy. We are also initiating an effort to sort and amplify single *Prochlorococcus* cells collected in the tropical South Pacific ocean, where we expect to find interesting genomic variants.
Rusch, Doug  
J. Craig Venter Institute

**PROCHLOROCOCCUS VARIANTS FROM THE GOS METAGENOME**

We have isolated a novel surface water *Prochlorococcus marinus* variant from the Global Ocean Survey metagenome. This variant is exclusive to the Pacific Ocean basin and is found to the exclusion of the other surface water strains. The genome was assembled using aggressive assembly techniques to approximately a 15-fold depth of coverage. On average it is approximately 20% divergent in nucleotide identity to the MIT9312 *Prochlorococcus* genome. Here we examine the genomic differences and catalog the environmental conditions that determine this Prochlorococcus range and role in the community.

Selph, Karen and Susan Brown  
University of Hawaii at Manoa, Department of Oceanography

**GRAZING DYNAMICS OF PROCHLOROCOCCUS**

Since the discovery of *Prochlorococcus*, and the realization of the key role it plays as the dominant primary producer in oligotrophic open ocean ecosystems, the dynamics of this organism have been of keen interest to biological oceanographers. Roughly coincident with the realization of its key ecosystem role, was a growing awareness of the importance of microzooplankton grazers in oceanic systems — a group which includes the most important grazers of *Prochlorococcus*. One widely used method to study the natural growth and mortality rates of phytoplankton, including *Prochlorococcus* and *Synechococcus*, is the seawater dilution technique, first reported by Landry and Hassett in 1982. This method allows the simultaneous measurement of growth and grazing rates in incubation experiments where the grazing impact is fractionally reduced in a dilution series consisting of natural seawater diluted with particle-free seawater. Flow cytometry and HPLC (divinyl chlorophyll) data will be presented showing the results of such experiments in a transect across the Pacific, including stations in the Western Warm Pool. Across the transect, average daily growth rates of *Prochlorococcus* down to the 25% light level (usually <50 m) are high, at ~1 doubling per day, and roughly equal to average daily mortality rates by microzooplankton. Growth rates increased with ammonia additions in the oligotrophic gyre, but not in the Warm Pool where ambient nitrate + nitrite concentrations were 10-fold higher. These data suggest that the lowest trophic levels in these systems are tightly coupled, with the high daily production of *Prochlorococcus*, the dominant phytoplankton in these systems, being consumed by protistan grazers concurrently. Thus, despite low chlorophyll standing stocks and the lack of obvious seasonal blooms in biomass, the turnover rate of the biota, and hence primary production of these systems, is potentially much higher than historically realized.
A MARINE HETEROTROPHIC BACTERIUM THAT INHIBITS THE GROWTH OF PROCHLOROCOCCUS IN CO-CULTURE

The abundance of Prochlorococcus and other cyanobacterial primary producers in the oceans is believed to be limited mainly through predation by eukaryotic grazers and/or lysis by phage. However, while these cyanobacteria are surrounded by a community of heterotrophic bacteria, little is known about how the heterotrophic community can directly affect their growth and/or mortality. Specifically, while it has been shown that many marine bacteria can inhibit the growth of other bacteria through the production of antibiotic substances, it is not known whether such antagonistic interactions occur between heterotrophs and cyanobacterial primary producers, and whether such interactions might affect primary productivity in the oceans.

To measure the effect of heterotrophic bacteria on the growth of Prochlorococcus, we have constructed a library of ~600 heterotrophic bacterial isolates from several depths at the Hawaii Time Series Station ALOHA, and used this library to screen for isolates able to affect the growth of Prochlorococcus in liquid co-culture. Using this approach, we have isolated a heterotrophic bacterium, termed HOT4E8, which is able to significantly inhibit the growth of many strains of Prochlorococcus, including both high light strains such as MIT9515 and AS9601 and low light strains such as NATL2A and SS120. In contrast, HOT4E8 did not inhibit the growth of Synechococcus WH8102 or CC9220. This inhibition takes place at ecologically relevant cell densities, with approximately 104 HOT4E8 cells/ml needed to significantly inhibit the growth of 105 Prochlorococcus NATL2A cells/ml. Interestingly, HOT4E8 did not inhibit the growth of the axenic Prochlorococcus strain MED4ax, raising the possibility that the inhibitory effect observed in other Prochlorococcus strains may be due to a three way interaction between HOT4E8, additional heterotrophic bacteria found in the non-axenic Prochlorococcus strains and the Prochlorococcus cells themselves. The mechanistic basis for this interaction is currently being studied. In contrast to HOT4E8, other bacterial strains were able to enhance the growth of Prochlorococcus. Our results suggest that antagonistic – and possibly synergistic - interactions between Prochlorococcus and different heterotrophic bacteria may affect the growth and abundance of these important marine primary producers.

FROZEN METABOLIC ACCIDENTS CONSTRAIN EVOLUTION OF THE CYANOBACTERIAL GENOME CORE

Cyanobacteria, the only known oxygenic photosynthetic bacteria, hold the key to the origin and evolution of oxygenic photosynthesis, the advent of which fundamentally changed the course of life on Earth. In the last two decades, concomitant with the advance in various aspects of cyanobacterial research, there has been a deluge of ever-growing genome sequence data. Yet, addressing molecular evolution on the genome scale has been challenging, not only because of
the unwieldiness of the unprecedented amount of data, but also because of the problems of substantial levels of horizontal gene transfer (HGT) in bacterial domain of life. Using a comparative genomics-based bioinformatic approach, we identified 682 conserved protein families from 13 genomes of cyanobacteria. By carefully filtering out genes that may have been subject to HGT, we considered only a “core” of genes that seem to have a coherent evolutionary history and used them to construct a robust phylogeny. This automated phylogenomic analysis greatly clarifies the evolutionary relationships among cyanobacteria. Moreover, our results convincingly demonstrate that photosynthetic and ribosomal proteins are key components of the cyanobacterial genome core. Many of key proteins tend to be encoded by tightly clustered putative operons which often are requisite of functional proteins that physically interact. This finding strongly suggests that the evolution of cyanobacteria is constrained by macromolecular interactions in complex metabolic pathways. In effect, these metabolic pathways have become frozen metabolic accident and sustained to the present time with very few modifications.

Sosik, Heidi M. and Robert J. Olson
Woods Hole Oceanographic Institution

SEASONALITY AND TEMPERATURE REGULATION OF SYNECHOCOCUS: NEW INSIGHTS FROM SUBMERSIBLE FLOW CYTOMETRY EMPHASIZE DIFFERENCES BETWEEN SHELF AND OPEN OCEAN ECOTYPES

Dramatic seasonal variations in Synechococcus populations are a common feature in temperate coastal zones where annual temperature ranges are large. We are taking advantage of the Martha’s Vineyard Coastal Observatory (MVCO), a cabled facility on the New England inner shelf, as a model system to better understand the physical and biological processes that interact to produce this variability. Our approach depends on high resolution (~hourly) multi-year time series of Synechococcus acquired with FlowCytobot, a custom-built automated submersible flow cytometer. At MVCO, Synechococcus abundance varies seasonally over more than three orders of magnitude, with a minimum in late winter followed by an approximately logarithmic increase through spring and early summer. From observed diel changes in cell size distributions and a matrix population model, we derive daily population growth rates that emphasize the importance of temperature limitation of Synechococcus in setting this seasonal pattern. Both observations for natural assemblages and laboratory experiments with isolates from MVCO support the conclusion that Synechococcus of the New England Shelf are adapted to growth at much lower temperatures than previously documented for open ocean ecotypes. While temperature regulation is critical, the time series also suggest an important role for grazing in determining aspects of the seasonal cycle. We are currently exploring the hypothesis that wintertime temperatures are an important source of interannual variability in timing of the Synechococcus spring bloom on the shelf.
A SYSTEMATIC MICROARRAY SCREEN FOR NCRNAS IN PROCHLOROCOCCUS

Small non-coding RNAs (ncRNAs) are functional RNA molecules, mostly without a protein-coding function, that have been found in all domains of life. In bacteria these functional RNA molecules range in size between 50 – 400 nt and frequently play a crucial role in regulatory networks particularly in response to environmental stress. ncRNAs are also known to control plasmid and viral replication, bacterial virulence and quorum sensing, while the function of others has remained unknown. Another class of regulatory RNAs – chromosomally encoded antisense RNAs (asRNAs) - is important for the regulation of mRNA stability. There are no systematic approaches to screen for asRNAs, but RNomics approaches have inadvertently revealed the presence of asRNAs in Escherichia coli. These cis-encoded asRNAs are transcribed from the opposite strand of the same genomic locus as the target (m)RNA and feature 100 % base complementarity. In contrast, ncRNAs that are mostly located in intergenic regions, act trans in a different genomic locus and exhibit only a short and imperfect base complementarity with their target transcripts.

Our analysis of microarray expression data of intergenic regions from Prochlorococcus MED4, together with a previous comparative genomics approach revealed the existence of more than 20 ncRNAs. The relative number of ncRNAs in Prochlorococcus thus is comparable with those found in enterobacteria like Escherichia coli, each with 1 – 2% of the genes coding for ncRNAs. Genome reduction in Prochlorococcus has particularly affected the number of genes coding for regulatory proteins, suggesting that regulation of gene expression through ncRNAs plays an important role in Prochlorococcus’ response to environmental cues. Some of these functional RNAs are likely to be involved in processes such as light stress adaptation or the response to phage infection as inferred from their mode of regulation. Furthermore, the enrichment in ncRNA genes in genomic islands of Prochlorococcus suggests that these islands are an important vehicle for the acquisition of ncRNAs.

VIRUS-ENCODED CYANOBACTERIAL METABOLIC GENES: WHAT CAN WE LEARN FROM THE EXPANDING DATABASES?

Cyanobacterial viruses (cyanophages) are abundant in the oceans, and the few cyanophage genomes sequenced to date often contain ‘auxiliary metabolic genes’ (AMGs) that are homologous to those from their hosts. Perhaps the most notable AMGs are the core reaction center photosynthesis genes that are nearly ubiquitous among the genomes, are expressed during infection and appear to generate diversity for their hosts. The many other AMGs that have been identified in these few genomes are not as universally distributed, but likely still play important roles during cyanophage infection. For example, the cyanophage-encoded
phycoerythrobilin synthase gene is found in only 1 of 4 myovirus genomes sequenced to date, but in that 1 cyanophage appears functional in vitro and in vivo. We wondered how expanding databases might inform our understanding of such sporadically distributed AMGs, what other cyanobacterial metabolisms are encoded by cyanophages, and more generally how wide-spread the AMG phenomenon is among oceanic viruses in wild populations. To this end we used the proteins from all available sequenced marine microbial genomes as blast queries against 20 cyanophage genomes and publicly available viral metagenomics databases. To date we have only analyzed the cyanobacteria-specific results. As expected, the relatively well-studied core photosynthetic proteins (eg. psbA, psbD) are a dominant signal in this group, as are high-light inducible proteins. Also prevalent in this expanded database are previously observed phosphate-stress response AMG’s (pstS, phoH) and those involved in carbon currency (talC and other pentose phosphate genes), while the low frequencies of other AMGs (e.g., a suite of previously described nucleotide metabolic genes – purHLMN, pyrE) suggest these pathway genes are either important for highly specialized cyanophage-host interactions, or that these AMGs are evolutionary transients in these cyanophage genomes. The expanded dataset also revealed novel AMGs that likely function in phosphate-stress response (alkaline phosphatase, phosphoregulation), carbon metabolism (acetyl coA synthase and carboxylase) and nitrogen metabolism (regulatory, synthetase and transporter genes). It is noteworthy that both “core” and “flexible” Prochlorococcus genes were found in the cyanophage AMG pool, suggesting that cyanophages carry genes that are critical for a diversity of hosts’ metabolisms (‘core’ genes) during phage infection, but that they also take advantage of metabolisms enabled by the niche-defining ‘flexible’ genes for more specific host-phage interactions.

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DOMINANCE OF SYNECHOCOCCUS CLADES I AND IV DURING A COASTAL MARINE TIME-SERIES

Marine cyanobacteria from the genus Synechococcus are found throughout the world’s oceans and are important contributors to global primary productivity and carbon cycling. Cultured isolates and environmental DNA clone libraries of Synechococcus have demonstrated the diversity of these microbes, however, the natural distribution of this diversity through space and time and the ecological significance of their distribution are still poorly understood. To understand the seasonal dynamics of Synechococcus diversity, we have developed a quantitative PCR strategy using the RNA polymerase C (rpoC) gene and applied it to a three-year time series of surface samples from the Scripps Institution of Oceanography pier (La Jolla, CA). Synechococcus from clades I and IV were dominant throughout the time-series and corresponded with total Synechococcus abundance. Of these two dominant clades, Synechococcus from clade IV were typically more abundant, however, those from clade I dominated during periods just prior to the annual spring bloom of Synechococcus. Synechococcus from clades II and III were absent during spring and early summer, but appeared at low abundances in late summer and winter. As the first long term time-series describing Synechococcus population diversity, these seasonal dynamics provide crucial information for understanding the interplay between genetic/genomic diversity, physiology, and the environment.
**PROCHLOROCOCCUS AND IRON**

Despite the ubiquity of *Prochlorococcus*, little is known about its minimum iron requirement and mechanisms of iron uptake. Given the diversity of *Prochlorococcus* ecotypes in terms of their light, nitrogen, and phosphorous physiology, as well as the natural gradients of iron concentrations over depth and over the geographical range of *Prochlorococcus*, we expect to observe differences in the iron physiology and iron requirement of the *Prochlorococcus* ecotypes. In order to understand the mechanism by which *Prochlorococcus* copes with iron stress, gene-expression of strains MED4 and MIT9313 was measured in response to abrupt iron deprivation using whole-genome microarrays. Also, the iron quota (Fe:C) of these two strains was measured over a range of iron concentrations and at two light intensities. Whole-genome expression results reveal that MED4 and MIT9313 use different sets of genes in their response to abrupt iron deprivation with the exception of the up-regulation of the known iron-stress related genes flavodoxin (isiB) and iron-deficiency-induced protein (idiA). Interestingly, MED4 lacks a stretch of genes that is up-regulated in MIT9313 (including a possible porin) and is present in most other high- and low-light ecotypes, in the environmental databases, and is predicted to be involved in iron uptake (Coleman and Chisholm 2007). In both strains, several genes of unknown function were differentially expressed in response to iron deprivation. Though MIT9313 is capable of steady-state growth at lower iron concentrations than MED4, the iron quota of these two strains is equal. The gene expression and iron quota measurements together suggest that MED4 and MIT9313 may use different systems of iron acquisition to maintain a similar iron quota. By beginning to describe the relationship between *Prochlorococcus* and iron we hope to better understand the link between the carbon and iron biogeochemical cycles in the ocean and the ecological factors that allow *Prochlorococcus* to dominate the microbial community of this oligotrophic environment.

**TRANSaLDOLASE IN VIRUSES INFECTING PROCHLOROCOCCUS: HIJACKING HOST CARBON METABOLISM WITH A NON-CYANOBACTERIAL ENZYME**

Among the several auxiliary metabolic genes (AMGs) carried by cyanophages infecting *Prochlorococcus* are genes for transaldolase, a key enzyme in the pentose phosphate pathway of cyanobacteria. Like the photosynthesis genes also carried by these cyanophage, the transaldolase gene (talC) is not found in any other type of virus. In the over 3,000 viral genomes in GenBank, including over 300 tailed bacteriophages, talC is found only in cyanophages infecting *Prochlorococcus* and *Synechococcus*. Unlike most other AMGs, however, talC does not resemble the transaldolase gene (talA) in the host; rather, it is most closely related to non-cyanobacterial genes. This raises the question of the evolutionary origin of this gene, and why the phage would have acquired it rather than the version carried by its host. If this viral talC encodes functional
transaldolase, potentially with augmented properties, it could significantly increase flux through the host’s pentose phosphate pathway, helping to generate ribose-5-phosphate and NADPH for phage nucleotide production. Here, we use structural data from an E. coli ortholog of talC to argue that the phage TalC protein has transaldolase activity. To test this hypothesis, recombinant talC from several Prochlorococcus phages was cloned, sequenced, and expressed in E. coli. The enzymes were purified to homogeneity and shown to have robust transaldolase activity, assayed using continuous spectrophotometric rate determination, with product formation coupled to NADH oxidation. Kinetic properties are comparable to those of other members of this enzyme family and suggest that cyanophage transaldolase could be active in vivo. Similar work on the transaldolase orthologs of Prochlorococcus (talA) shows that they too have transaldolase activity as predicted. Ongoing efforts are comparing kinetic features between phage and host enzyme pairs from organisms known to interact naturally, with the goal of identifying key differences that may explain the presence of talC in marine cyanophages.

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**PROBING THE STRUCTURE AND FUNCTION OF* PROCHLOROCOCCUS*: FROM GENOME TO THREE-DIMENSIONAL CELLULAR ARCHITECTURE**

Our recent work on the near-native, three-dimensional architecture of *Prochlorococcus* identified major differences that have evolved in closely-related strains in key structures, such as the cell wall and the intracytoplasmic lamellae, where polypeptides involved in photosynthesis are localized (Ting et al. (2007) J. Bact. 189:4485-4493). We are investigating the physiological implications of these structural differences and how they impact the molecular responses of individual *Prochlorococcus* strains to abiotic stress. Results of our global comparative genomic analyses underscore the dynamic character of the *Prochlorococcus* chromosome. Major gene rearrangements and dissimilarities in gene content, including in stress response related genes, distinguish the genomes of strains that are deeply branched and strains that belong to the clade of more recently differentiated lineages. Notably, in contrast to other cyanobacteria and bacteria, we have found that thermal stress does not induce the synthesis of many polypeptides in MED4. This strain belongs to the large clade of recently differentiated lineages and possesses one of the smallest genomes of any photosynthetic organism. Furthermore, our data indicate that thermal stress results in damage to the Photosystem II (PSII) reaction center of the MED4 strain. Western analyses reveal heat stress-induced declines in PsbA, a 32 kDa core PSII subunit, but not in PsaC, a Photosystem I-associated polypeptide. Our data suggest that fundamental differences exist in the ability of this strain to maintain active photosynthesis and productive protein folding, assembly, and stabilization at elevated temperatures. These studies will broaden our understanding of how predicted changes in global climate and the ocean environment could affect populations of this ecologically important microorganism.
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BIOCHEMICAL STOICHIOMETRY OF PROCHLOROCOCCUS CELLS

The uniquely small genome and cell size of *Prochlorococcus* strongly influence its ecology and evolution. Studies over the past twenty years have generated sufficient information about the elemental, chemical and physical composition of *Prochlorococcus* cells to provide a first-order estimate of the stoichiometry of the principal cellular components. This picture of cellular composition highlights some of the adaptations that have allowed *Prochlorococcus* to thrive in oligotrophic regions of the ocean. Notably, as much as half of cellular phosphate is in the chromosome, very little is in lipids, and only a small proportion of a cell’s genome is transcribed into mRNA at any given time. The resource-saving effect of genome reduction and shift to low G+C content between low-light and high-light ecotypes is predicted to be relatively small in and of itself, but may contribute to overall cellular streamlining and economization. Several key gaps in our knowledge of cell composition are also apparent, including in the biochemical distributions of nitrogen and trace metals, and in reconciling observed rates of carbon fixation and photosynthetic electron transport with the inventories of proteins that enable those processes. These considerations also help to constrain the effect of lytic phage infection on cellular biochemical stoichiometry, and its implications for water-column element cycling.
THE APPLICATION OF FLOW CYTOMETRY TO ENUMERATION AND SIZING OF MARINE PHYTOPLANKTON POPULATIONS

The use of flow cytometry in marine systems was instrumental in the discovery of the planet’s most abundant primary producer, Prochlorococcus. Flow cytometry continues to be a powerful tool for enumerating marine pico- and nano-plankton populations. We are interested in evaluating the relative contributions of the cyanobacteria Prochlorococcus and Synechococcus as well as their eukaryotic counterparts, the picophytoeukaryotes. Because of the broader distribution and variability in cell size of picophytoeukaryotes (as well as Prochlorococcus) our interest has been in calibrating flow cytometers to render an estimate of cell volume from light scatter parameters. To this end, experiments have been conducted using a range of mid-exponential growth picophytoplankton cultures. Physical properties measured include forward angle light scatter (FALS), pulse width, side scatter (SSC), Coulter Multisizer volume and carbon per cell via CHN analysis. The flow cytometer in use is the InFlux Mariner (Cytopeia Corp). These measurements have been interrelated to develop an algorithm allowing a reasonable estimation of population biomass. In addition, the influence of various fixation procedures have been evaluated on the same culture series. Similar measurements have been made on live populations at-sea, and post fixation. Our instrument cannot discriminate Prochlorococcus populations in oligotrophic surface waters, due to low signal to noise ratios in the red channel. However, with that caveat, these methods are providing refined insight into the contributions of individual picoplankton populations, not only in terms of abundance but also biomass and production.

PICOPHYTOPLANKON COMMUNITY DYNAMICS AT A TROPICALLY INFLUENCED TIME-SERIES TRANSECT

Photosynthetic picoplankton are dominant primary producers in open-ocean regions of the world. Knowledge regarding the distribution and genomic capabilities of Prochlorococcus has led to a refined understanding of the dynamics and distribution of this genus. Prochlorococcus co-exists with a diverse assemblage of other microbes, including photosynthetic eukaryotes. Given the tremendous advances in understanding of dynamics of both Prochlorococcus and its relative Synechococcus, we have focused on third highly diverse group, the picoeukaryotes. At a tropically influenced time-series transect, Prochlorococcus was found to always dominate, both in terms abundance and biomass. Picoeukaryotes were responsible for a large fraction, second to Prochlorococcus, of biomass in this fraction, while Synechococcus contributed relatively little overall. The dominant taxa across are pico-prymnesiophytes, with sequenced representatives belonging solely to uncultured groups. The relationship between these pico-prymnesiophytes and Prochlorococcus is being explored through FISH, Q-PCRC and culture independent whole genome sequencing.
TEMPERATURE AND REACTIVE OXYGEN SPECIES AS ECOLOGICAL DETERMINANTS FOR PROCHLOROCOCCUS

The first twenty years of research on Prochlorococcus has taught us much about the global distribution and the genetic and physiological diversity within this numerically-dominant lineage. One of the key challenges for the Prochlorococcus research community in the 21st century is to identify the physiological traits that determine the abundances and activities of the Prochlorococcus lineages in nature. Our laboratory has focused on two environmental factors that strongly influence Prochlorococcus growth and survival: temperature and oxidative stress. Lineages of Prochlorococcus are broadly distributed into high-light- and low-light-adapted ecotypes, and optimization for growth at different temperatures further partitions the niche between the two high-light adapted ecotypes. Our analysis of Prochlorococcus in the Pacific Ocean, and in particular the Western Pacific Warm Pool - with temperatures exceeding 30°C – confirms and extends these observations. Laboratory and field studies have further indicated that Prochlorococcus cells are especially sensitive to reactive oxygen species, and we have discovered that their heterotrophic bacterial neighbors play a critical role in protecting them from these harmful agents.
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