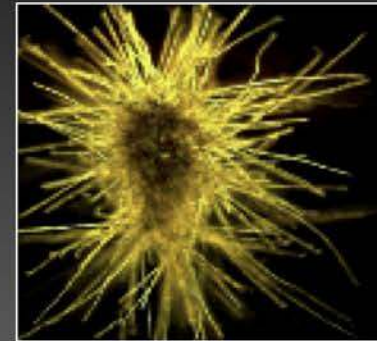


Vignettes

- From genome to biome: Tracking the metabolism and microbiome of a keystone N_2 fixer

Genome - enabled



- Co-existing in a sea of competition: Leveraging transcriptome data to identify the physiological ecology of phytoplankton from key groups

Transcriptome - enabled



Complex community dynamics driven in part by resources



Complex community dynamics driven in part by resources

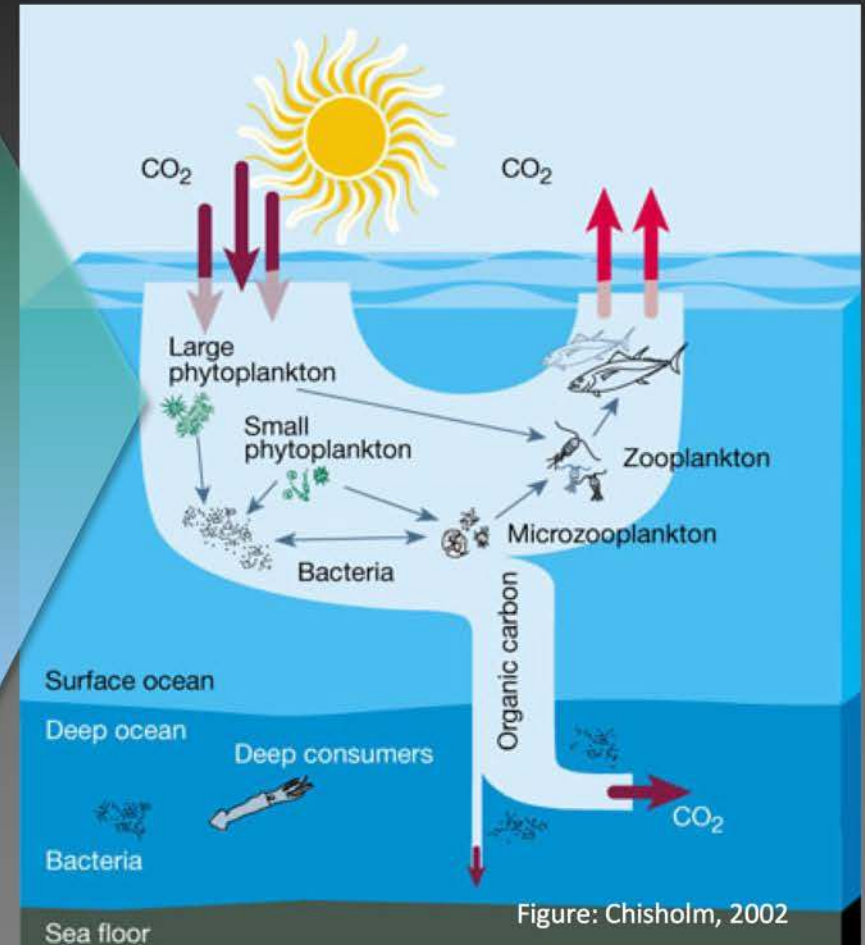
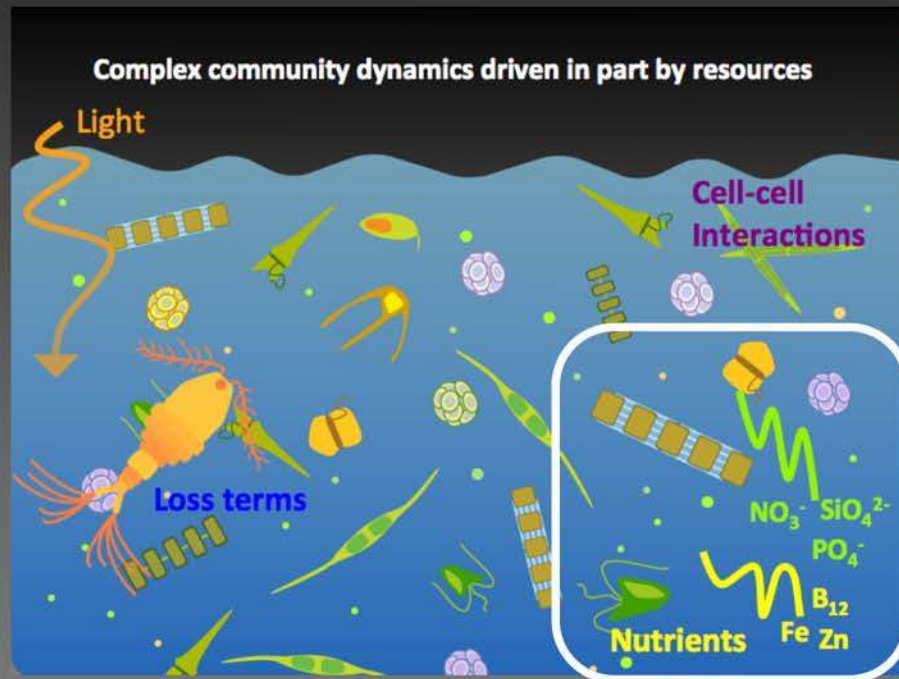


Complex community dynamics driven in part by resources



Tracking phytoplankton physiological ecology

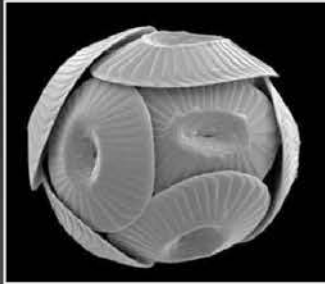
Ecosystem function and biogeochemistry



How do resources drive phytoplankton distributions and activities?

Focus on keystone groups

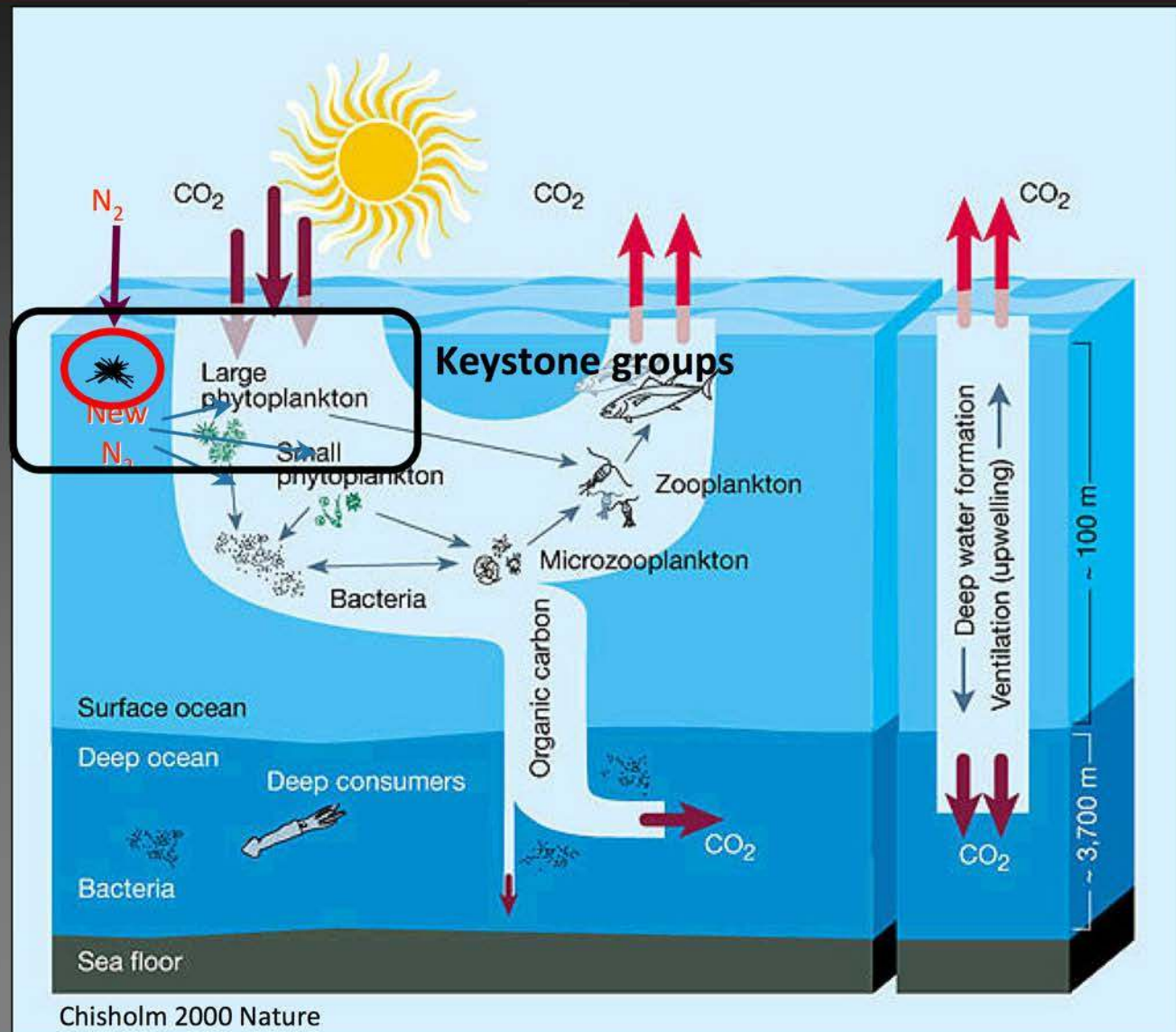
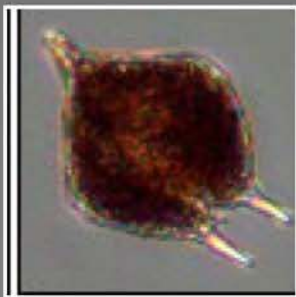
Haptophytes



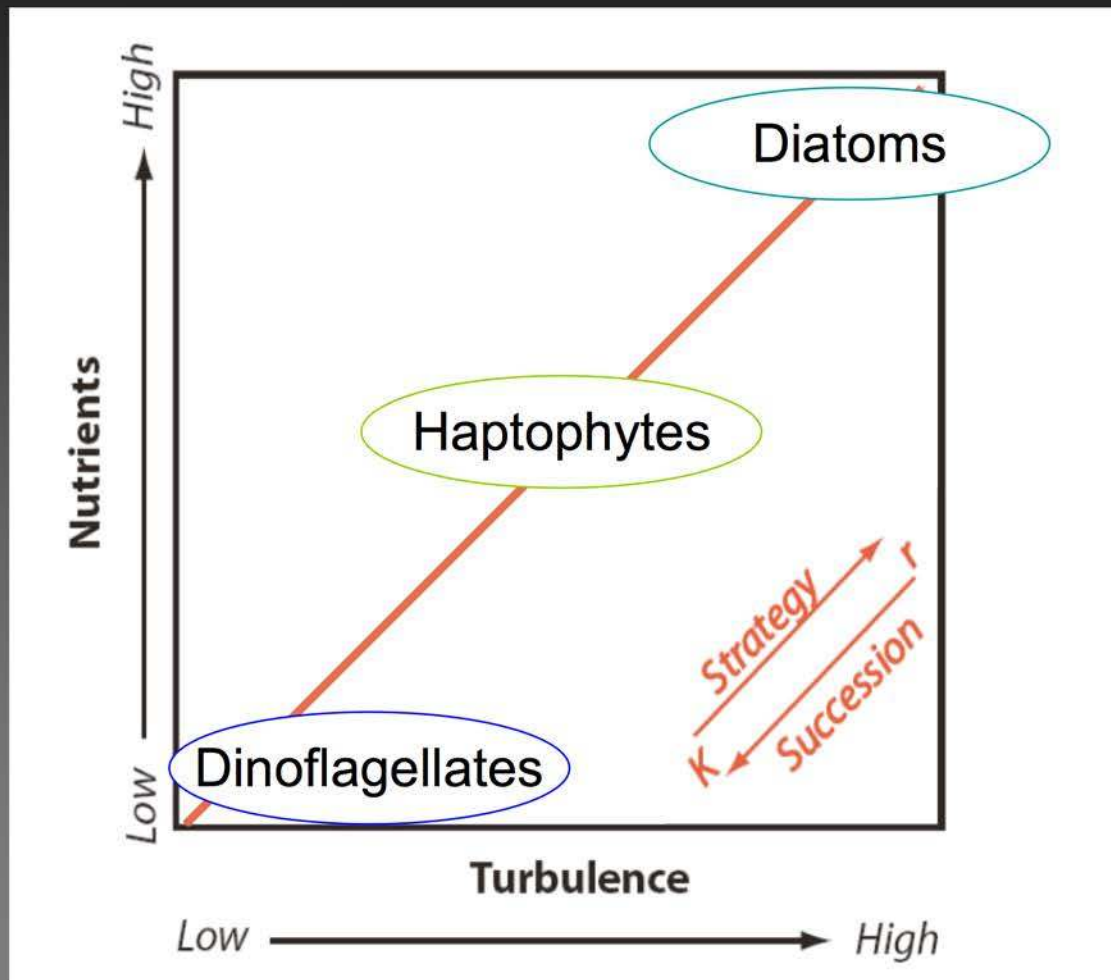
Diatoms



Dinoflagellates

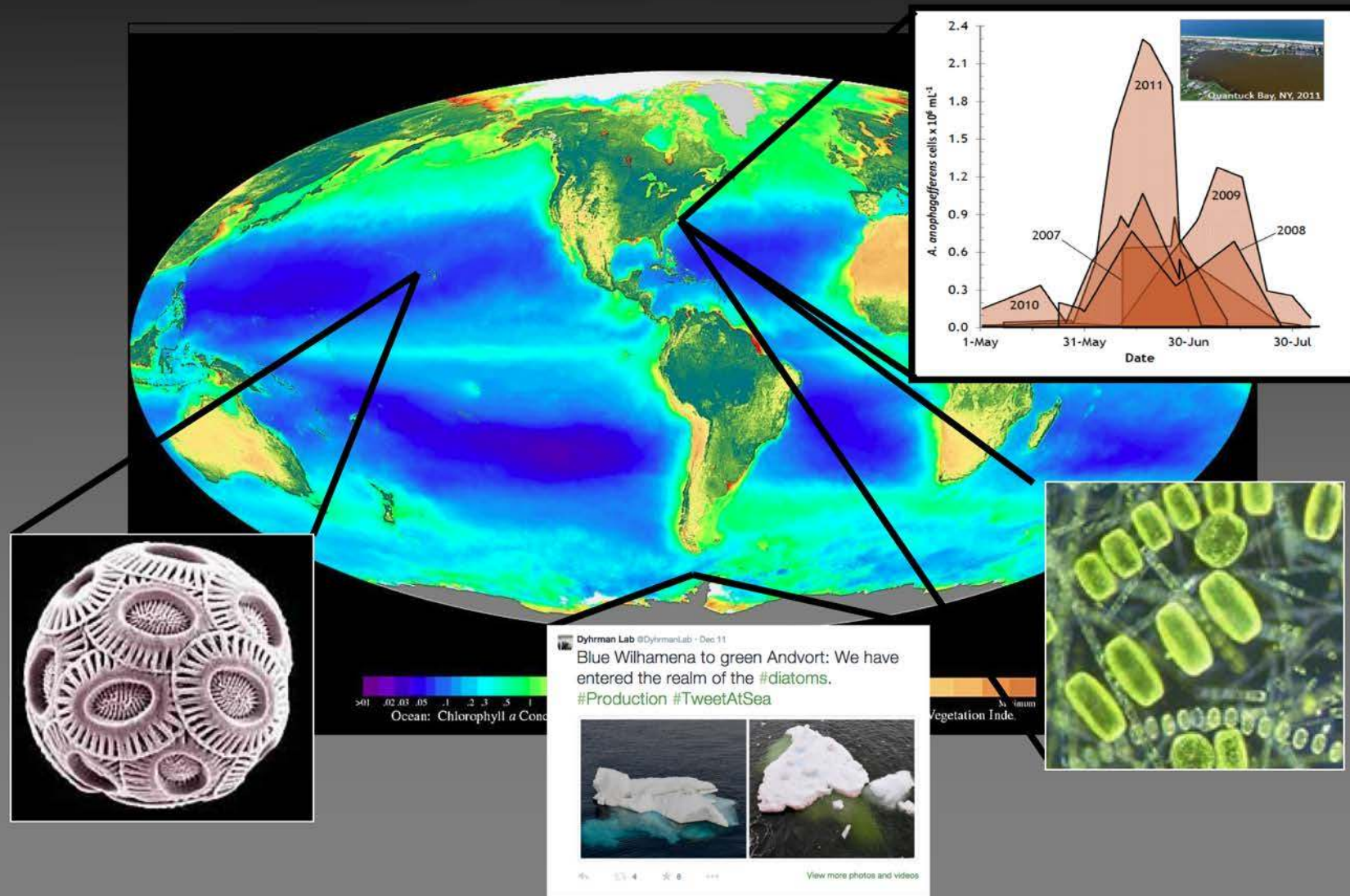


Margalef's Mandala - succession and ecological traits



Adapted from Margalef 1978

Tracking phytoplankton with metatranscriptomics - roles of competition, resource availability, light and viruses



Two themes

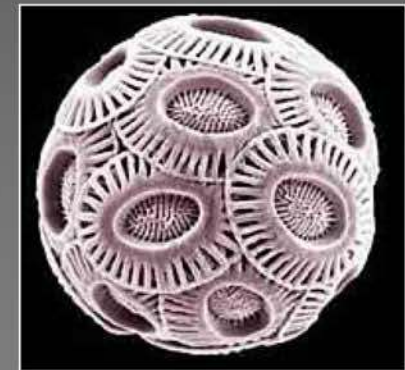
Eco-evolutionary traits

- Are there functional group traits that drive the bloom dynamics that structure the low nutrient North Pacific Subtropical Gyre?



Metabolic plasticity

- How do resources drive the physiological ecology of a keystone coccolithophore?



The significance of the NPSG

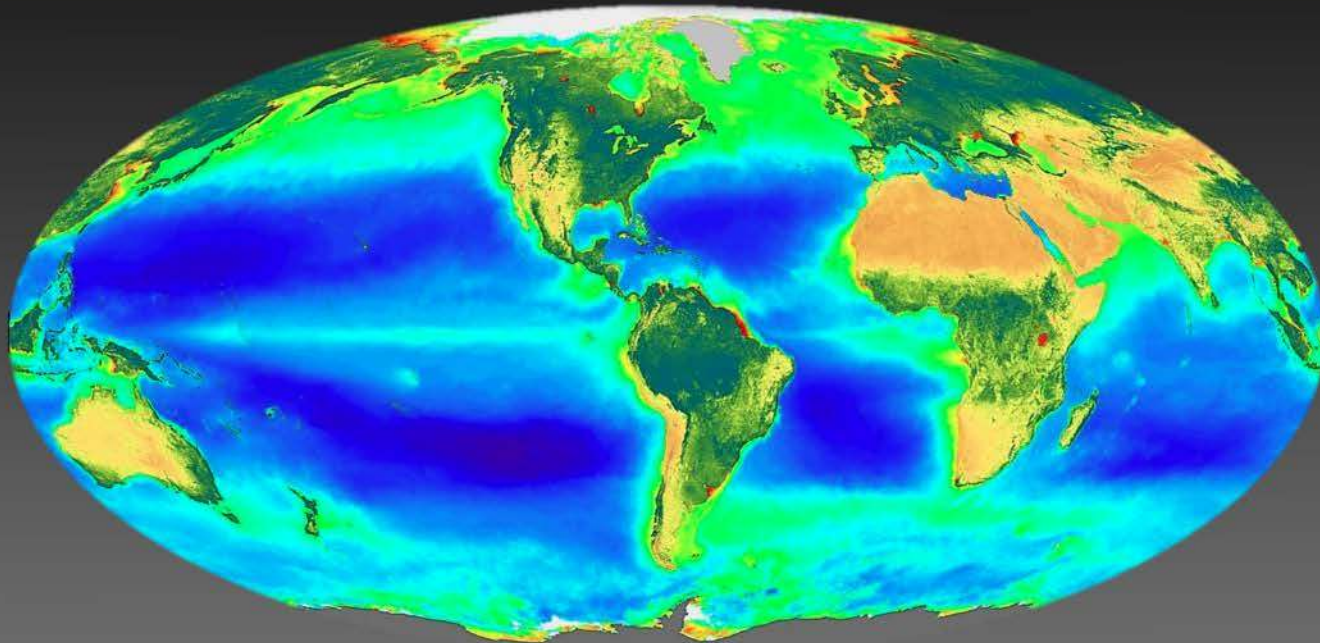
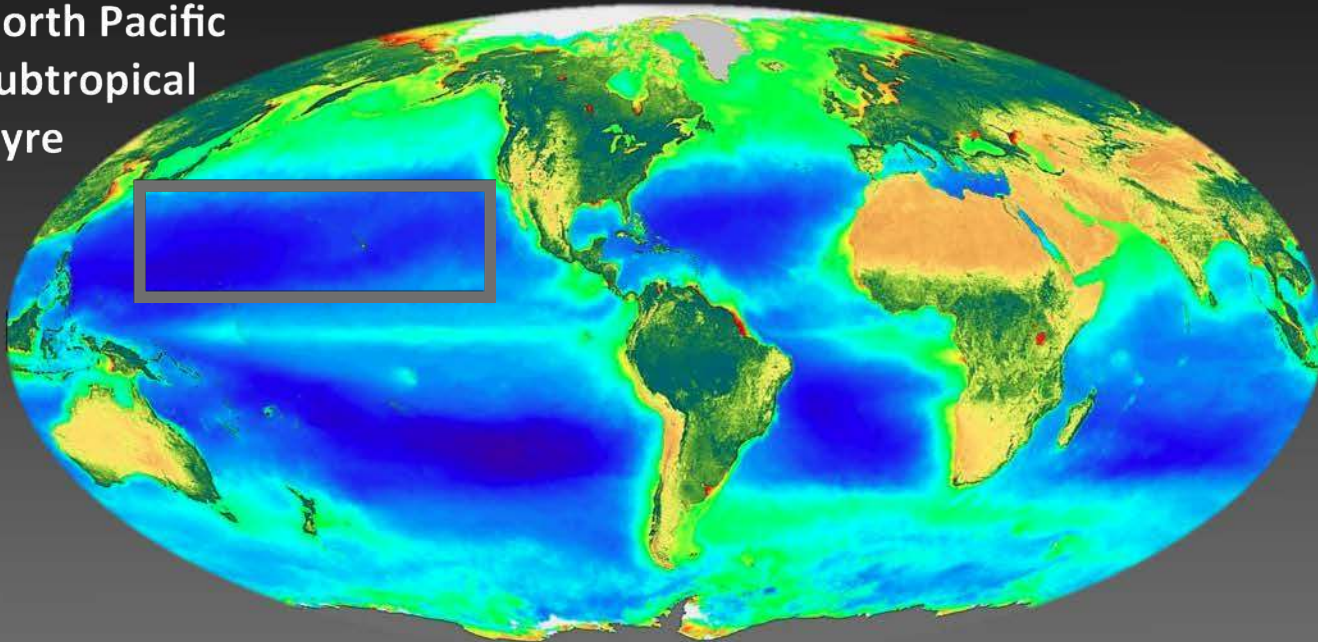


Image credits: SeaWiFS Global Chlorophyll

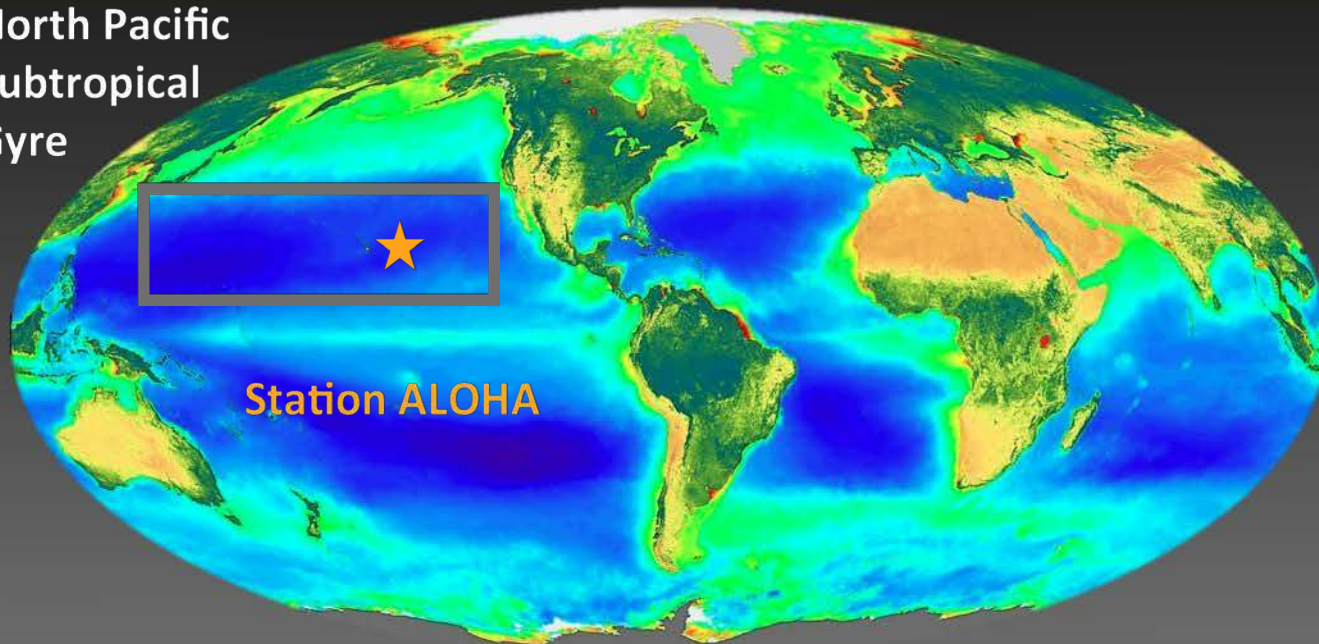
The significance of the NPSG

North Pacific
Subtropical
Gyre



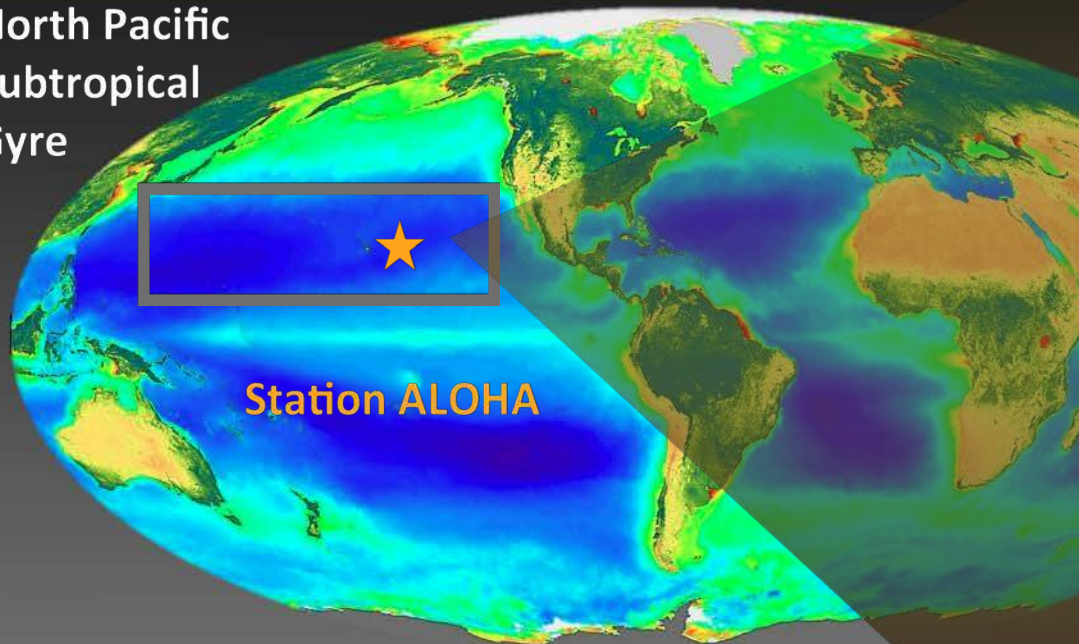
The significance of the NPSG

North Pacific
Subtropical
Gyre



The significance of the NPSG

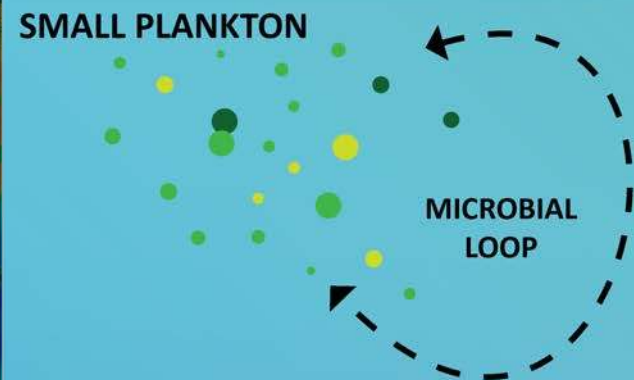
North Pacific
Subtropical
Gyre



Station ALOHA

NORMAL OLIGOTROPHIC STATE

SMALL PLANKTON



MICROBIAL
LOOP

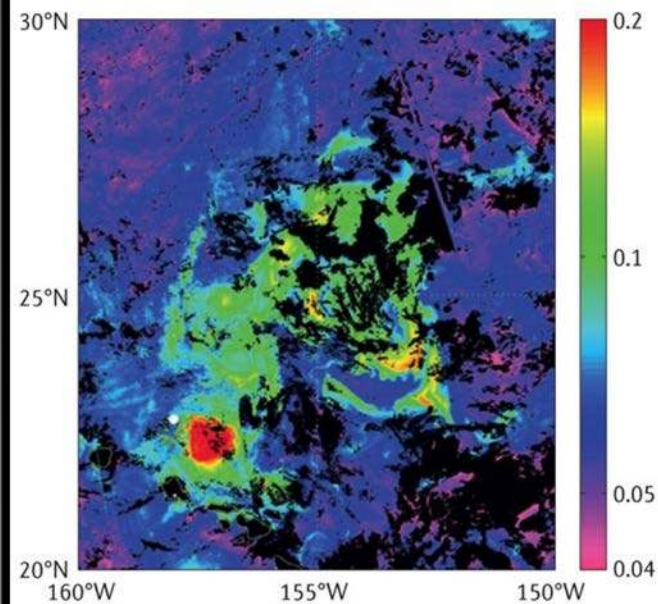
RARE LARGE EUKARYOTES

The significance of the NPSG

North Pacific
Subtropical
Gyre



Station ALOHA



(Karl and Church, Nature Rev. Microbiol., 2014)

NORMAL OLIGOTROPHIC STATE

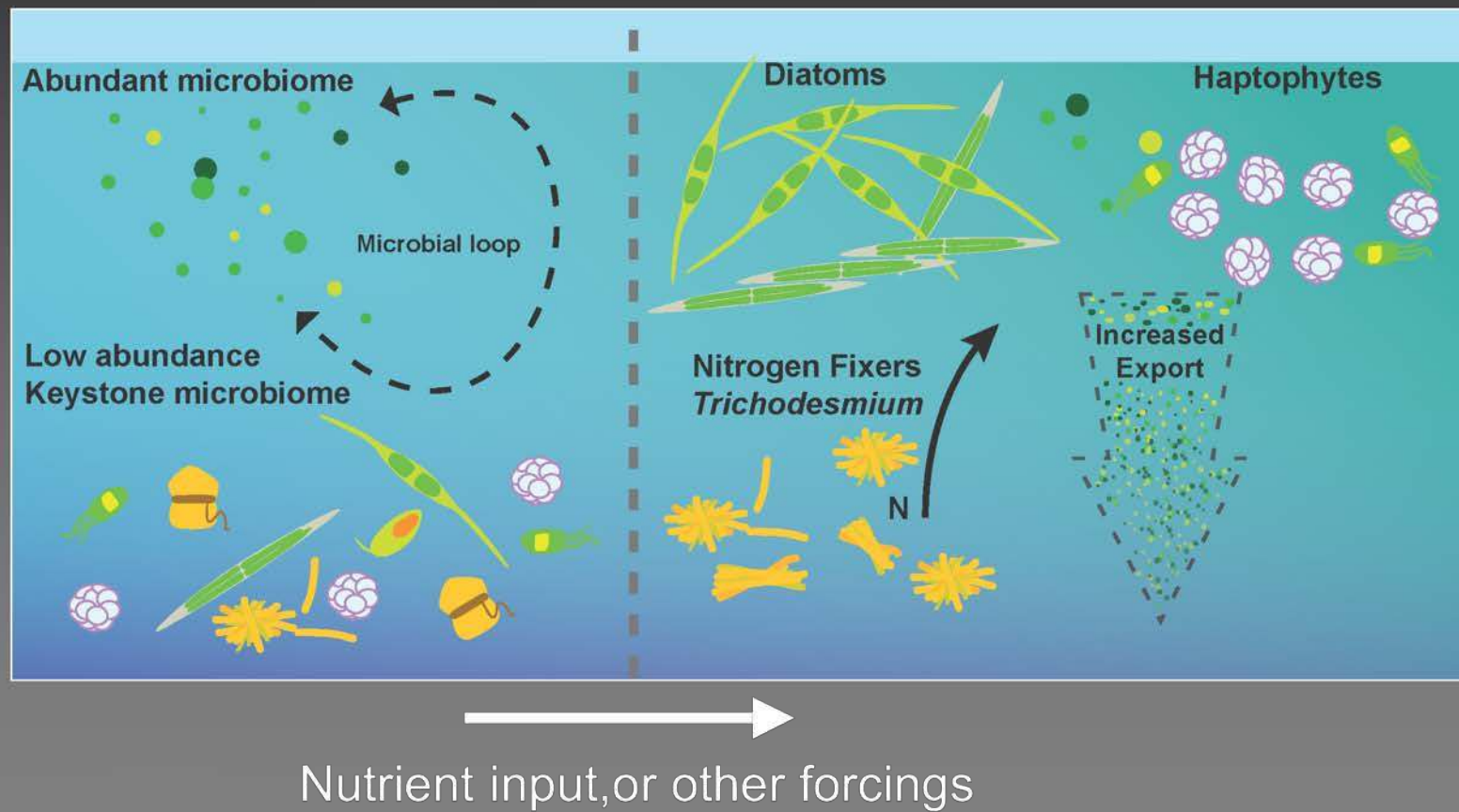
SMALL PLANKTON

MICROBIAL
LOOP

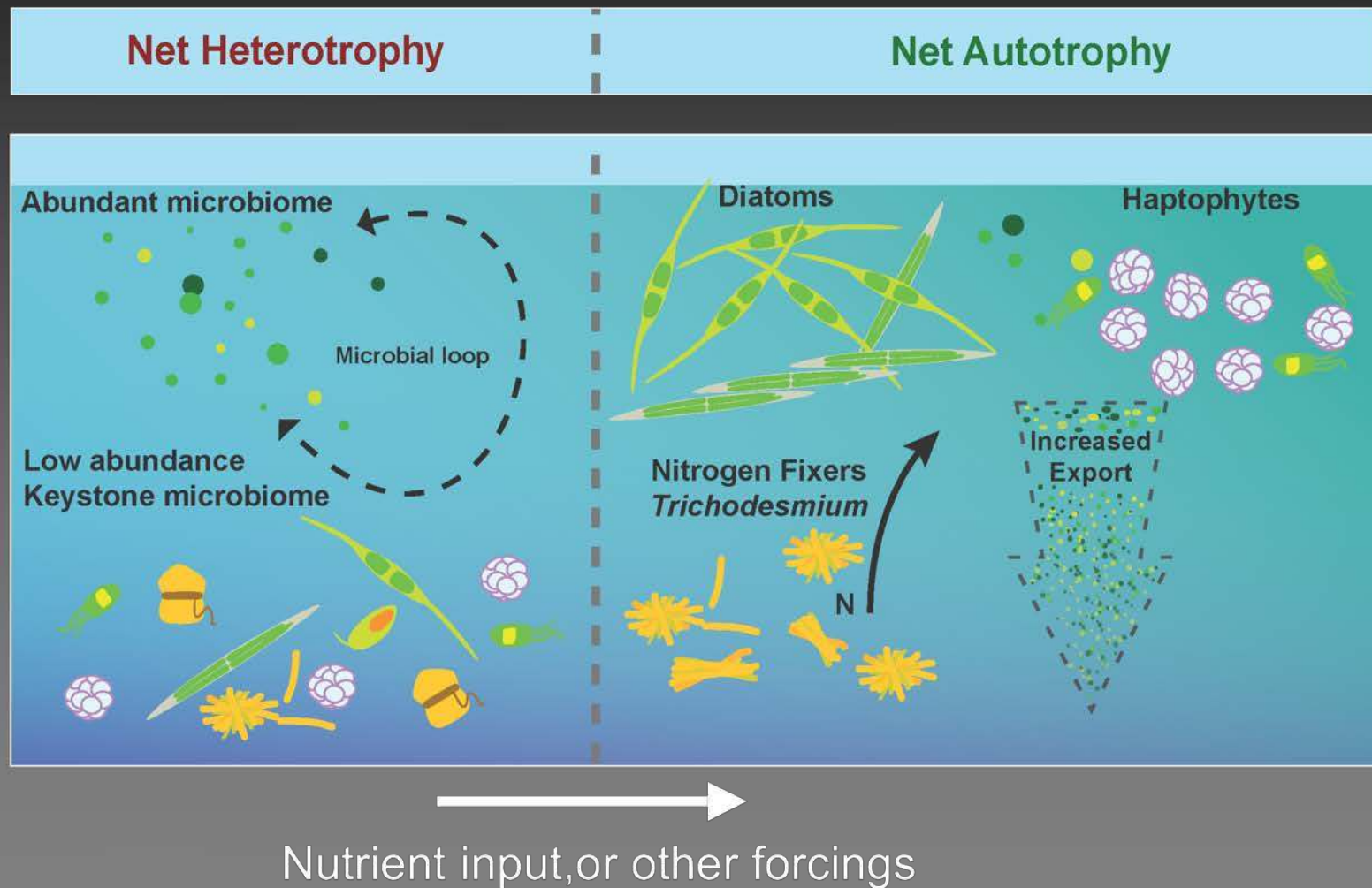
RARE LARGE EUKARYOTES



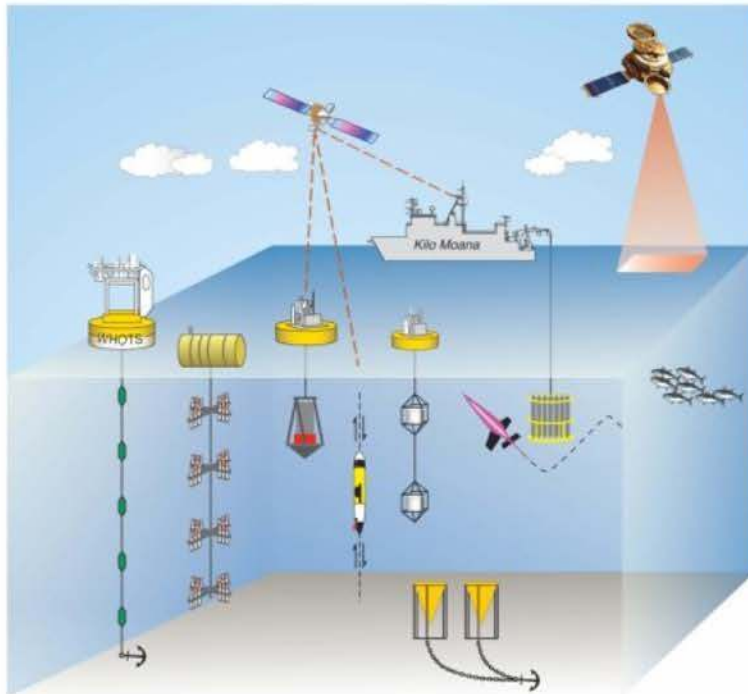
Blooms of keystone species can shift ecosystem state



Blooms of keystone species can shift ecosystem state



Hawaii Ocean Experiment: Dynamics of Light and Nutrients



Wilson et al. 2015 *GBC*

Global Biogeochemical Cycles

AN AGU JOURNAL

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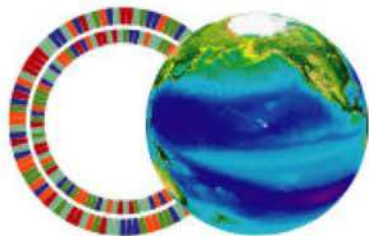
Research Article

Short-term variability in euphotic zone biogeochemistry and primary productivity at Station ALOHA: A case study of summer 2012

Samuel T. Wilson , Benedetto Barone,
Francois Ascani, Robert R. Bidigare, Matthew J. Church,
Daniela A. del Valle, Sonya T. Dyhrman, Sara Ferrón,
Jessica N. Fitzsimmons, Laurie W. Juranek,
Zbigniew S. Kolber, Ricardo M. Letelier,
Sandra Martínez-García, David P. Nicholson,
Kelvin J. Richards, Yoshimi M. Rii, Mónica Rouco,
Donn A. Viviani, Angelicque E. White, Jonathan P. Zehr,
David M. Karl



[View Issue TOC](#)
Volume 29, Issue 8
August 2015
Pages 1145-1164

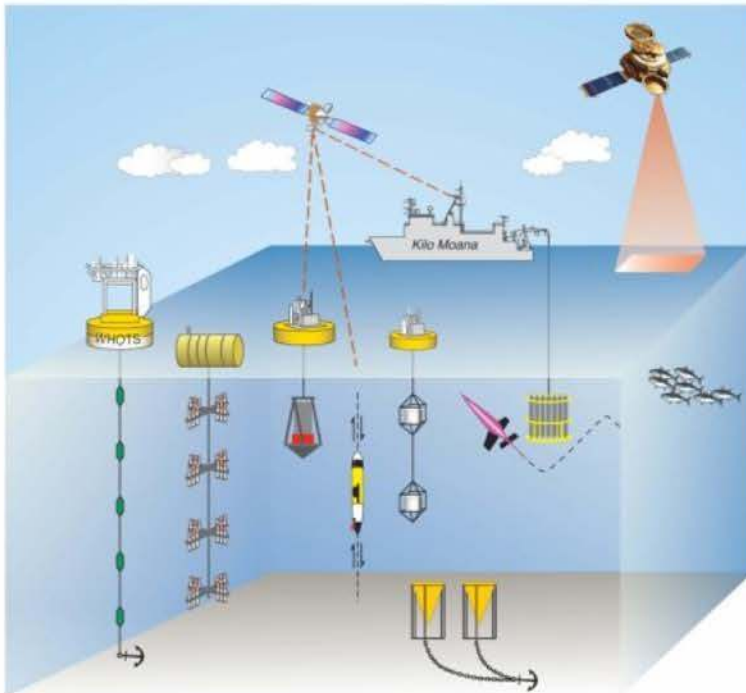


center for microbial oceanography: research and education

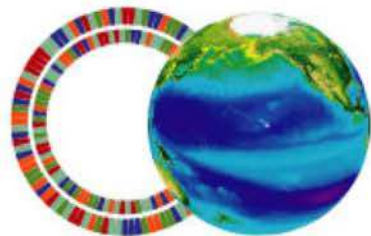
C-MORE *linking genomes to biomes*

(HOE-DYLAN)

Hawaii Ocean Experiment: Dynamics of Light and Nutrients



Wilson et al. 2015 GBC

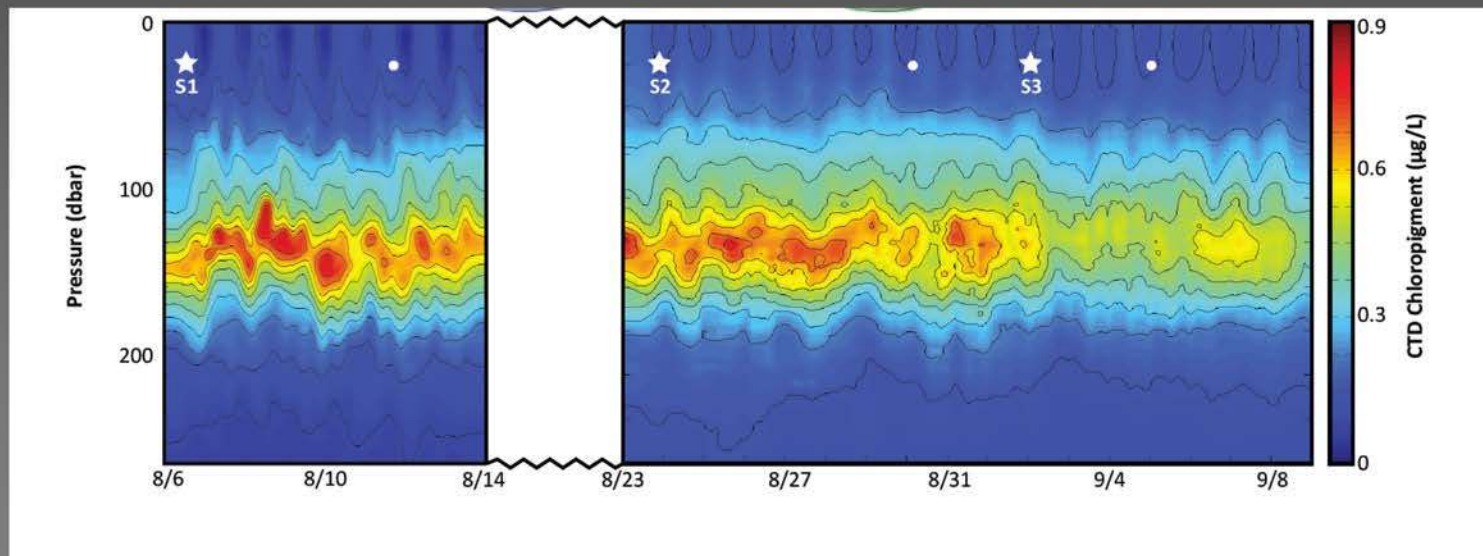


center for microbial oceanography: research and education

C·more *linking genomes to biomes*

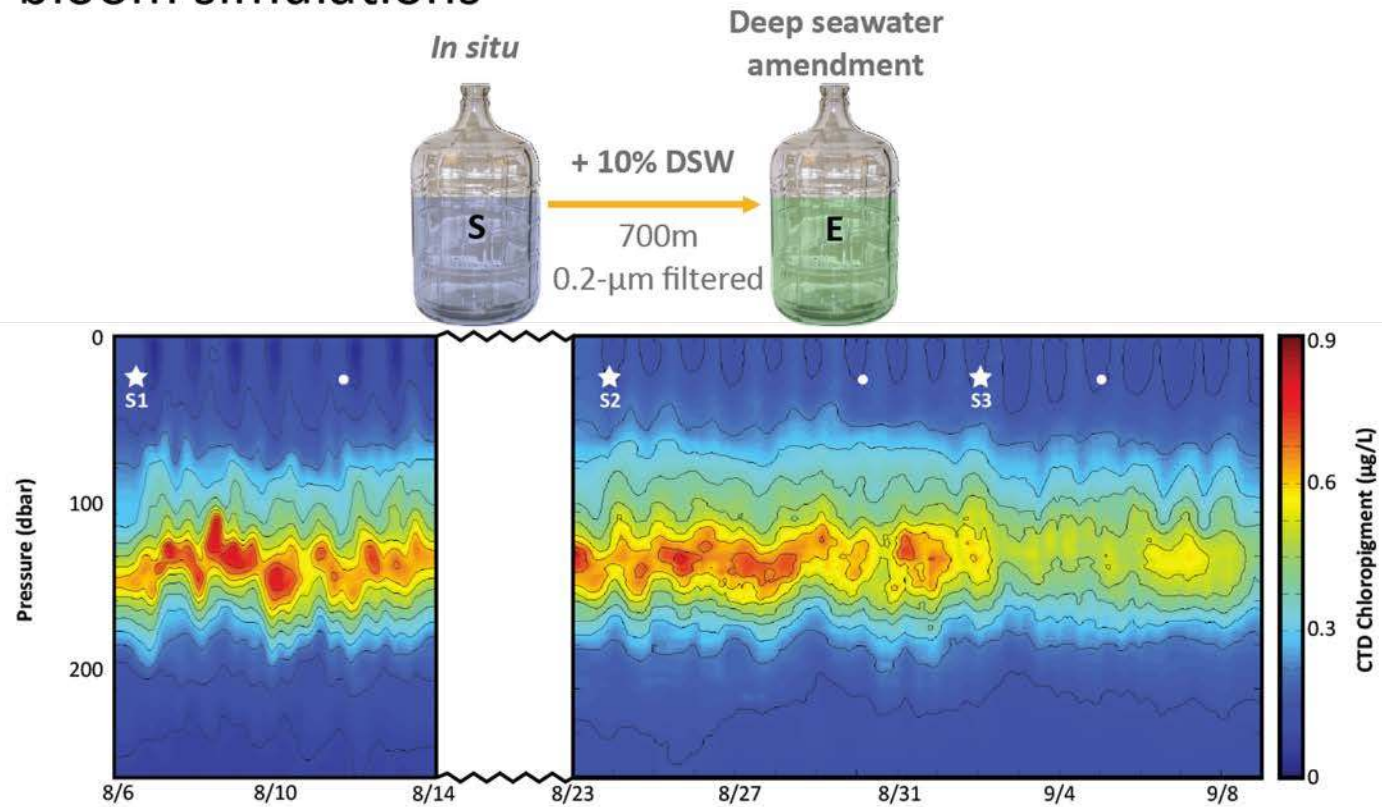
(HOE-DYLAN)

Sampling a bloom



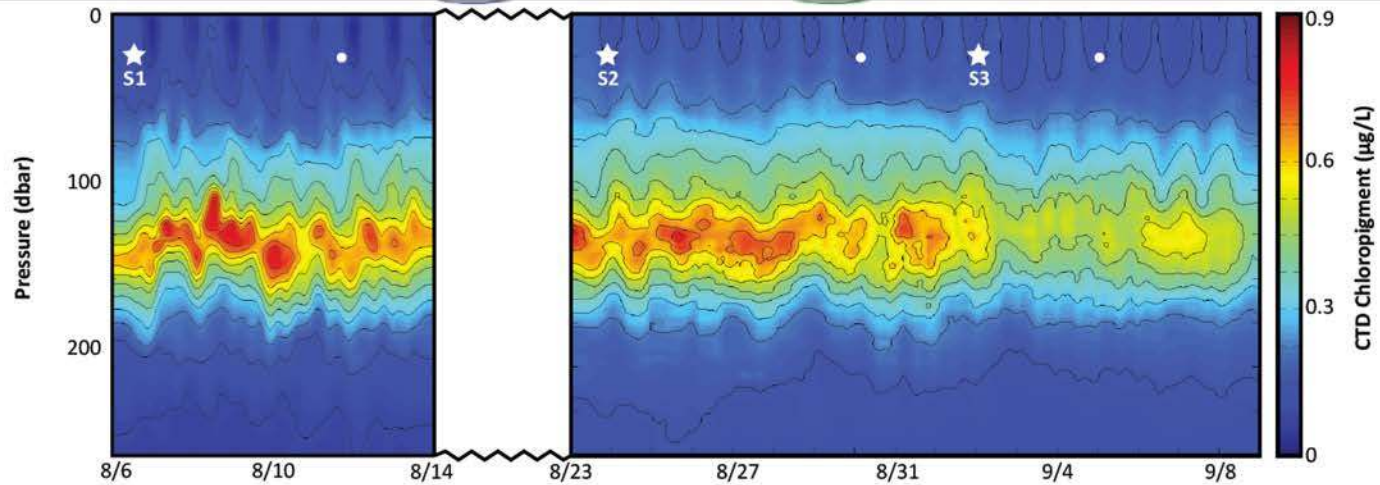
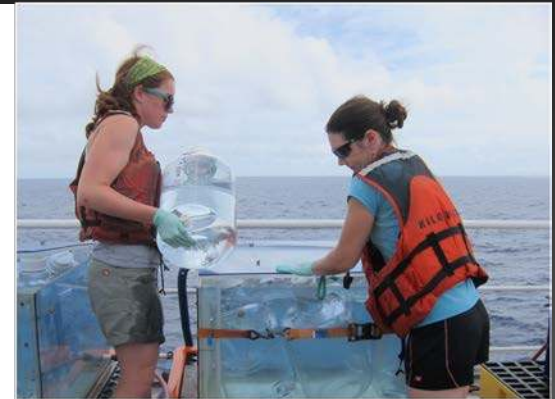
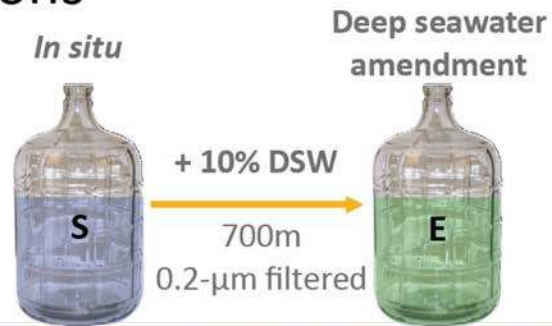
Sampling a bloom

Sampling at Station ALOHA coupled with bloom simulations

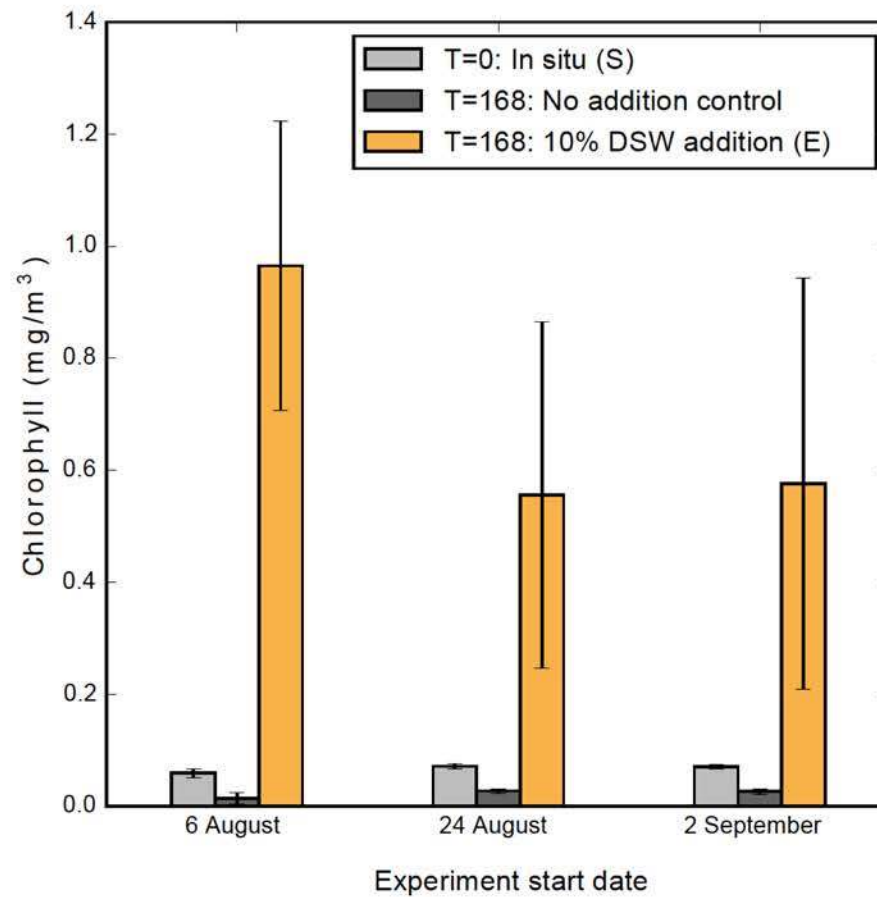


Sampling a bloom

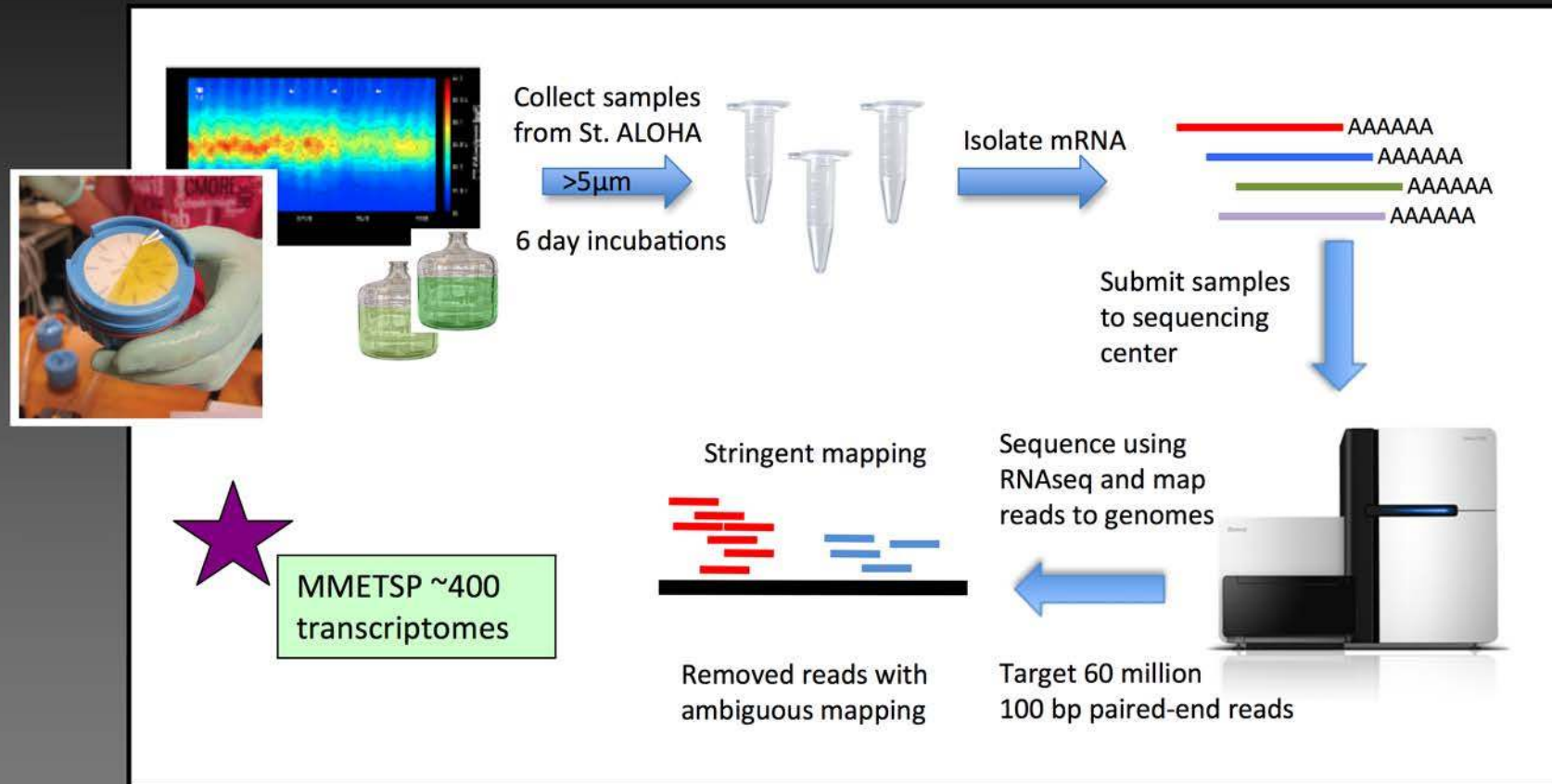
Sampling at Station ALOHA coupled with bloom simulations



Deep water addition led to simulated “bloom”

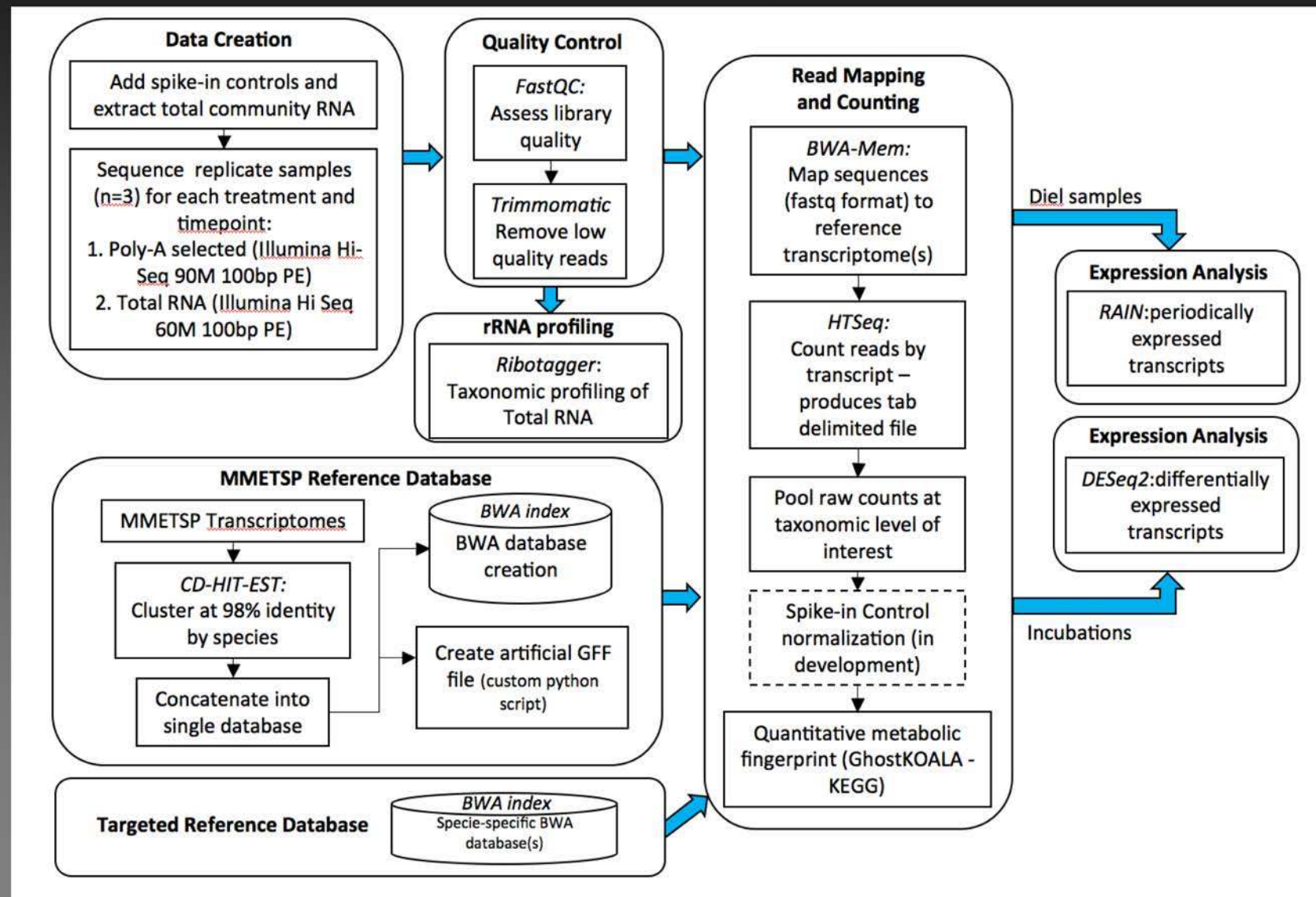


Sampling and pipeline

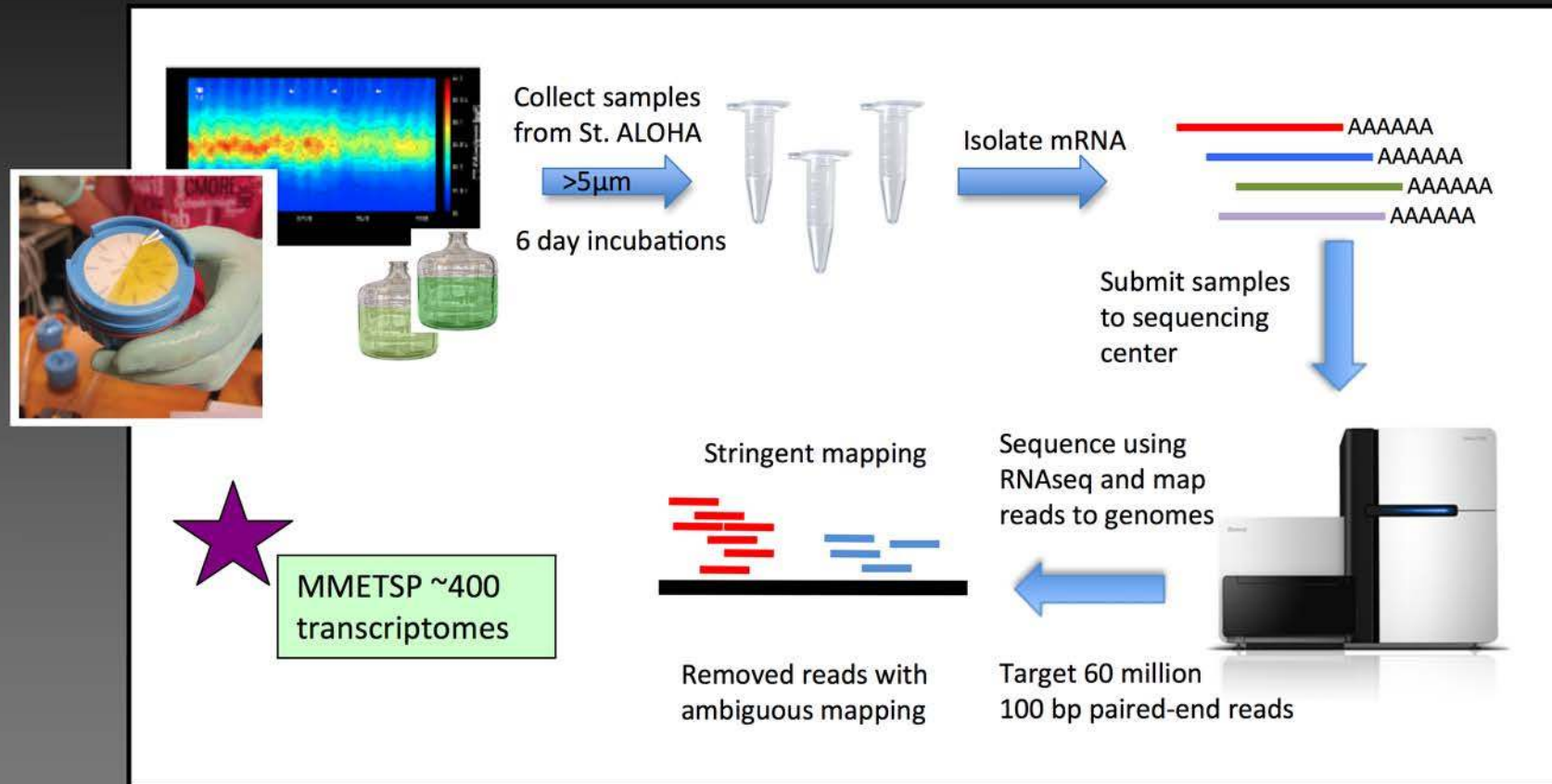


MMETSP = Marine Microbial Eukaryotic Transcriptome Project

Sequencing and analysis strategy



Sampling and pipeline



MMETSP = Marine Microbial Eukaryotic Transcriptome Project

Marine Microbial Eukaryote Transcriptome Sequencing Project

OPEN ACCESS Freely available online

PLOS BIOLOGY

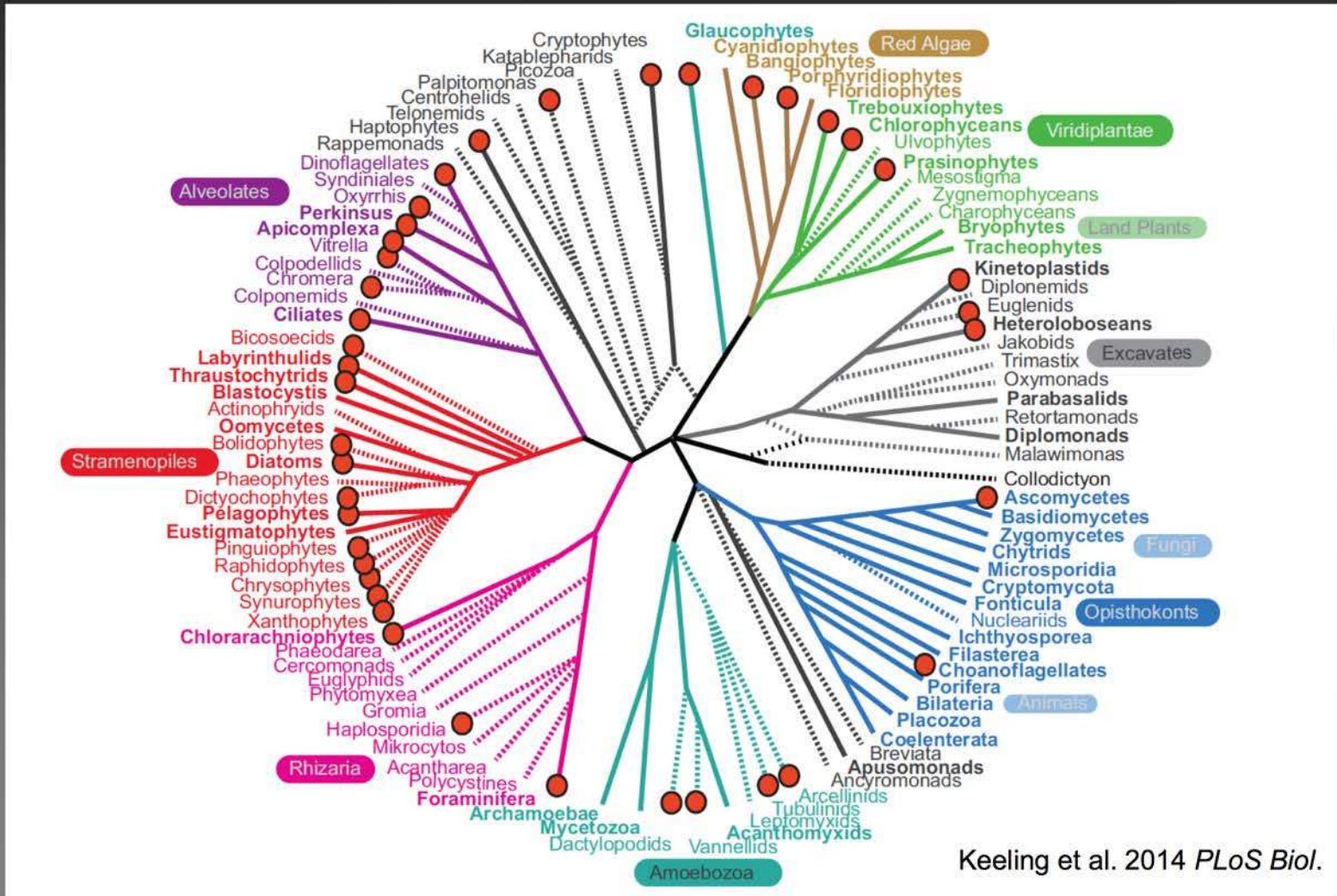
Community Page



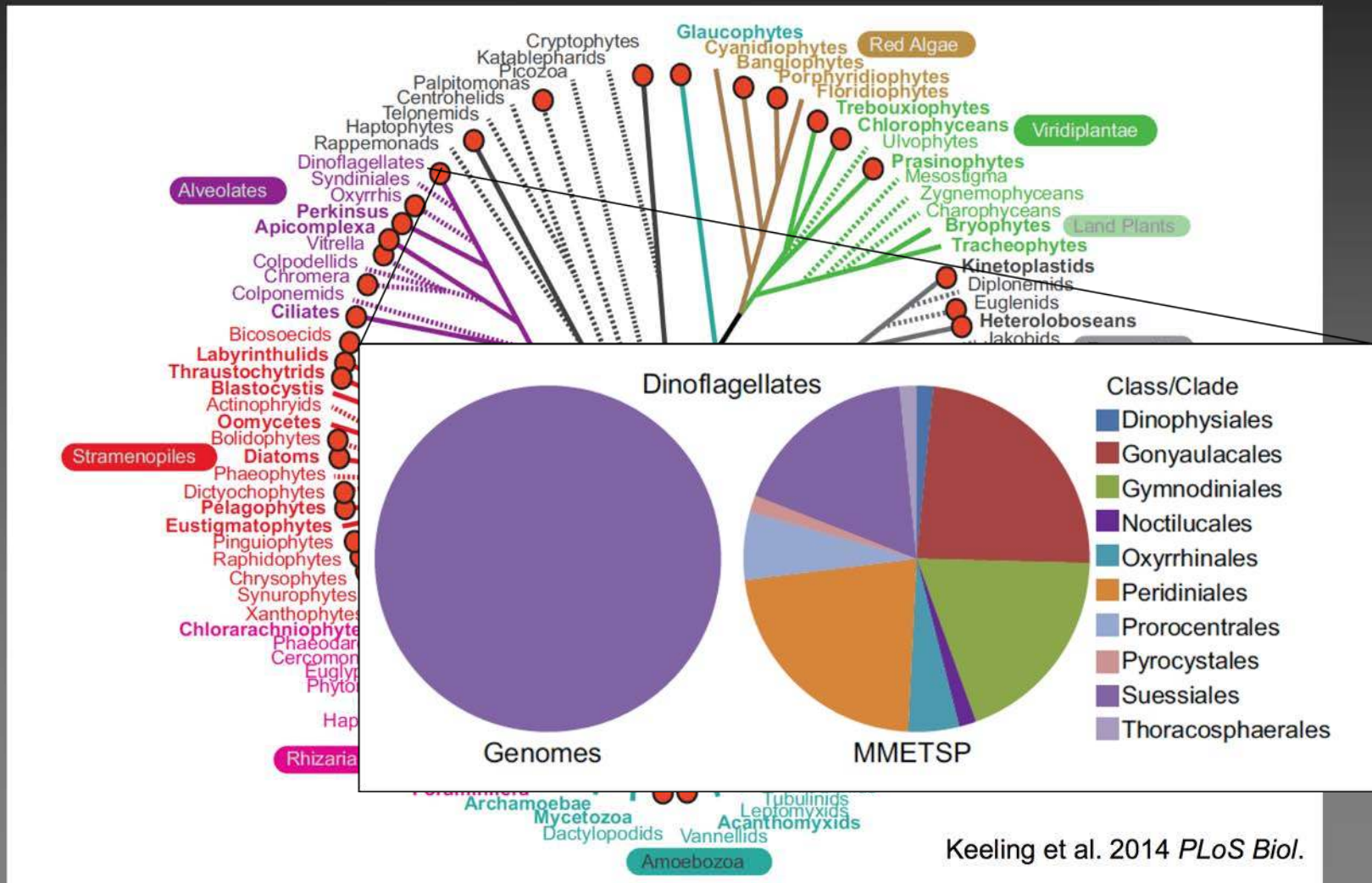
The Marine Microbial Eukaryote Transcriptome Sequencing Project (MMETSP): Illuminating the Functional Diversity of Eukaryotic Life in the Oceans through Transcriptome Sequencing

Patrick J. Keeling^{1,2*}, Fabien Burki¹, Heather M. Wilcox³, Bassem Allam⁴, Eric E. Allen⁵, Linda A. Amaral-Zettler^{6,7}, E. Virginia Armbrust⁸, John M. Archibald^{2,9}, Arvind K. Bharti¹⁰, Callum J. Bell¹⁰, Bank Beszteri¹¹, Kay D. Bidle¹², Connor T. Cameron¹⁰, Lisa Campbell¹³, David A. Caron¹⁴, Rose Ann Cattolico¹⁵, Jackie L. Collier⁴, Kathryn Coyne¹⁶, Simon K. Davy¹⁷, Phillipe Deschamps¹⁸, Sonya T. Dyhrman¹⁹, Bente Edvardsen²⁰, Ruth D. Gates²¹, Christopher J. Gobler⁴, Spencer J. Greenwood²², Stephanie M. Guida¹⁰, Jennifer L. Jacobi¹⁰, Kjetill S. Jakobsen²⁰, Erick R. James¹, Bethany Jenkins^{23,24}, Uwe John¹¹, Matthew D. Johnson²⁵, Andrew R. Juhl¹⁹, Anja Kamp^{26,27}, Laura A. Katz²⁸, Ronald Kiene²⁹, Alexander Kudryavtsev^{30,31}, Brian S. Leander¹, Senjie Lin³², Connie Lovejoy³³, Denis Lynn^{34,35}, Adrian Marchetti³⁶, George McManus³², Aurora M. Nedelcu³⁷, Susanne Menden-Deuer²⁴, Cristina Miceli³⁸, Thomas Mock³⁹, Marina Montresor⁴⁰, Mary Ann Moran⁴¹, Shauna Murray⁴², Govind Nadathur⁴³, Satoshi Nagai⁴⁴, Peter B. Ngam¹⁰, Brian Palenik⁵, Jan Pawlowski³¹, Giulio Petroni⁴⁵, Gwenael Piganeau^{46,47}, Matthew C. Posewitz⁴⁸, Karin Rengefors⁴⁹, Giovanna Romano⁴⁰, Mary E. Rumpho⁵⁰, Tatiana Ryneerson²⁴, Kelly B. Schilling¹⁰, Declan C. Schroeder⁵¹, Alastair G. B. Simpson^{2,52}, Claudio H. Slamovits^{2,9}, David R. Smith⁵³, G. Jason Smith⁵⁴, Sarah R. Smith⁵, Heidi M. Sosik²⁵, Peter Stief²⁶, Edward Theriot⁵⁵, Scott N. Twary⁵⁶, Pooja E. Umale¹⁰, Daniel Vaultot⁵⁷, Boris Wawrik⁵⁸, Glen L. Wheeler^{51,59}, William H. Wilson⁶⁰, Yan Xu⁶¹, Adriana Zingone⁴⁰, Alexandra Z. Worden^{2,3*}

Greatly expanded reference sequences in the tree of life

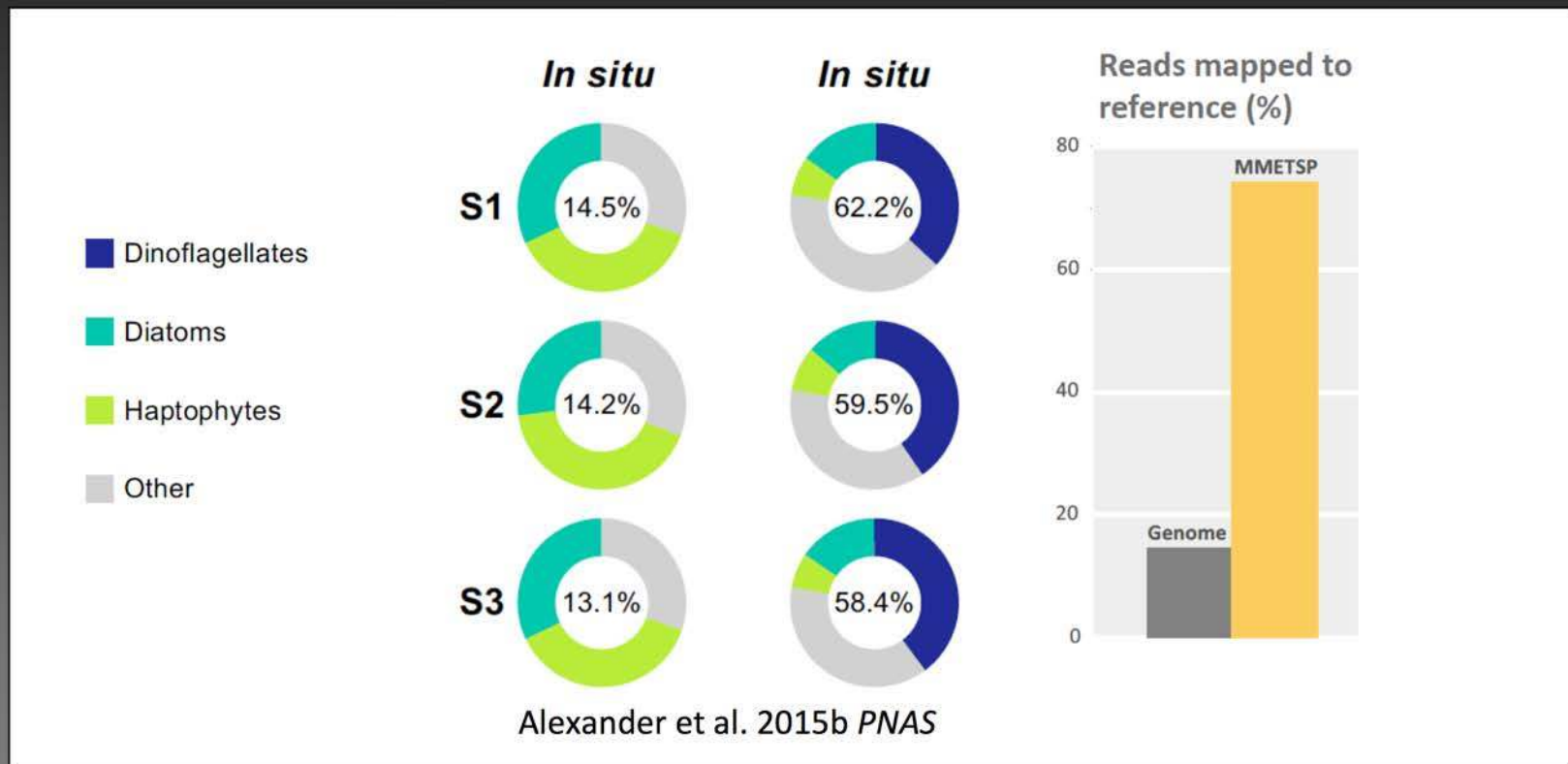
Keeling et al. 2014 *PLoS Biol.*

Greatly expanded reference sequences in the tree of life



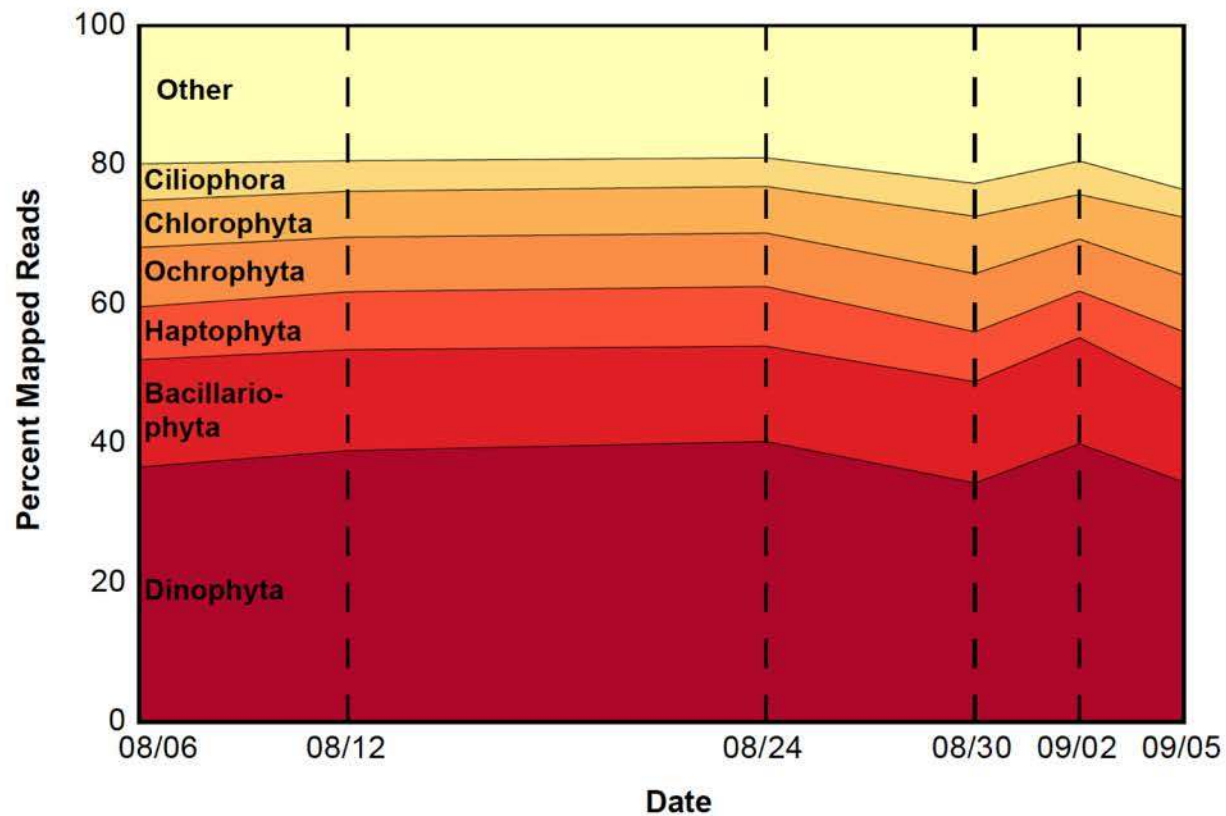
MMETSP improves read identification

Read mapping against genomes v. MMETSP at St. ALHOA



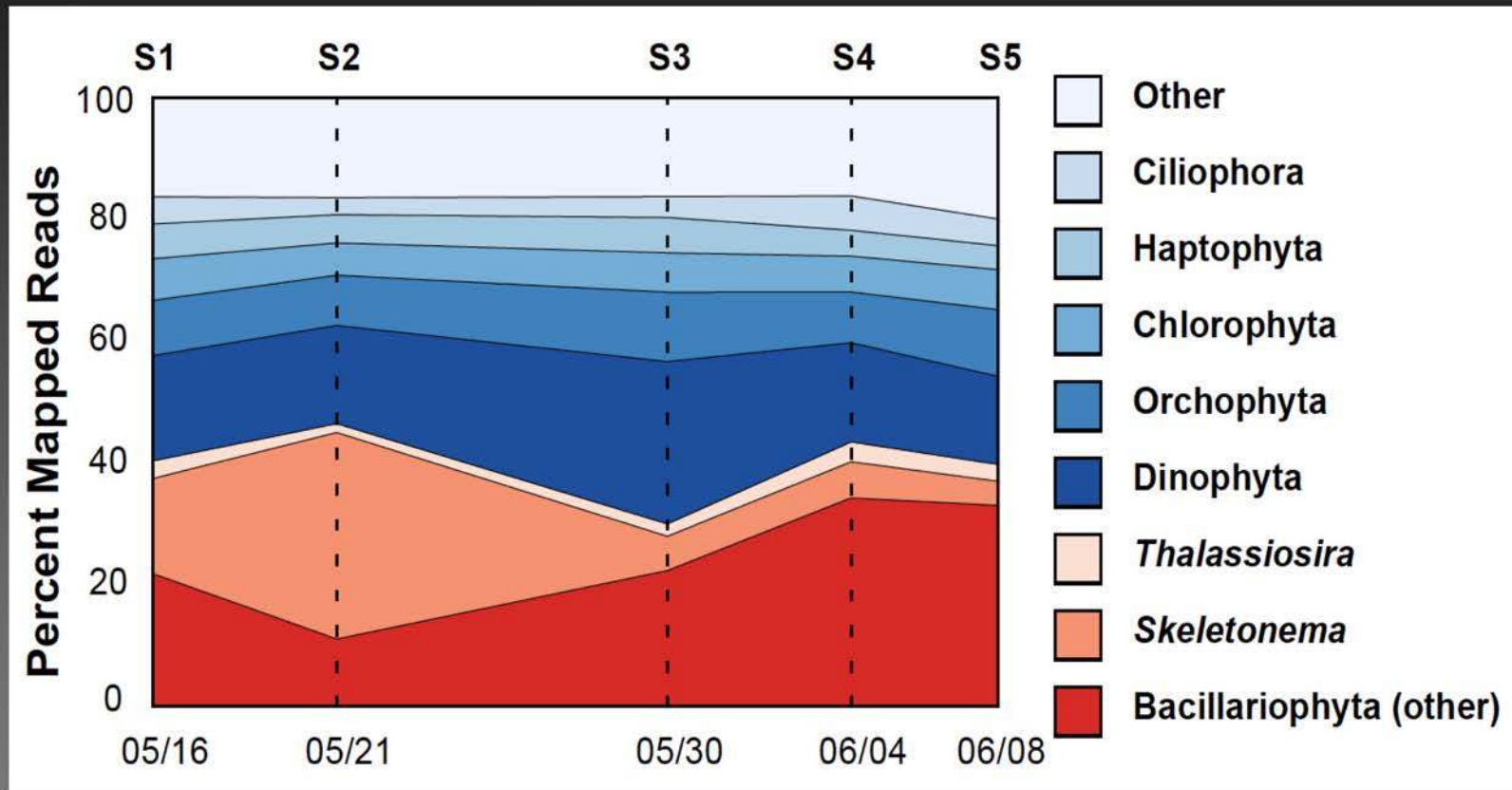
Sequence read identification is substantially improved over using phytoplankton genomes which do not capture the same diversity.

Taxonomic distribution of reads



Distributions is highly stable, much more so than what was observed in coastal system.

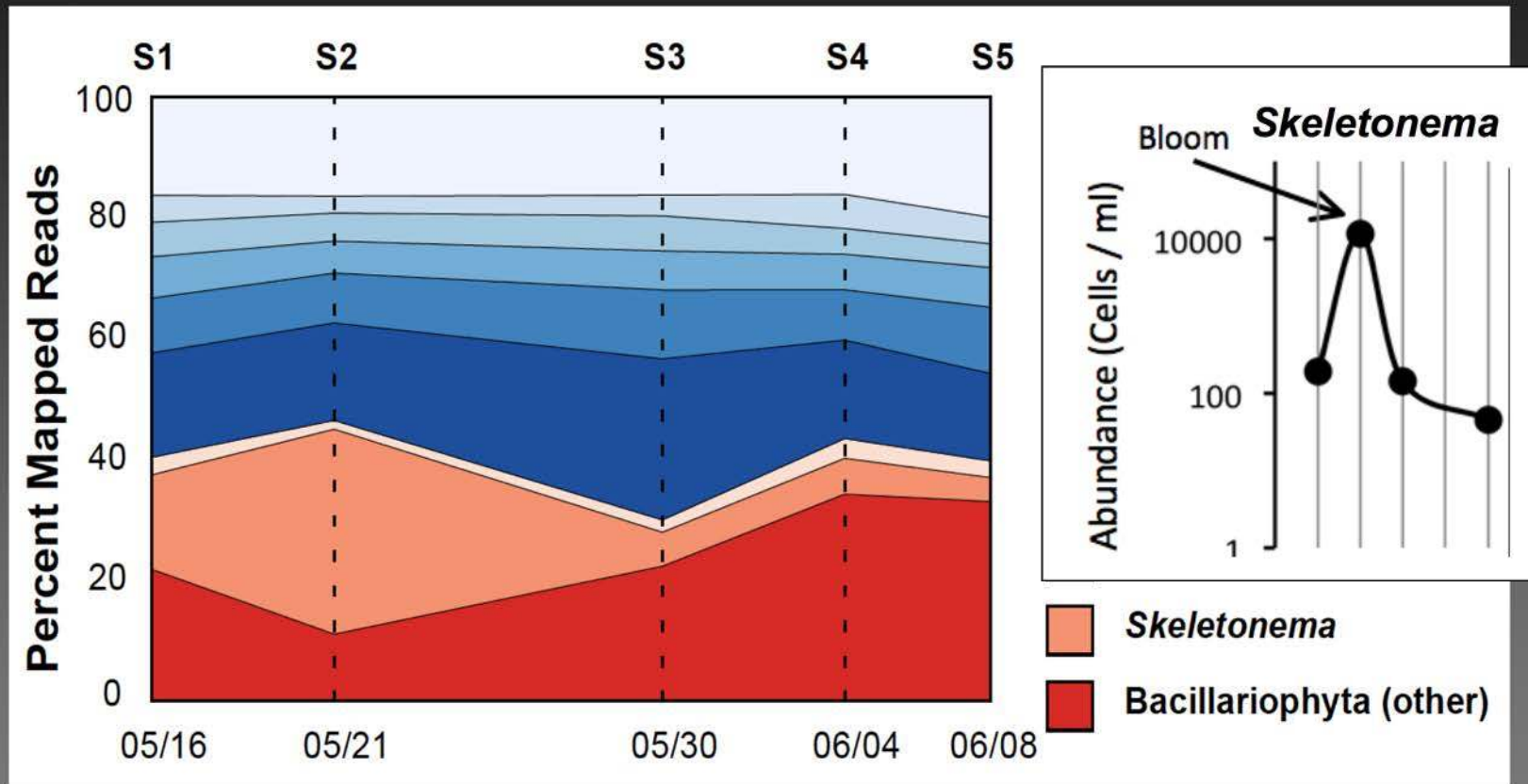
Taxonomic distribution of reads - coastal bloom



Alexander et al. 2015 *PNAS*

Taxonomic distribution of reads is more variable in a coastal system

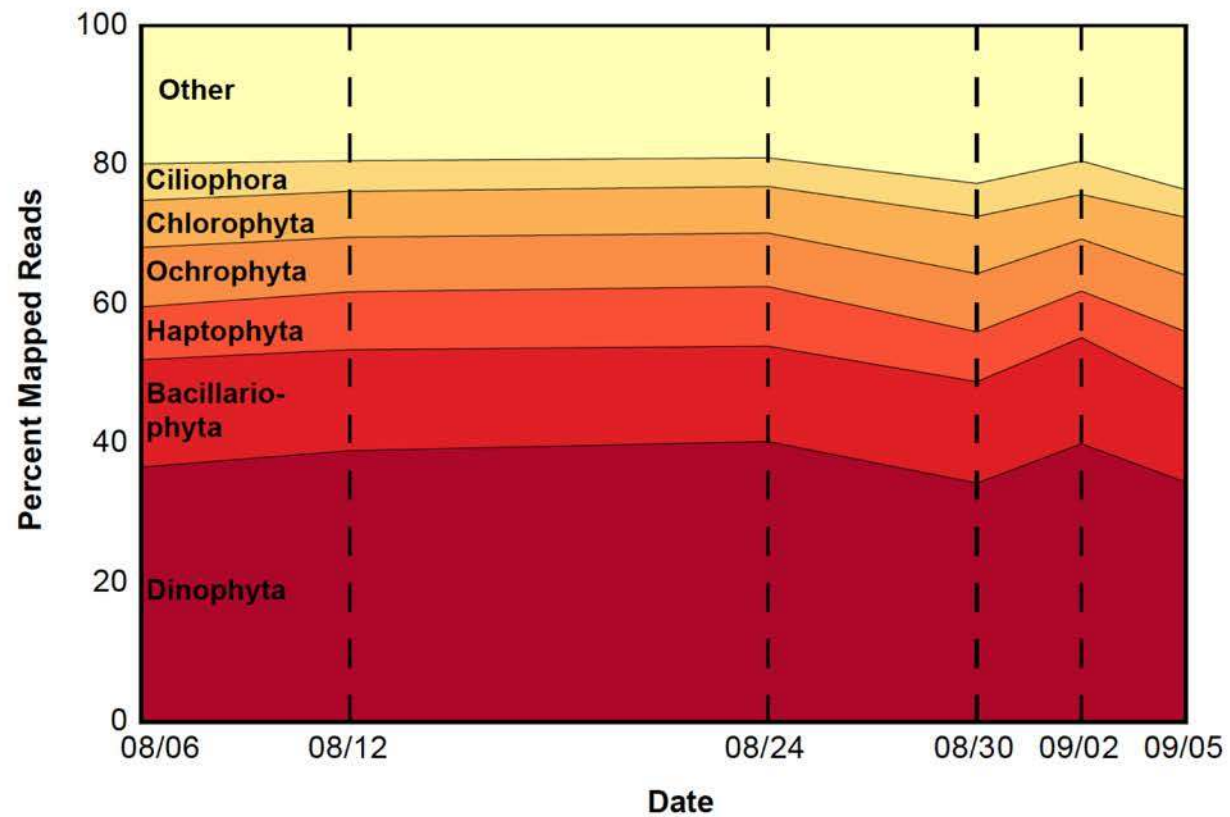
Taxonomic distribution of reads - coastal bloom



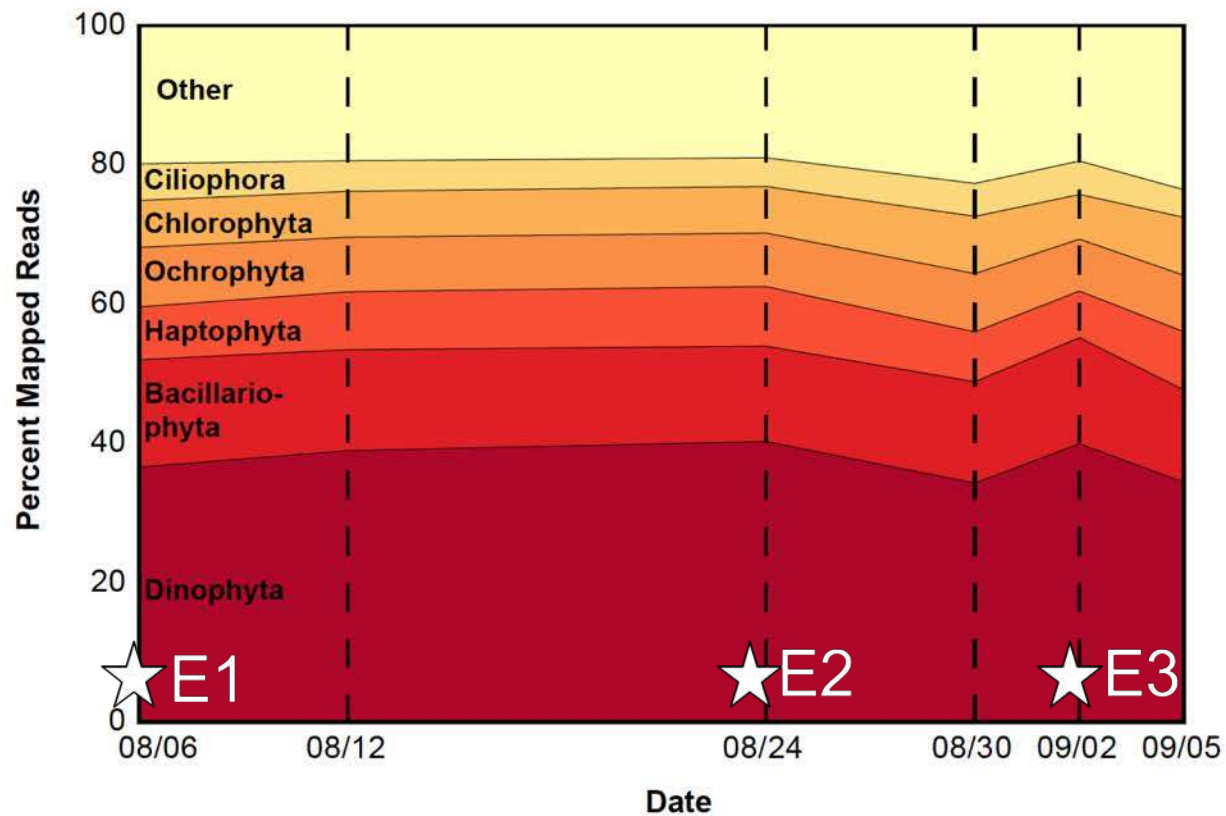
Alexander et al. 2015 *PNAS*

Taxonomic distribution of reads is more variable in a coastal system

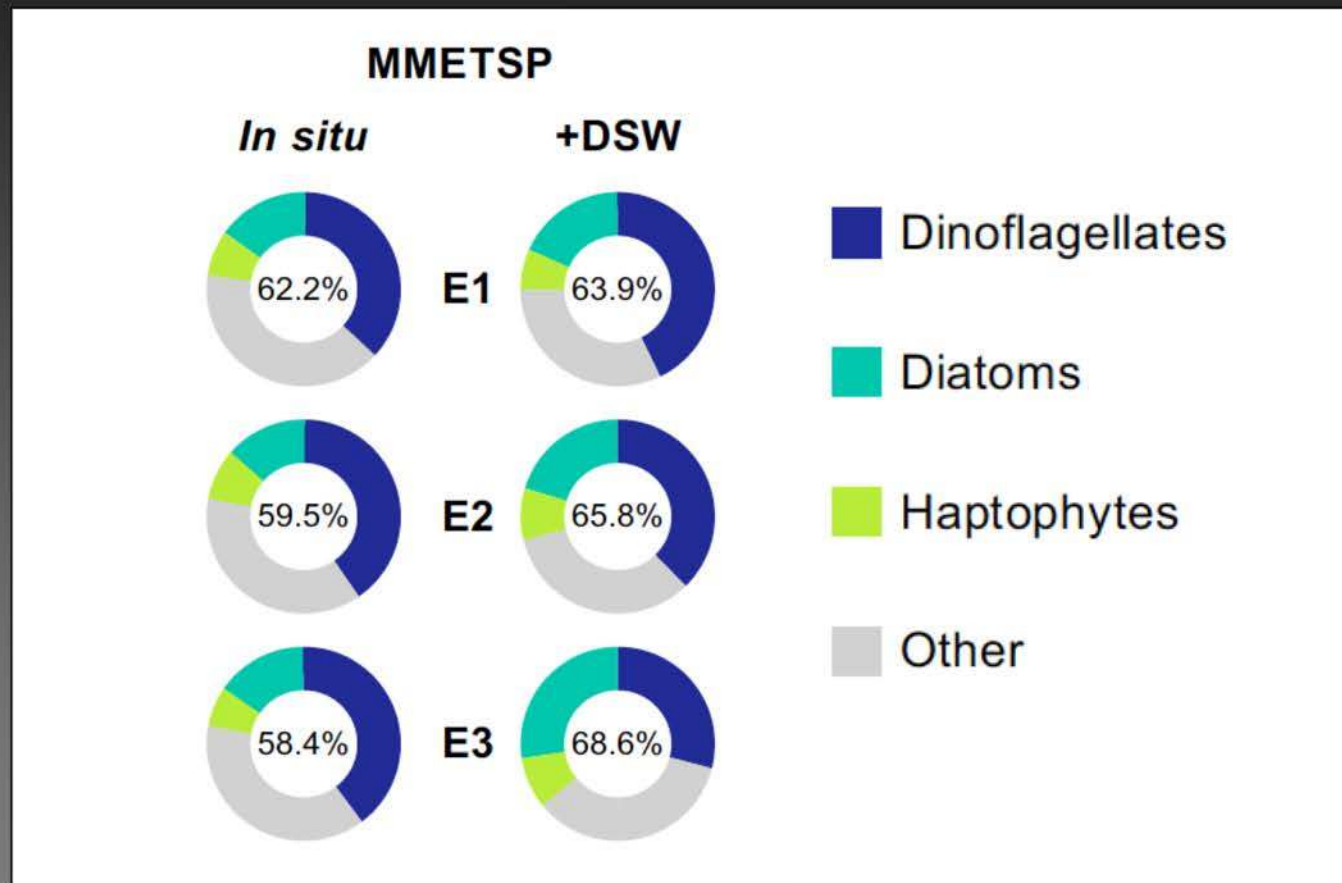
Taxonomic distribution of reads



Taxonomic distribution of reads

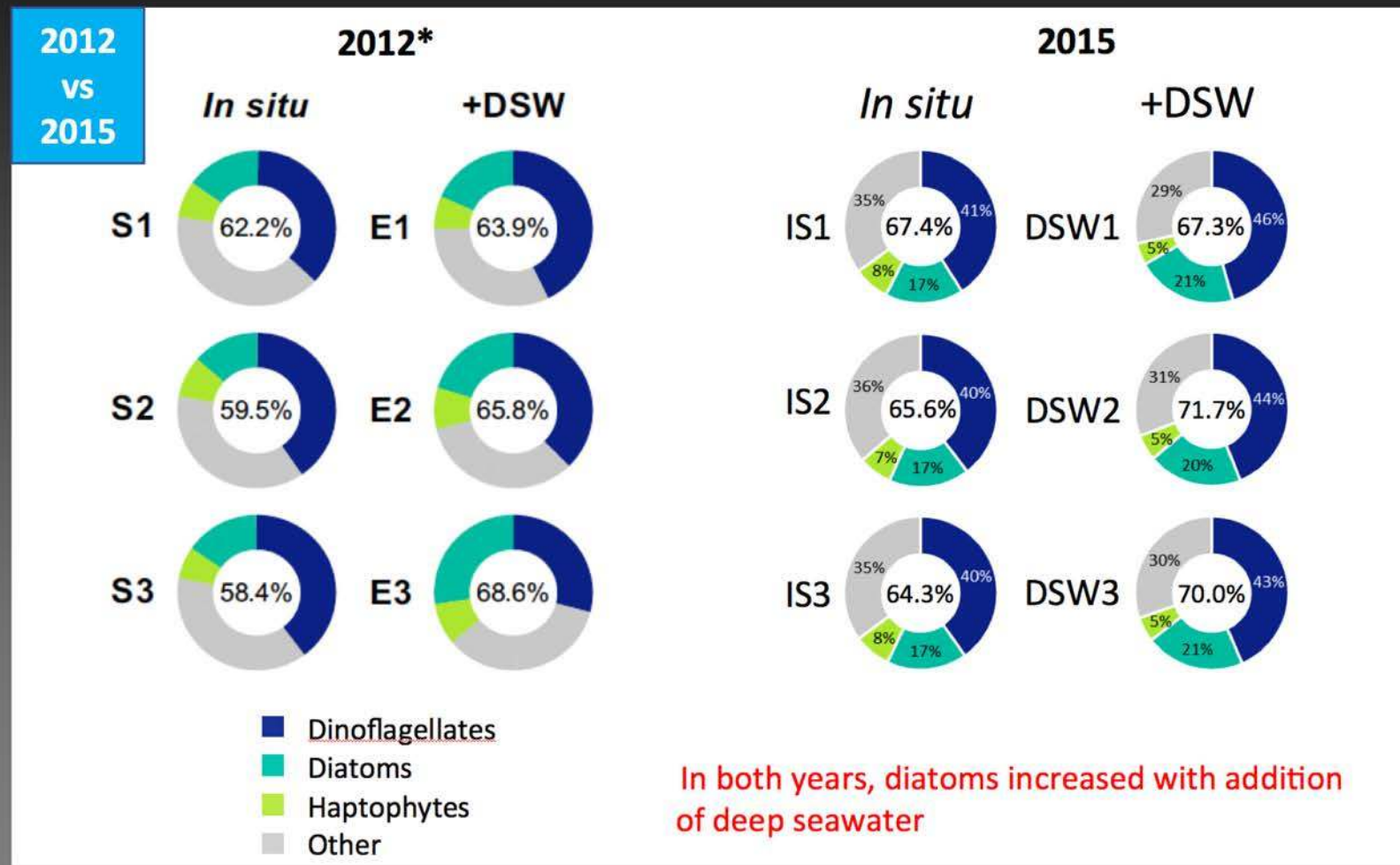


Increase in diatoms during simulated blooms



Read identification is robust, most are dinoflagellates, but diatoms increase in simulated blooms (+DSW)

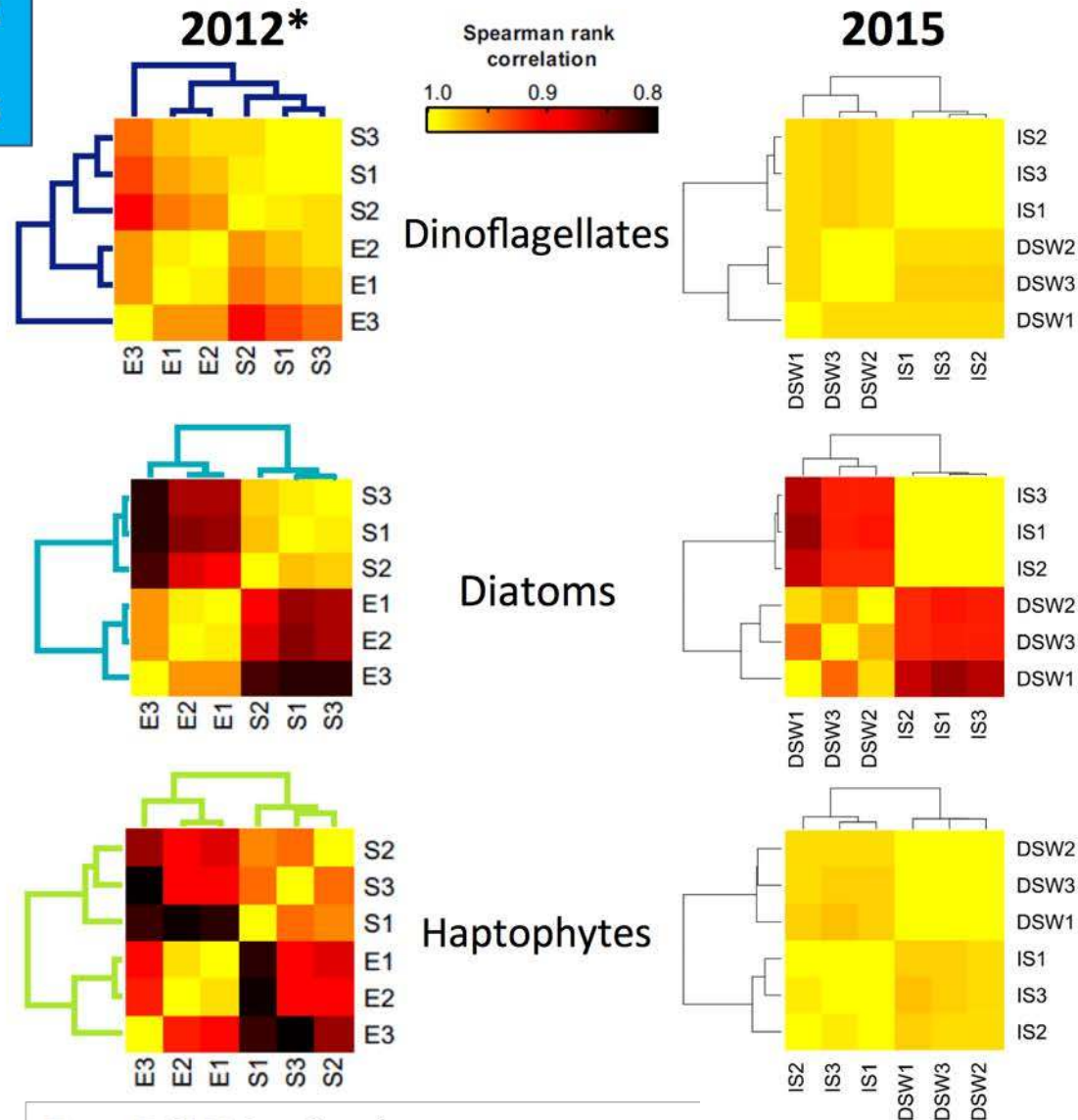
Simulated bloom response was reproducible 3 years later



Read identification increases with larger database, remarkable similarity in response between years

Community composition shifts in bloom condition

2012
vs
2015



Community composition shifts in bloom condition

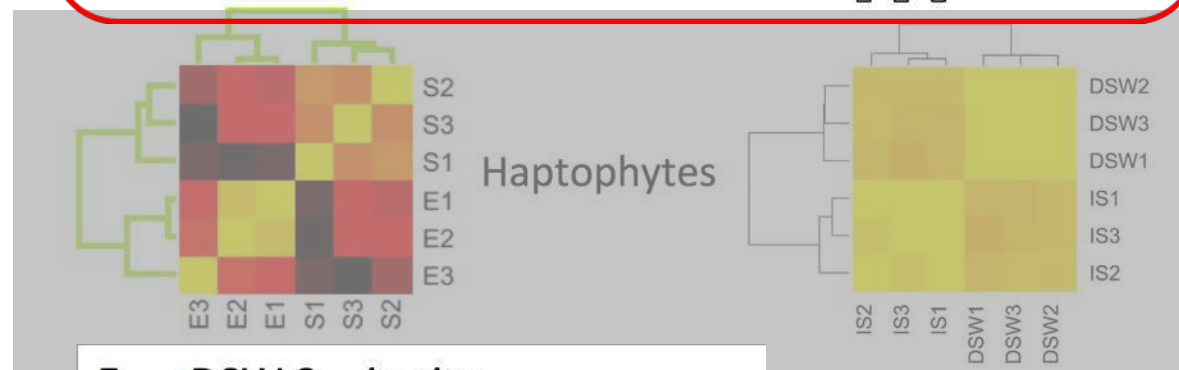
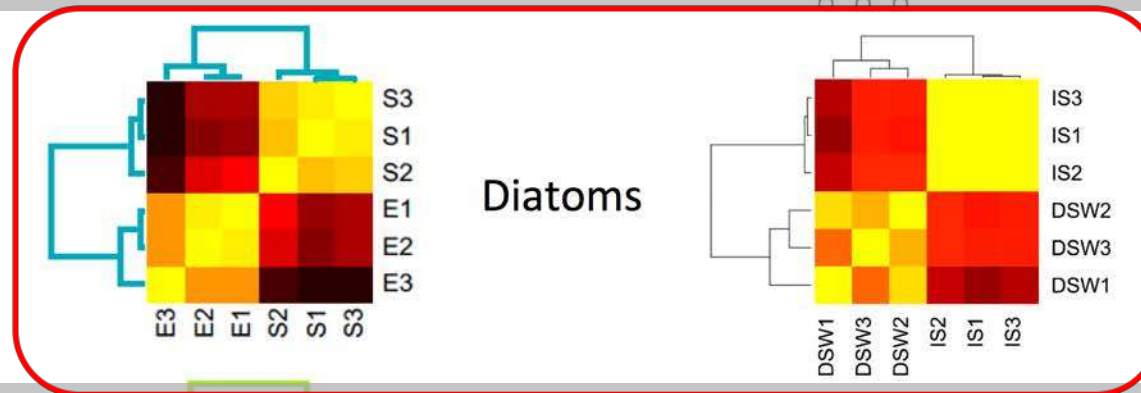
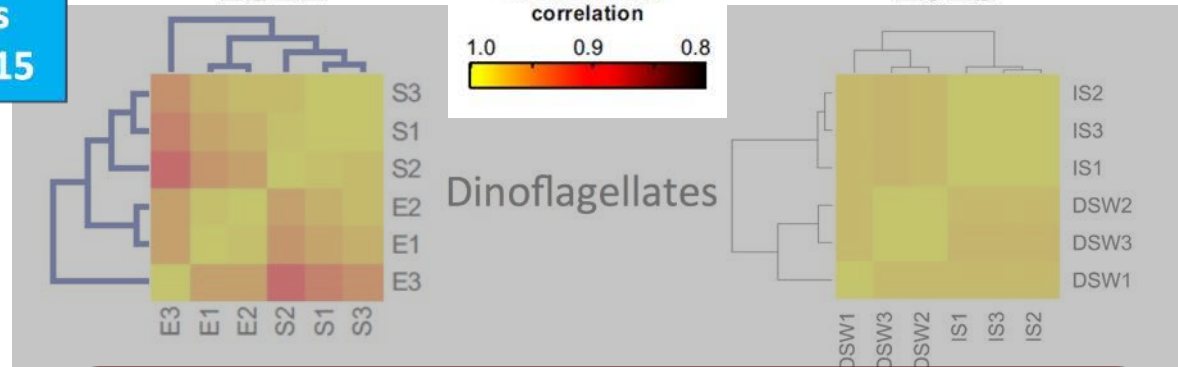
2012
vs
2015

2012*

Spearman rank
correlation

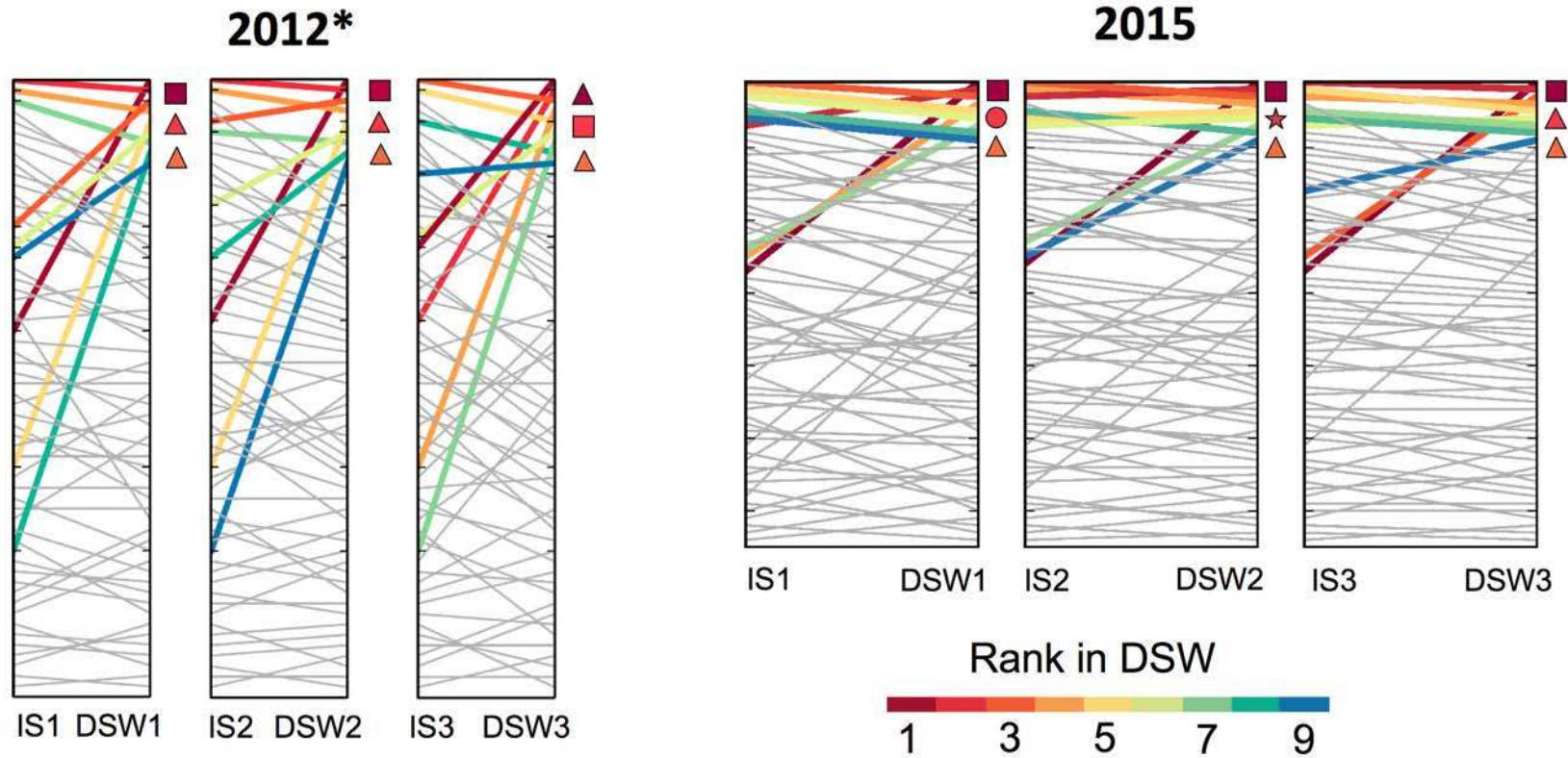


2015



E = +DSW S = *in situ*

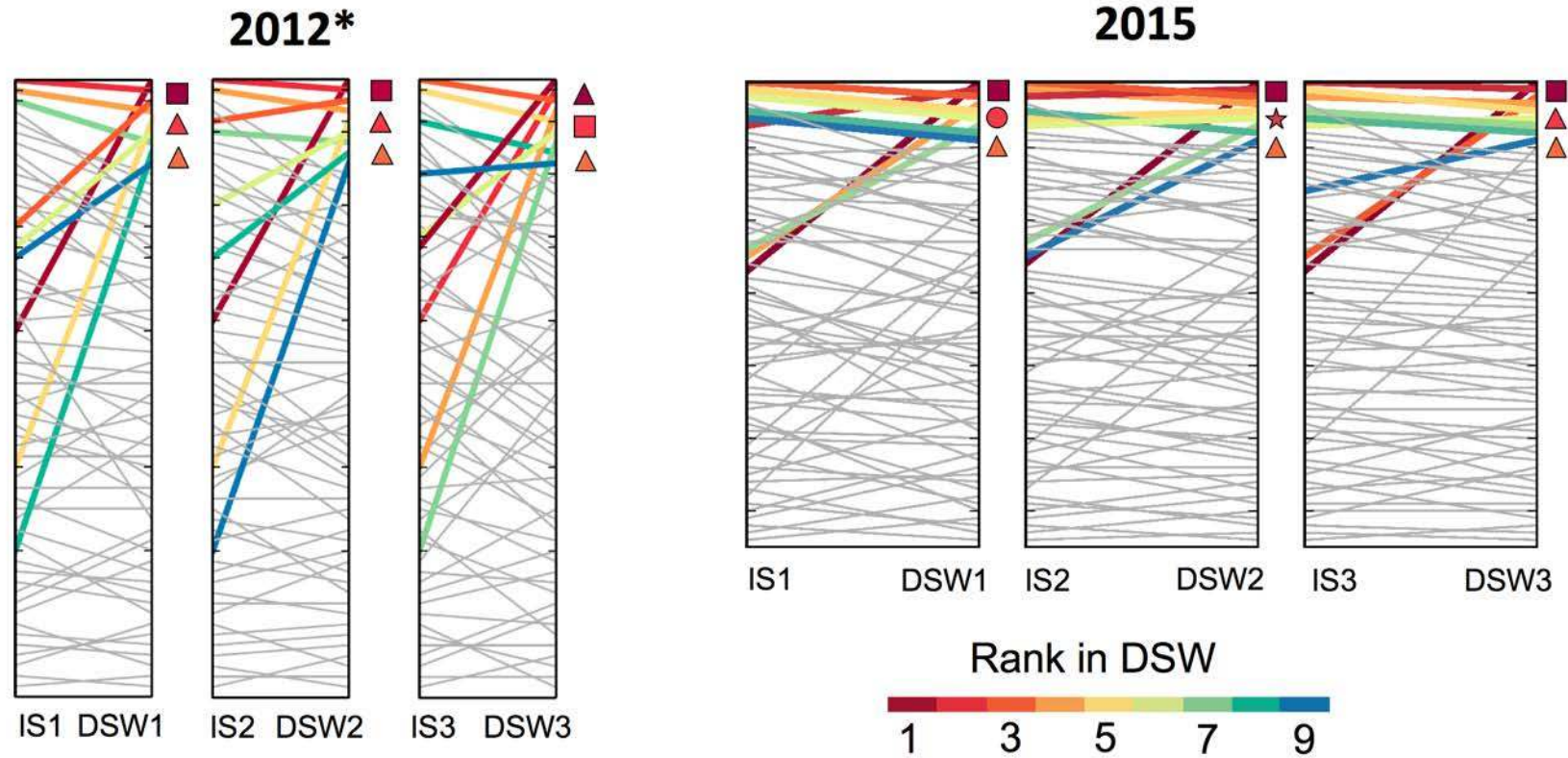
Its even the same species changing...



- *Cylindrotheca* sp.
- △ *Pseudo-nitzschia* sp.
- *Chaetoceros* sp.
- ☆ *Ditylum* sp.

2012
vs
2015

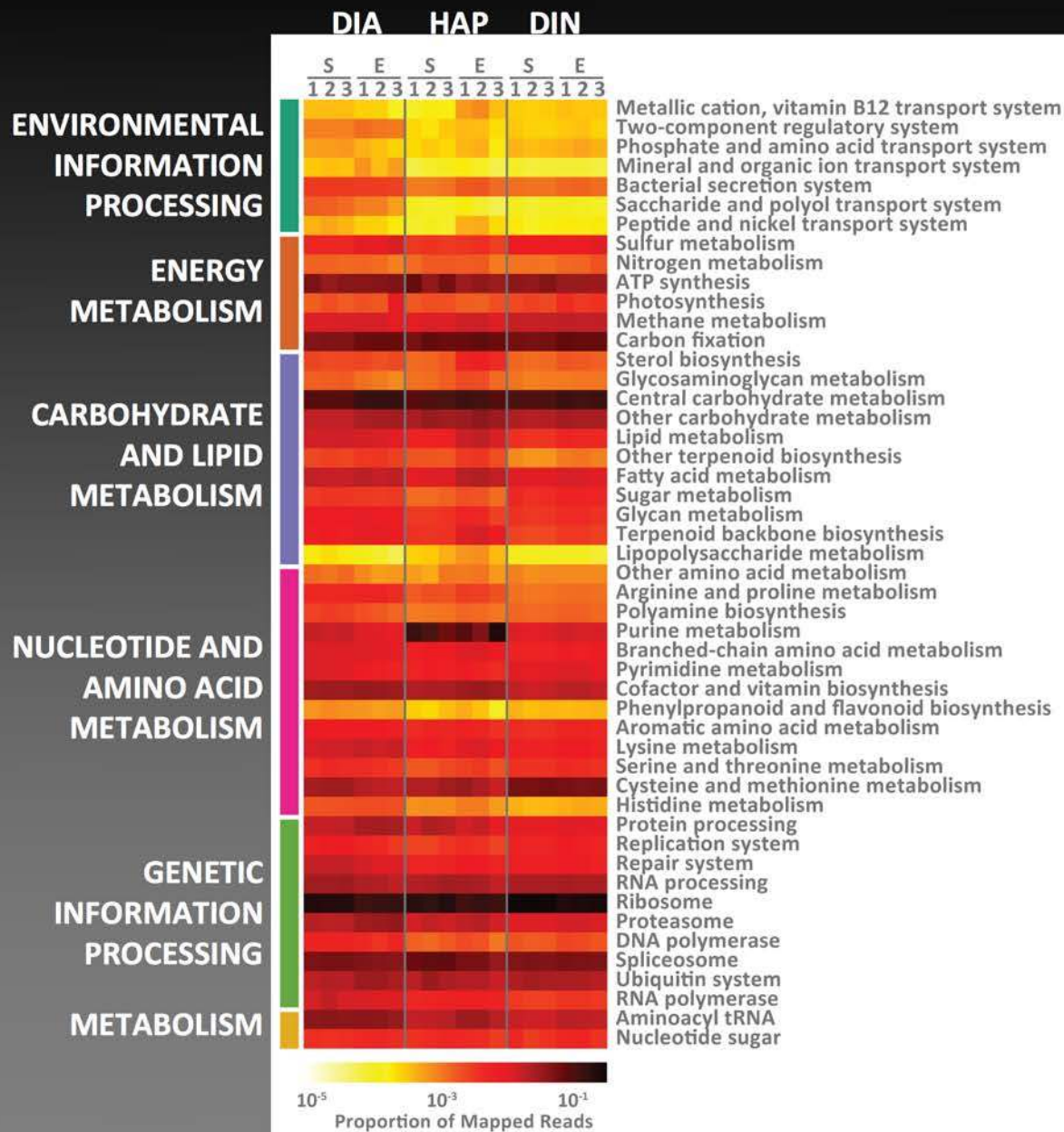
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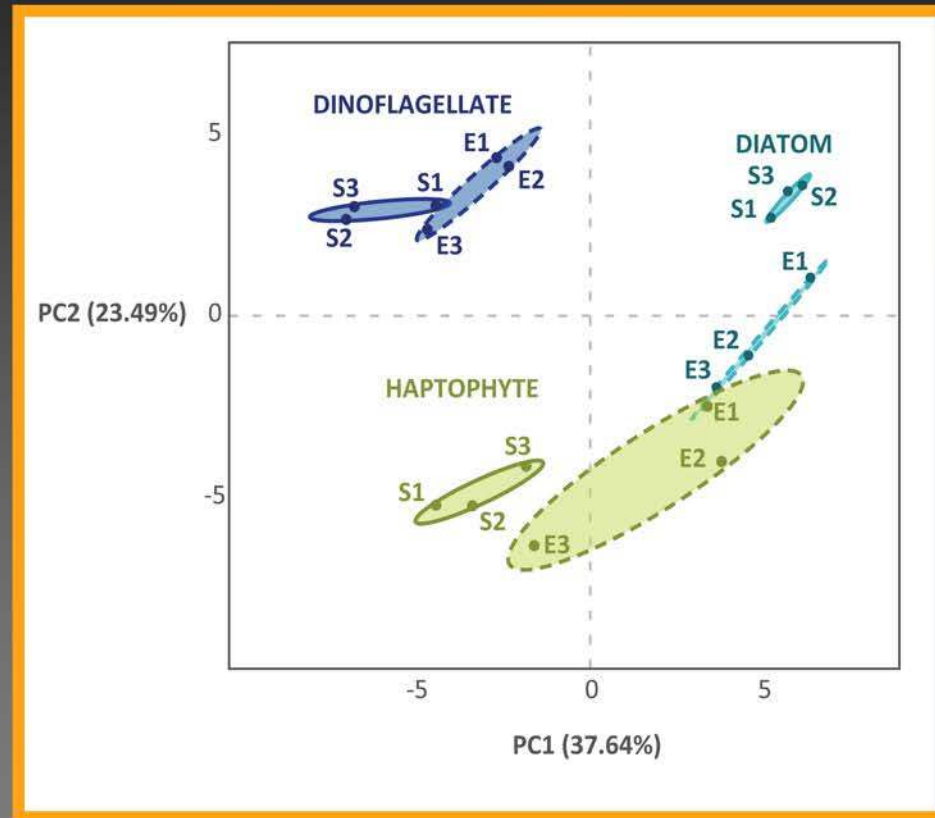
- *Cylindrotheca* sp.
- △ *Pseudo-nitzschia* sp.
- *Chaetoceros* sp.
- ☆ *Ditylum* sp.

2012
vs
2015

In both years, *Cylindrotheca* sp. and *Pseudo-nitzschia* sp. dominate with DSW addition

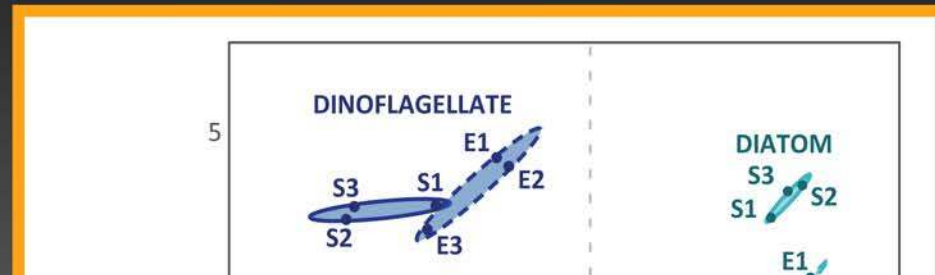


Metabolic fingerprints are distinct



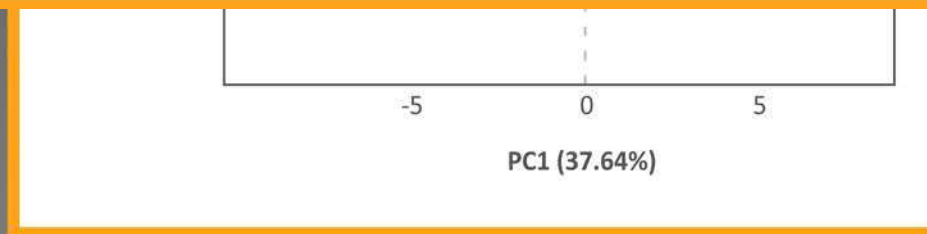
Species are distinct from each other with 95% confidence, and all but dinoflagellates significantly shift in the simulated blooms

Metabolic fingerprints are distinct



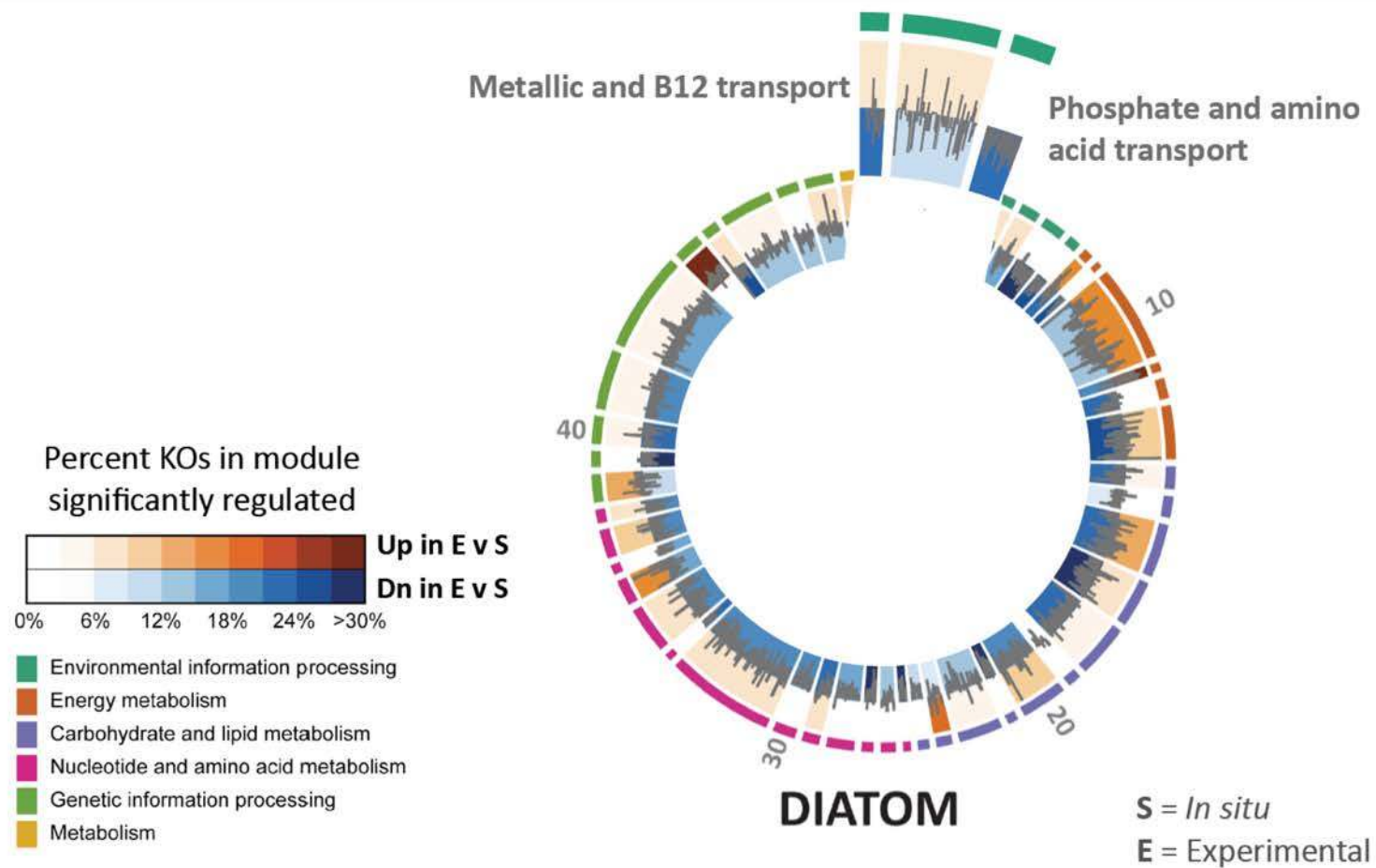
For each gene determine

Significance Post- $p > 0.95$ for 2-fold change

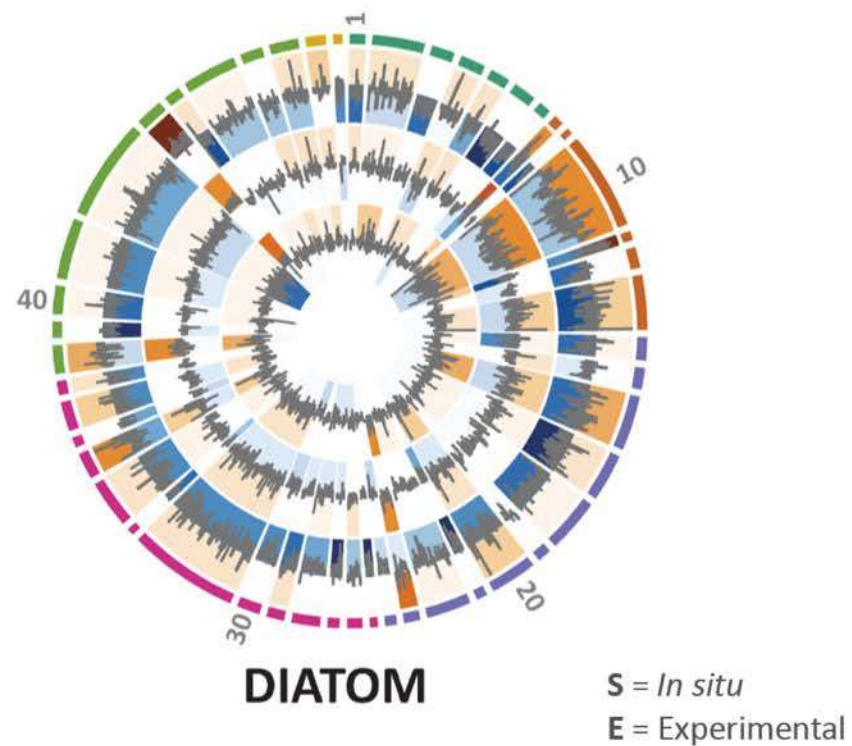
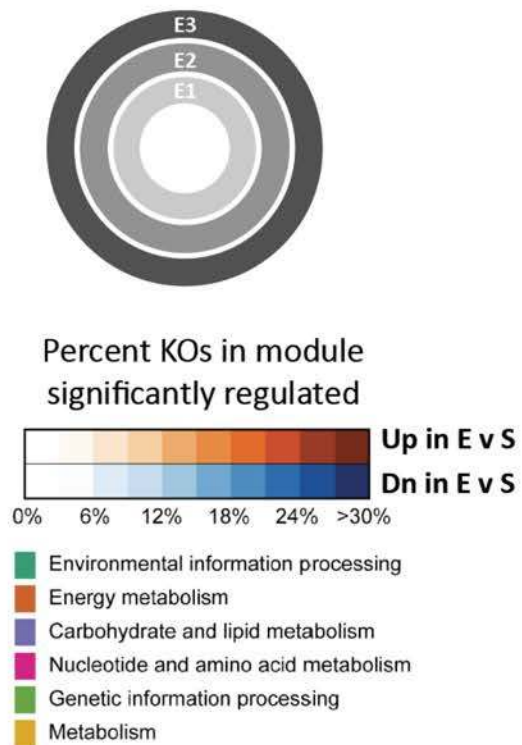


Species are distinct from each other with 95% confidence, and all but dinoflagellates significantly shift in the simulated blooms

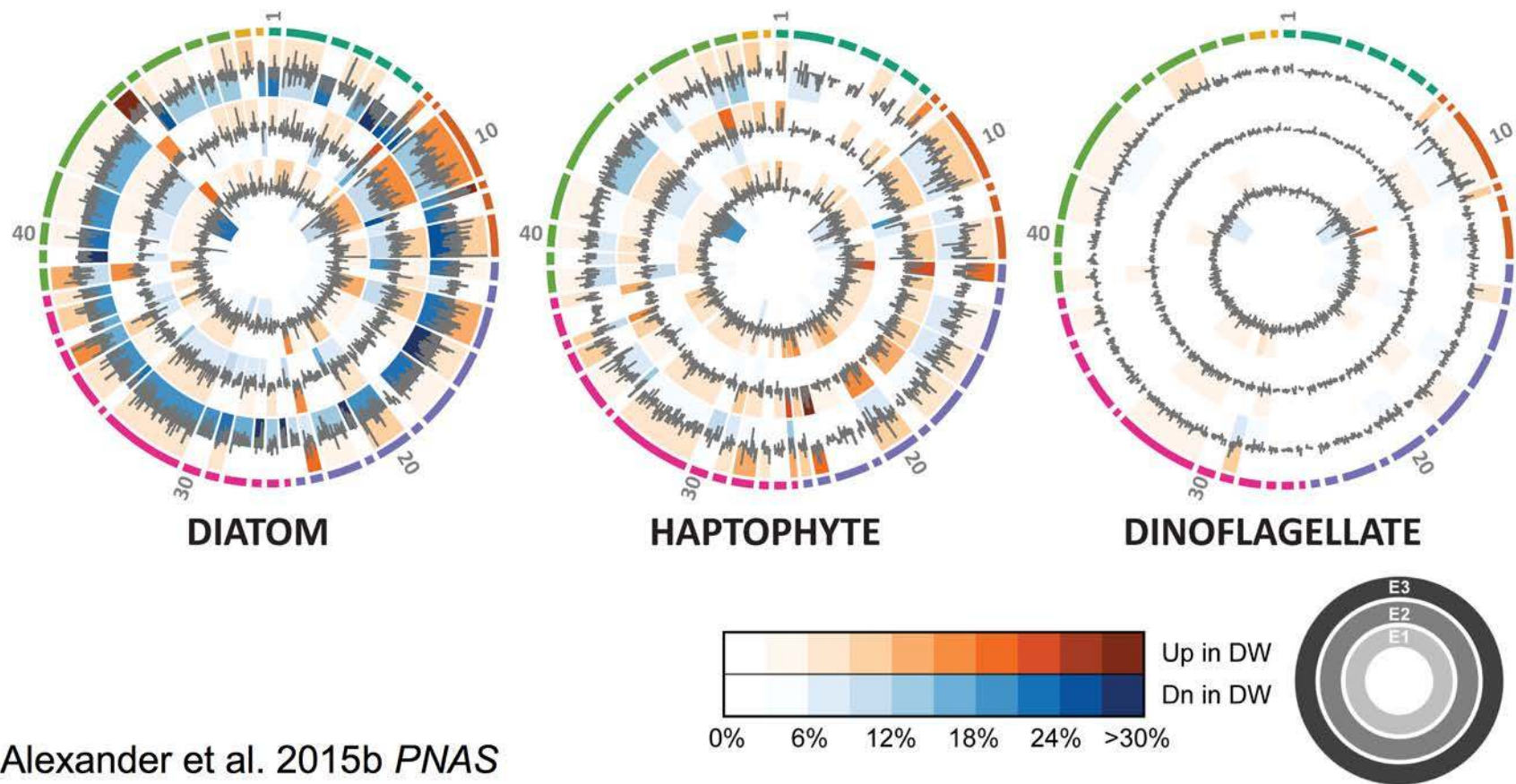
Gene shifts in diatoms



Gene shifts in diatoms



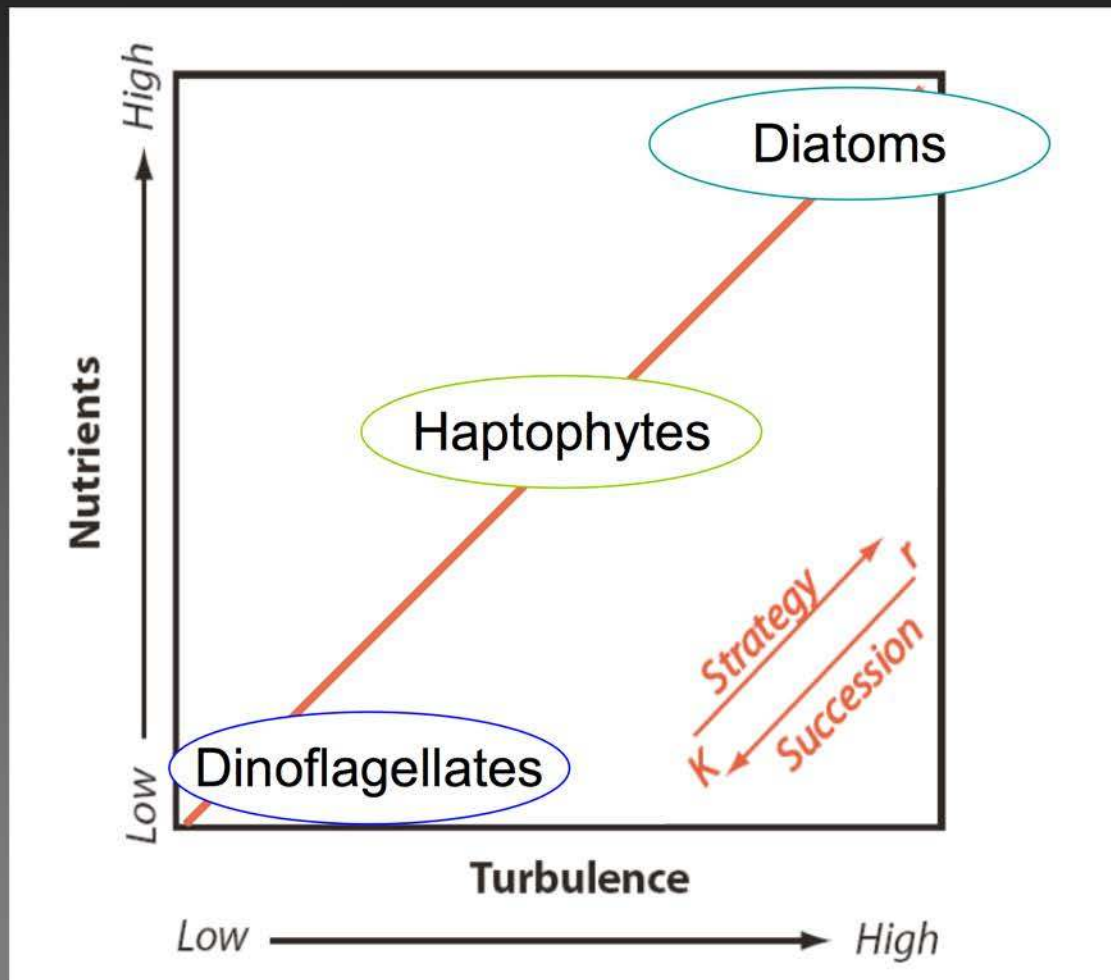
Transcriptional response during simulated blooms



Alexander et al. 2015b *PNAS*

Functional groups have distinct and reproducible transcriptional response during blooms driven by nutrient input

Margalef's Mandala - succession and ecological traits



Adapted from Margalef 1978

Transcriptional responses underscore functional group traits

Dinoflagellates



FEW significant shifts



Alternative trophic modes?

Diatoms



BROAD transcript decreases
TARGETED transcript increase



“the scavengers”
r-selected

Haptophytes



MUTED increase and decreases

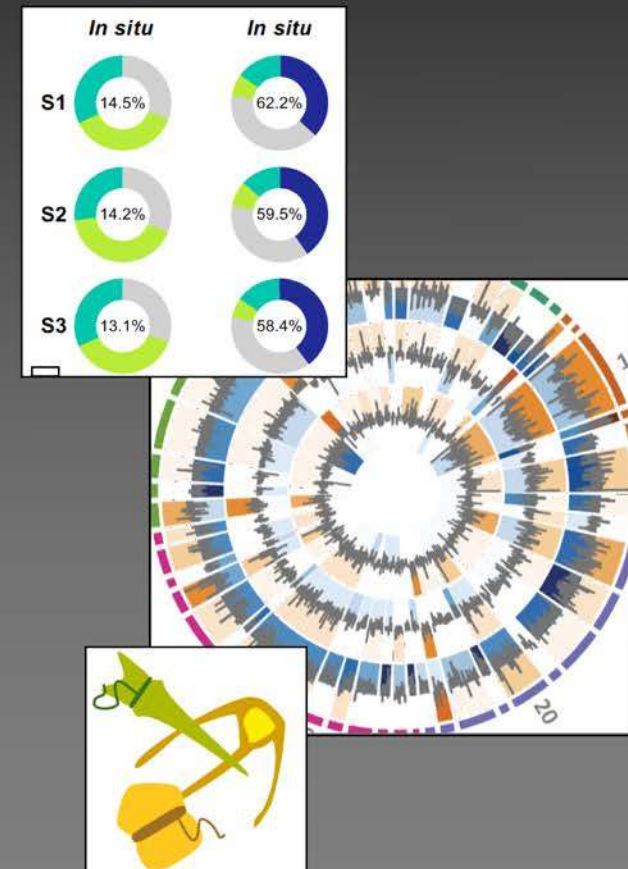


“the survivalists”
K-selected

Summary - Eco-evolutionary traits

Are there functional group traits that drive the structure and function of the NPSG?

- **Transcriptomes:** The better the reference database (MMETSP) the better resolution
- **Metatranscriptomes:** Phytoplankton groups appear to be limited by resource availability in the NPSG with remarkable year to year consistency
- **Metatranscriptomes:** Dinoflagellates have little transcriptional response to nutrient input - will need other methods
- Diatom are particularly responsive ($VTAR > 1$) to nutrient input which likely underpins their dominance in blooms



Two themes

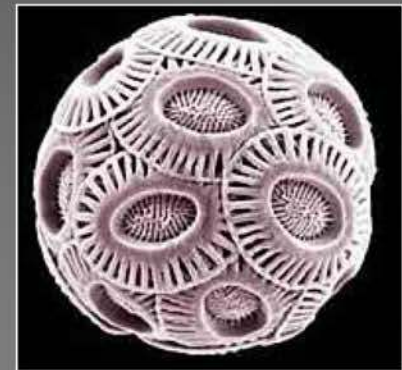
Eco-evolutionary traits

- Are there functional group traits that drive the bloom dynamics that structure the low nutrient North Pacific Subtropical Gyre?

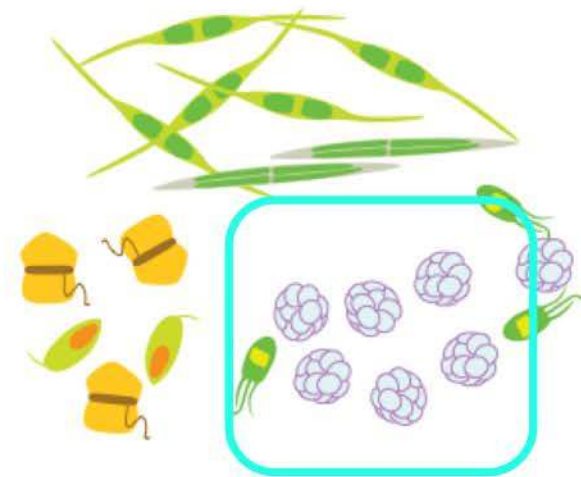
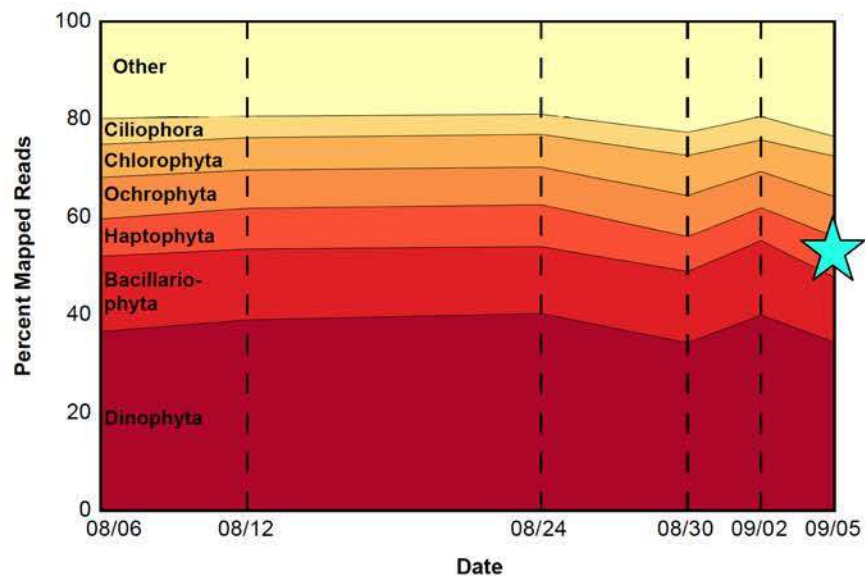


Metabolic plasticity

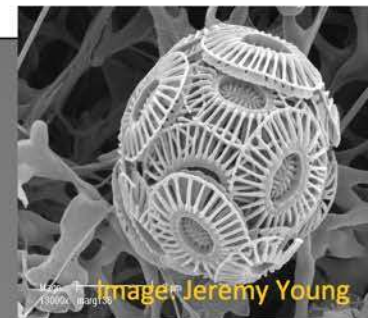
- How do resources drive the physiological ecology of a keystone coccolithophore?



Diving beyond the functional group...

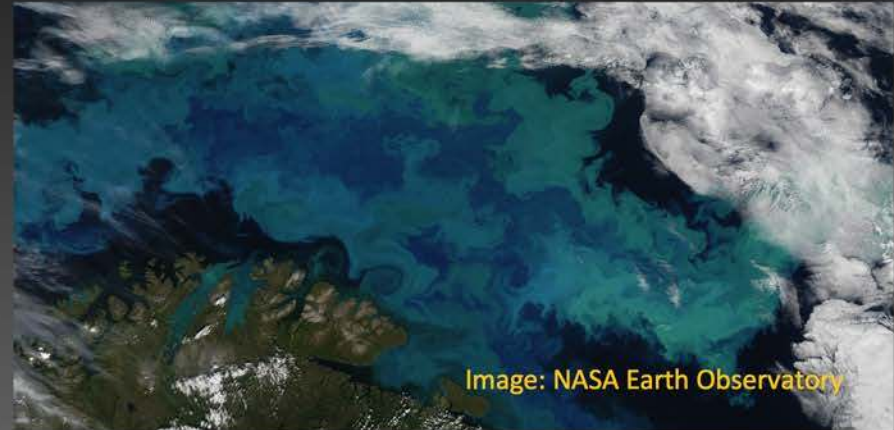


Tracking strain specific responses in the calcifying haptophyte, *Emiliana huxleyi* (Ehux)



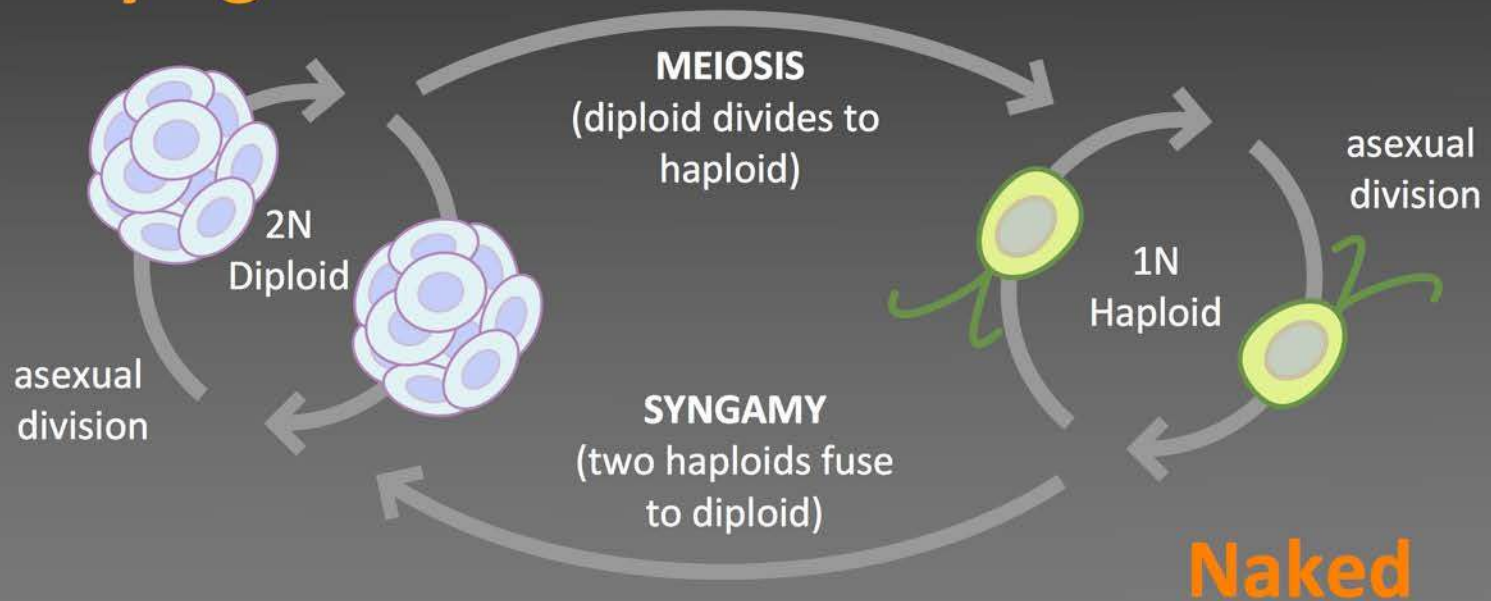
Emiliana huxleyi: a cosmopolitan, globally significant species

- Calcification - critical role in global carbon cycle and strongly linked to climate driven ocean acidification
- Source of paleoproxies for climate reconstructions
- Form dense blooms, drivers largely unknown
- First marine phytoplankton to have multiple strains sequenced, identifying pan genome



E. huxleyi life cycle

Calcifying



Emiliana huxleyi has many diverse isolates

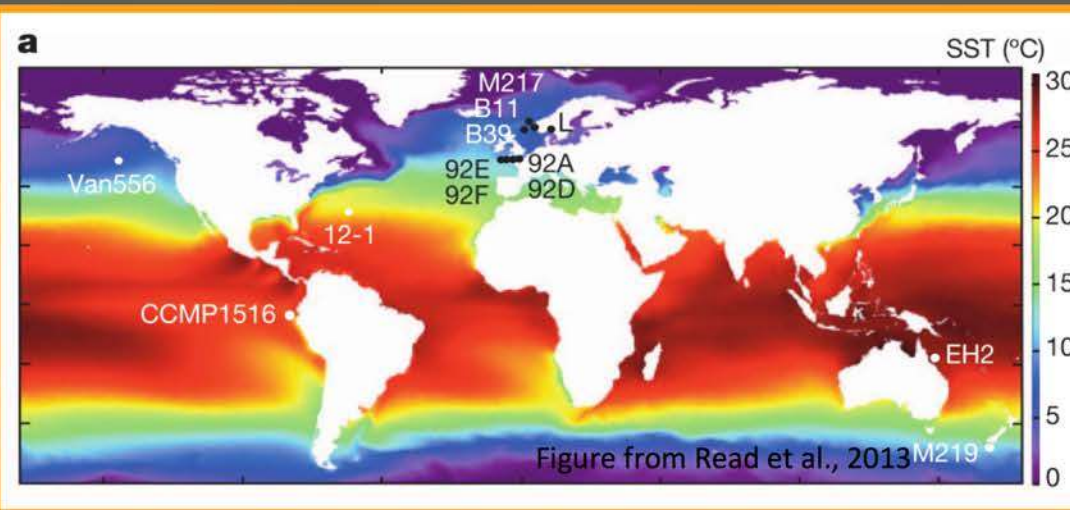
LETTER

OPEN

doi:10.1038/nature12221

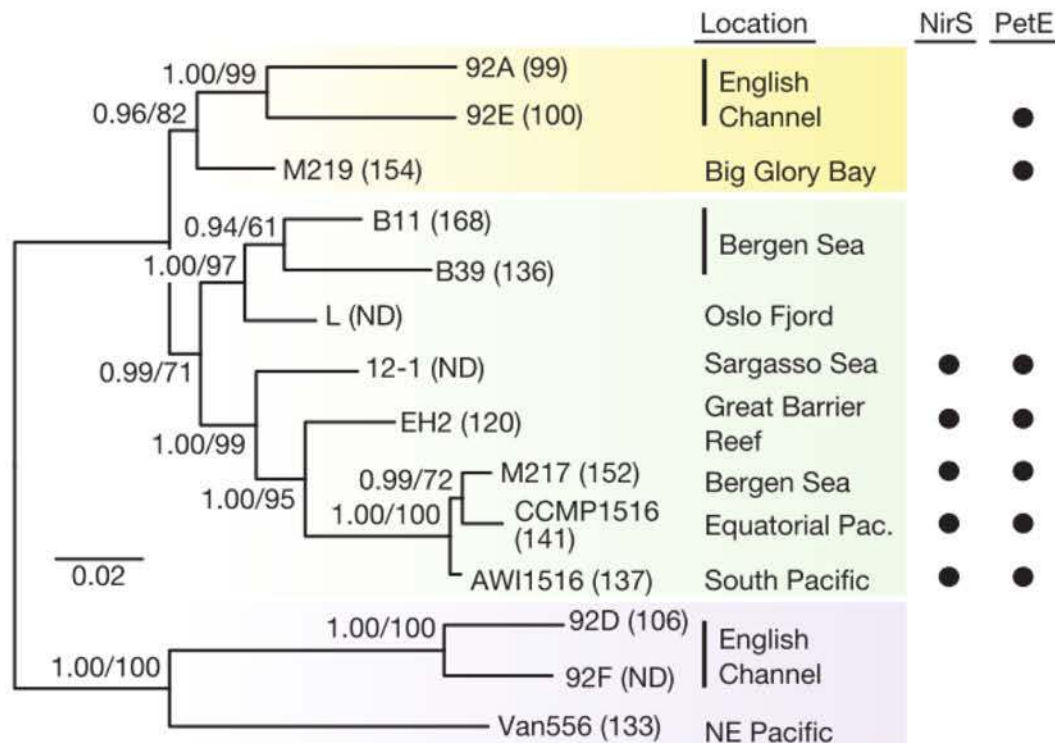
Pan genome of the phytoplankton *Emiliana* underpins its global distribution

Betsy A. Read¹, Jessica Kegel², Mary J. Klute³, Alan Kuo⁴, Stephane C. Lefebvre⁵, Florian Maumus⁶, Christoph Mayer^{7,8}, John Miller⁹, Adam Monier¹⁰, Asaf Salamov⁴, Jeremy Young¹¹, Maria Aguilar³, Jean-Michel Claverie¹², Stephan Frickenhaus^{2,13}, Karina Gonzalez¹⁴, Emily K. Herman³, Yao-Cheng Lin¹⁵, Johnathan Napier¹⁶, Hiroyuki Ogata¹², Analissa F. Sarno¹, Jeremy Shmutz^{4,17}, Declan Schroeder¹⁸, Colomán de Vargas¹⁹, Frederic Verret²⁰, Peter von Dassow²¹, Klaus Valentin², Yves Van de Peer¹⁵, Glen Wheeler^{18,22}, *Emiliana huxleyi* Annotation Consortium†, Joel B. Dacks^{3*}, Charles F. Delwiche^{9*}, Sonya T. Dyhrman^{23,24*}, Gernot Glöckner^{25*}, Uwe John^{2*}, Thomas Richards^{26*}, Alexandra Z. Worden^{10*}, Xiaoyu Zhang^{27*} & Igor V. Grigoriev⁴



Cultured strains are highly diverse - isolated from a broad temperature range and displaying considerable physiological diversity

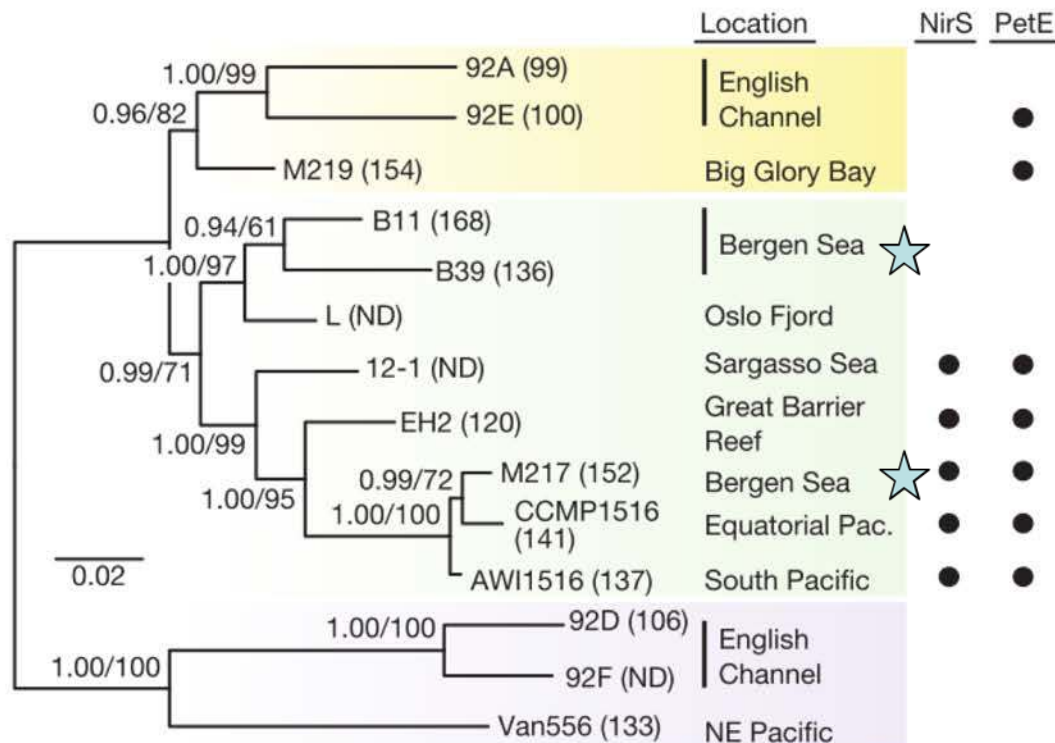
E. huxleyi has a pan genome, with core and variable gene content



Read et al., 2013 *Nature*

Key functional genes are variably distributed across cultured isolates, even from the same location

E. huxleyi has a pan genome, with core and variable gene content

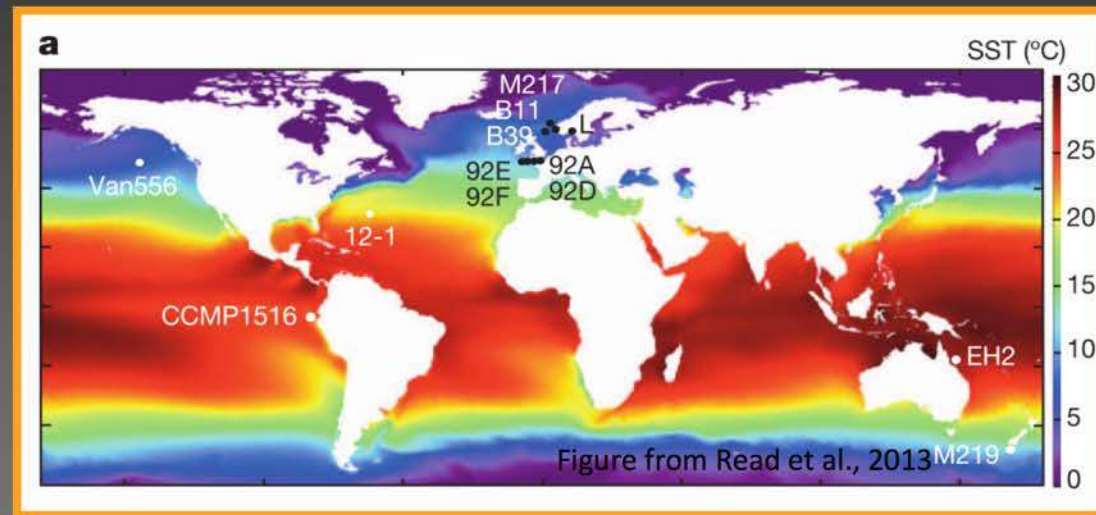


Read et al., 2013 *Nature*

Key functional genes are variably distributed across cultured isolates, even from the same location

Baas Becking hypothesis

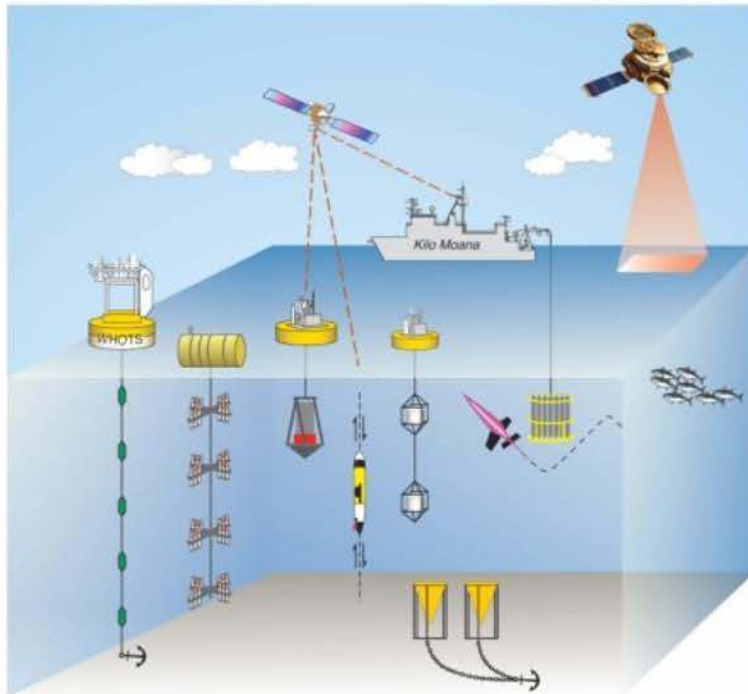
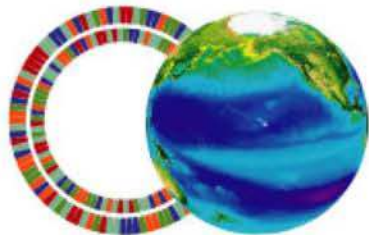
“Everything is every where, but
the environment selects”



How do resources drive physiological ecology?

Does the variable component of the pan-genome underpin
Response to changing environment?

Hawaii Ocean Experiment: Dynamics of Light and Nutrients

Wilson et al. 2015 *GBC*

center **for** microbial oceanography: research and education

C·more *linking genomes to biomes*
(HOF D)

(HOE-DYLAN)

Global Biogeochemical Cycles

AN AGU JOURNAL

[Explore this journal >](#)

Research Article

Short-term variability in euphotic zone biogeochemistry and primary productivity at Station ALOHA: A case study of summer 2012

Samuel T. Wilson , Benedetto Barone,
Francois Ascani, Robert R. Bidigare, Matthew J. Church,
Daniela A. del Valle, Sonya T. Dyhrman, Sara Ferrón,
Jessica N. Fitzsimmons, Laurie W. Juranek,
Zbigniew S. Kolber, Ricardo M. Letelier,
Sandra Martínez-García, David P. Nicholson,
Kelvin J. Richards, Yoshimi M. Rii, Mónica Rouco,
Donn A. Viviani, Angelicque E. White, Jonathan P. Zehr,
David M. Karl



View issue TOC
Volume 29, Issue 8
August 2015
Pages 1145–1164

Responses to shifts in resource ratios



Control Deep seawater
amendment

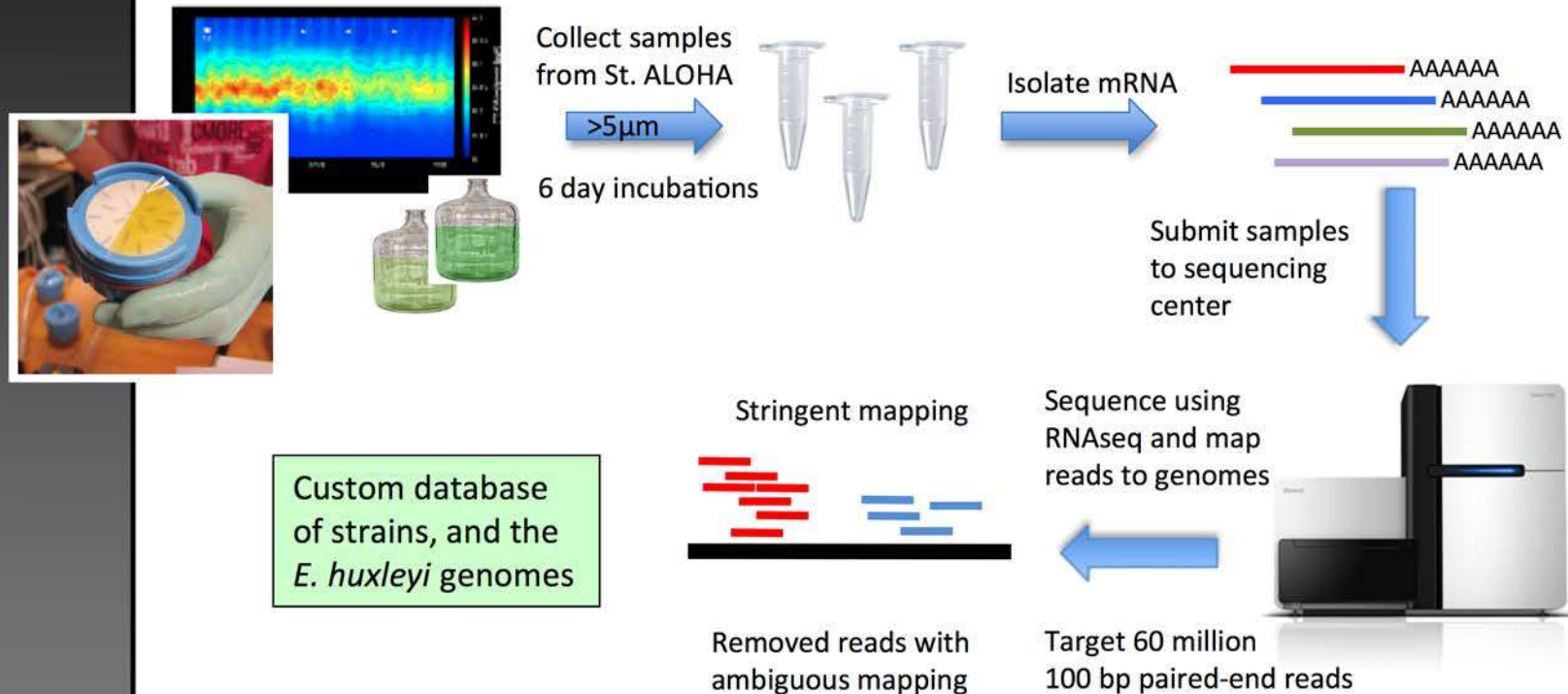


Treatments with added N



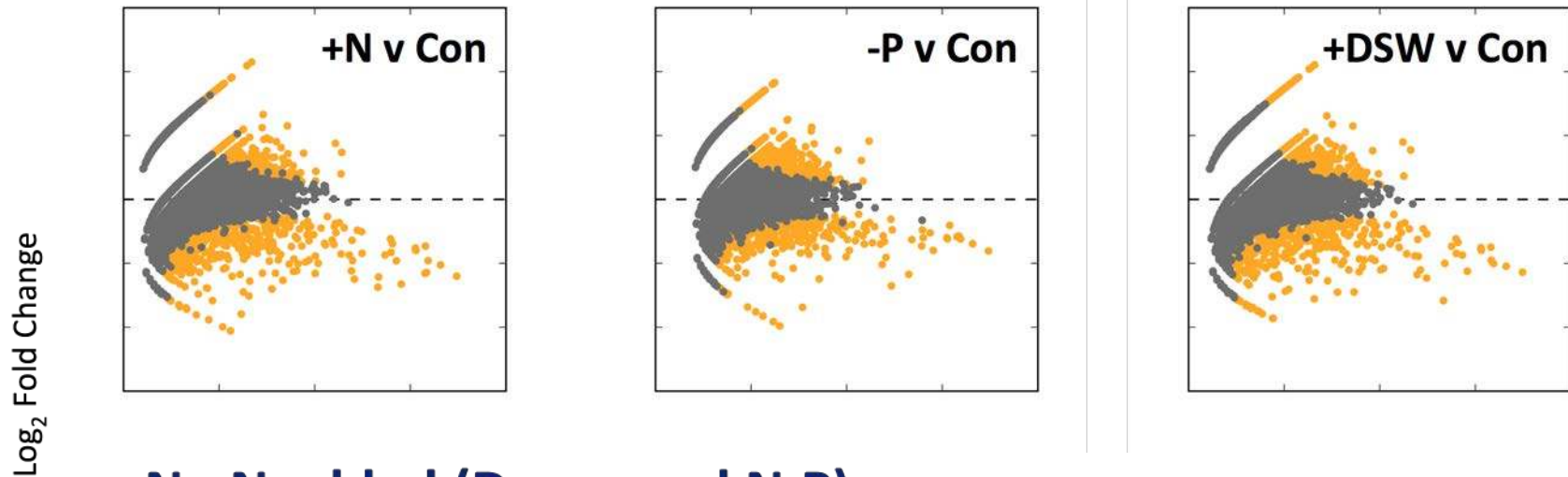


Sampling and pipeline



E. huxleyi physiological response suggests N control

N added (Increased N:P)



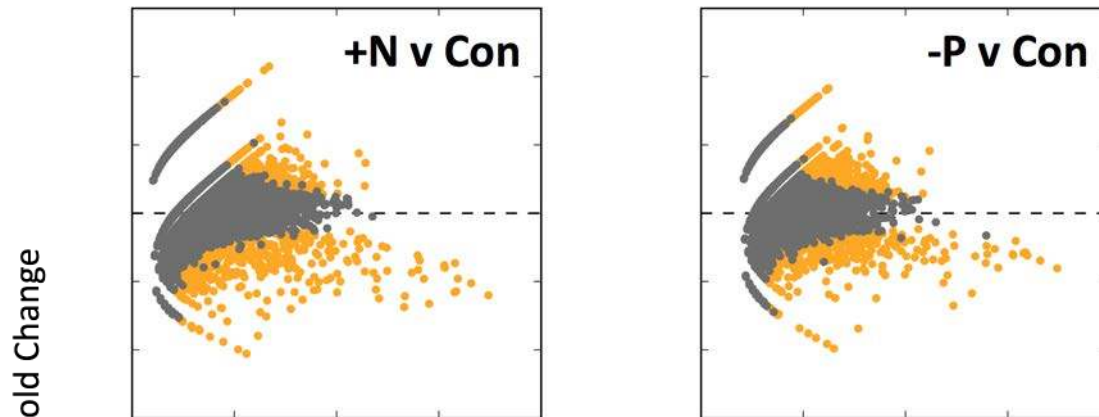
No N added (Decreased N:P)

Alexander et al. (in review)

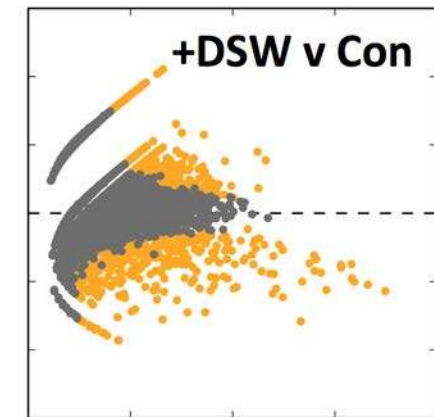
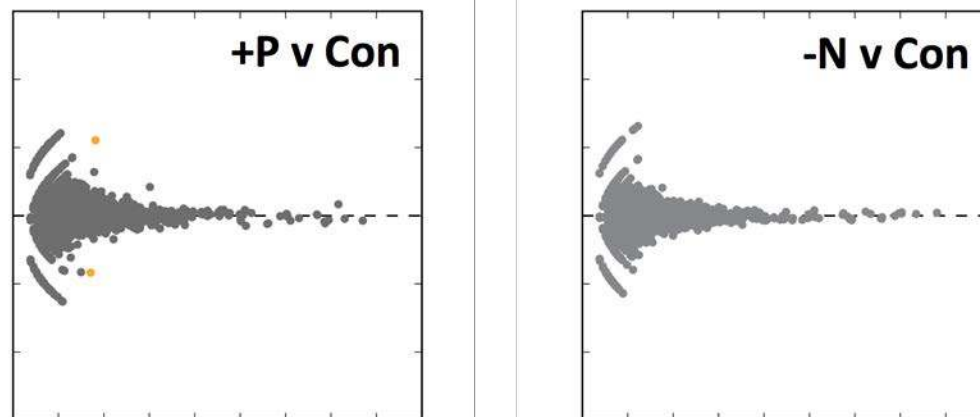
Log₂ Average Abundance

E. huxleyi physiological response suggests N control

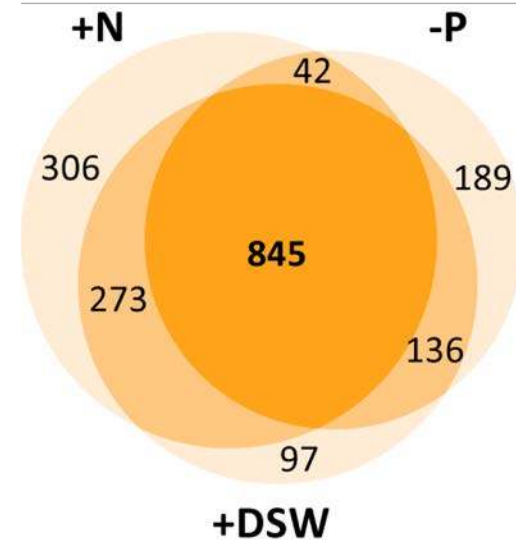
N added (Increased N:P)



No N added (Decreased N:P)



Significantly Differentially Abundant Genes

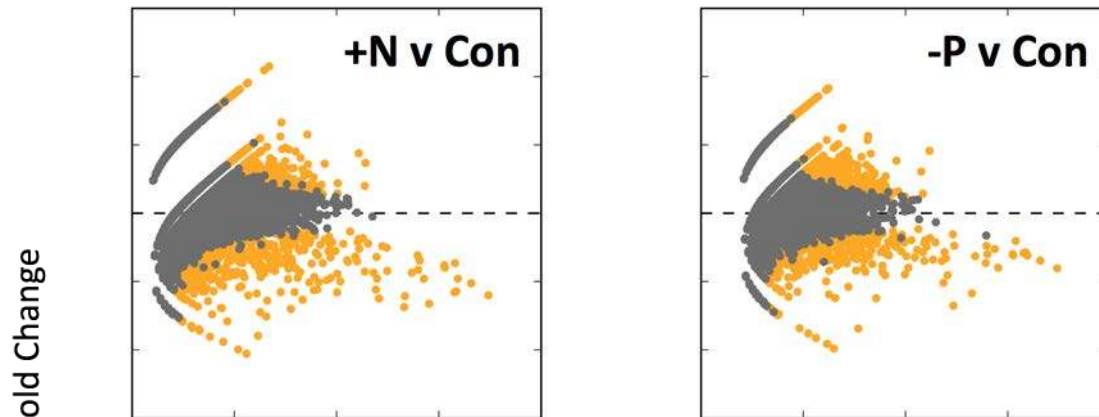


Alexander et al. (in review)

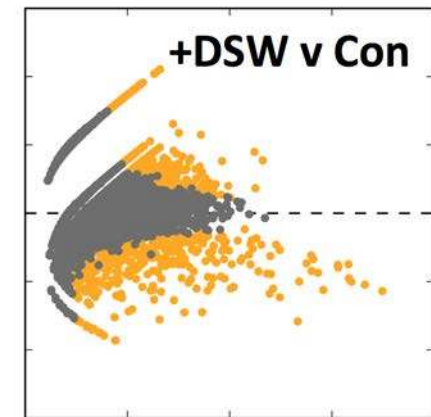
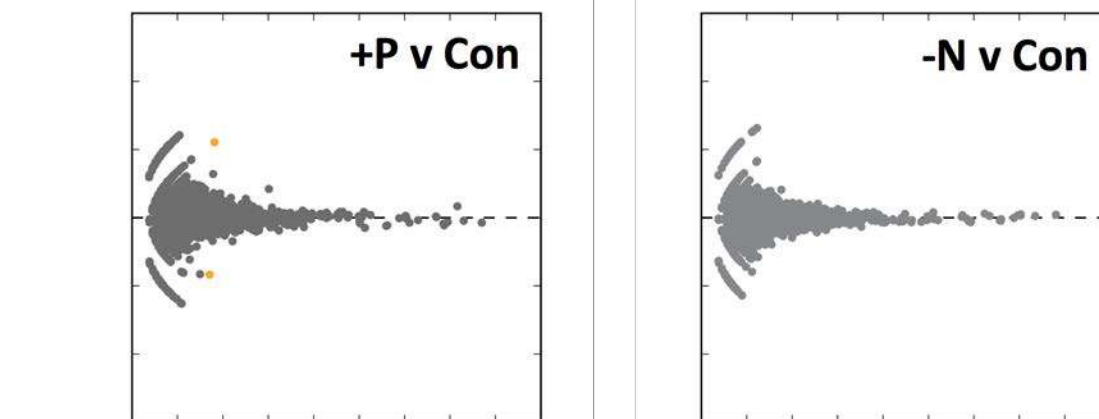
Log₂ Average Abundance

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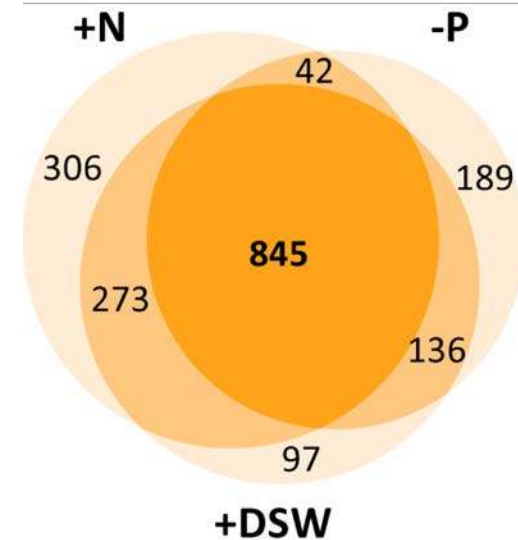
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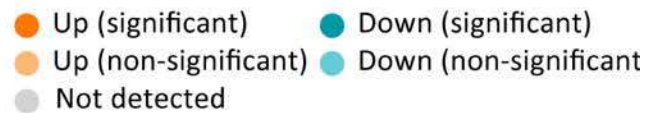
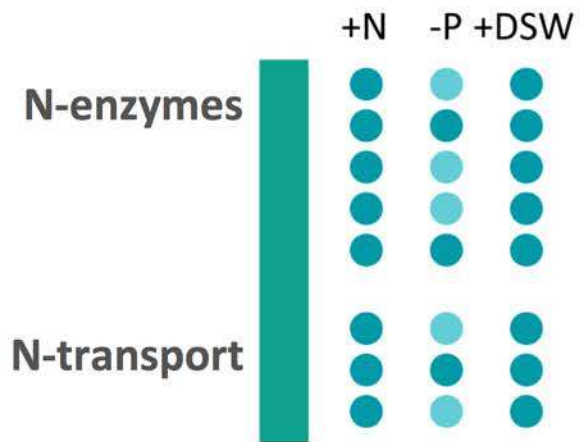
Significantly Differentially Abundant Genes



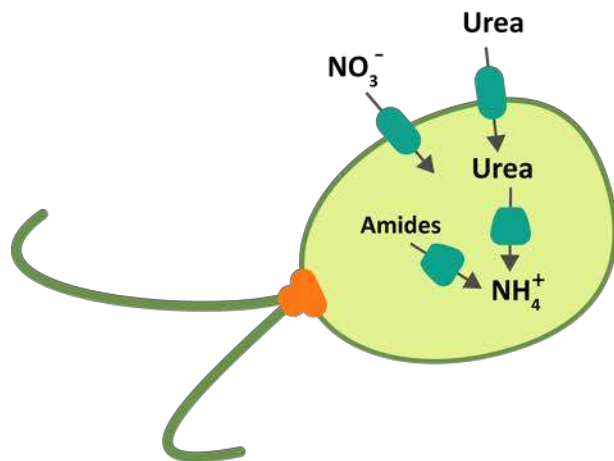
Alexander et al. (in review)

Log₂ Average Abundance

Nitrogen

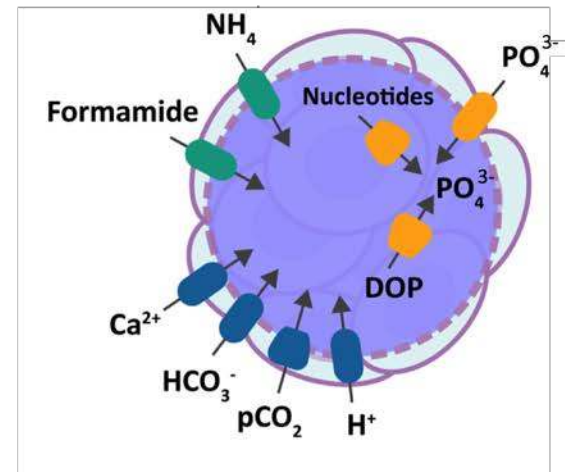


1N, non-calcifying, N-limited

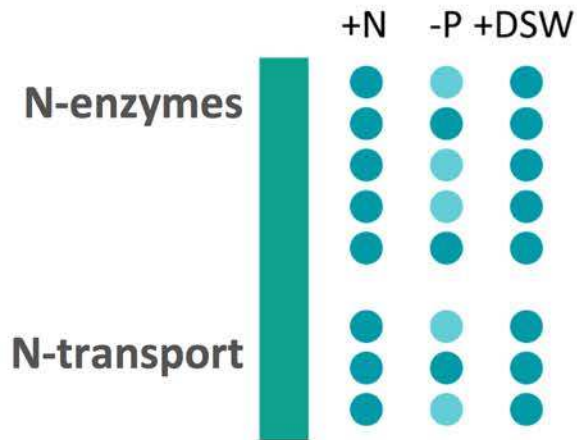


N added

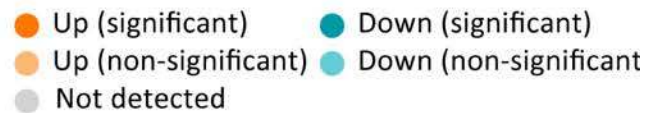
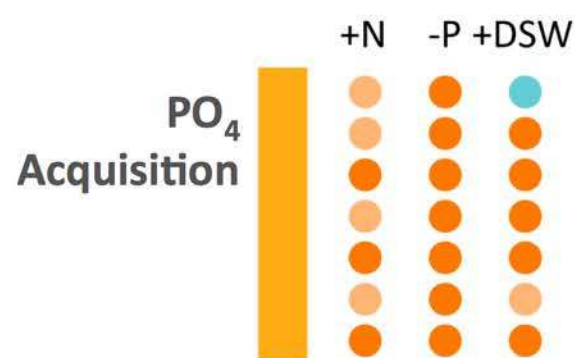
2N, calcifying, P-limited



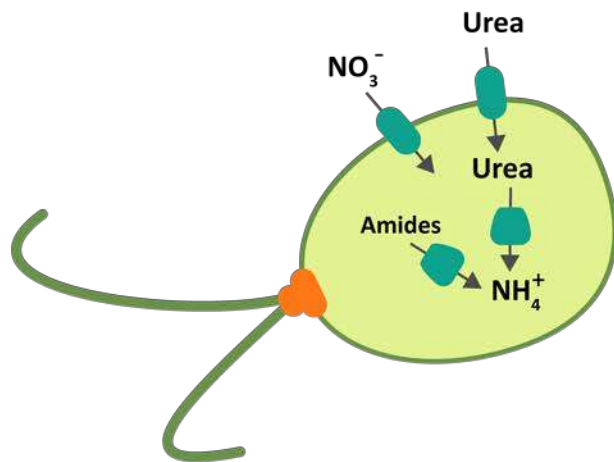
Nitrogen



Phosphorus

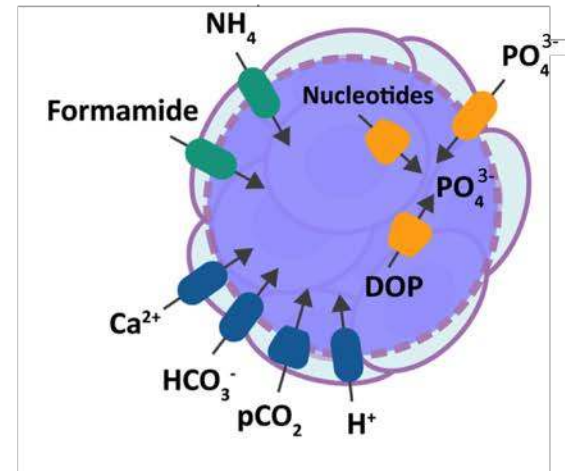


1N, non-calcifying, N-limited

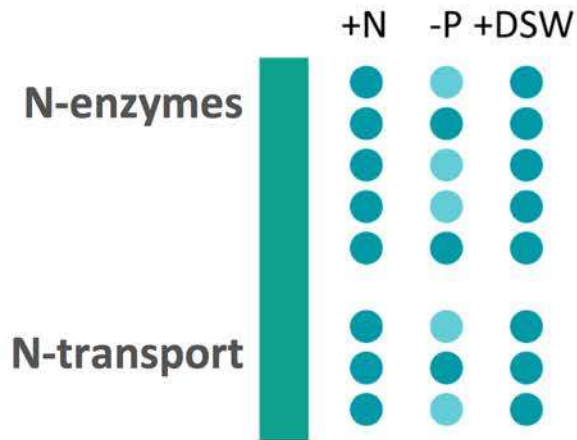


N added

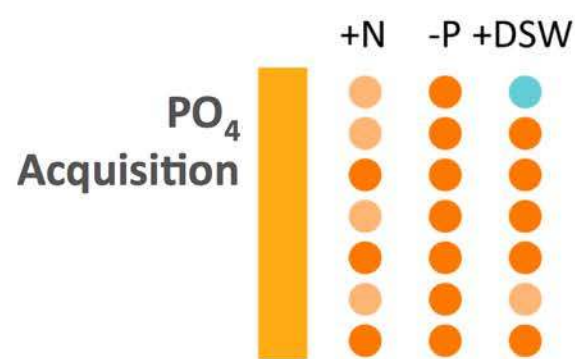
2N, calcifying, P-limited



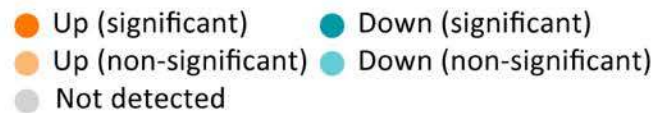
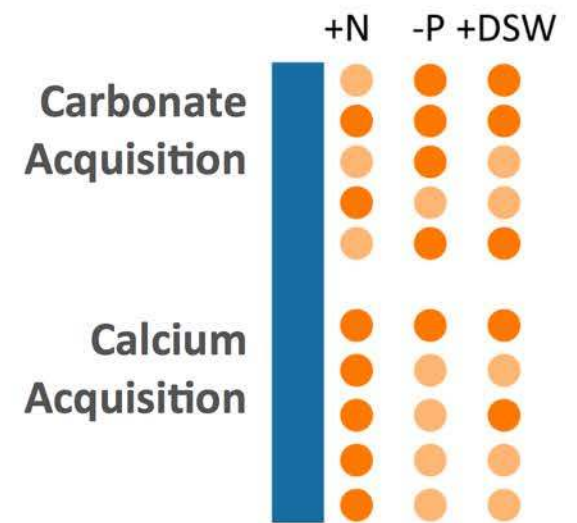
Nitrogen



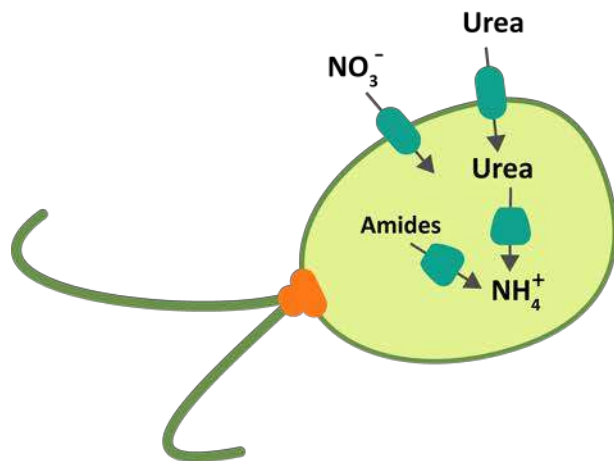
Phosphorus



Calcification

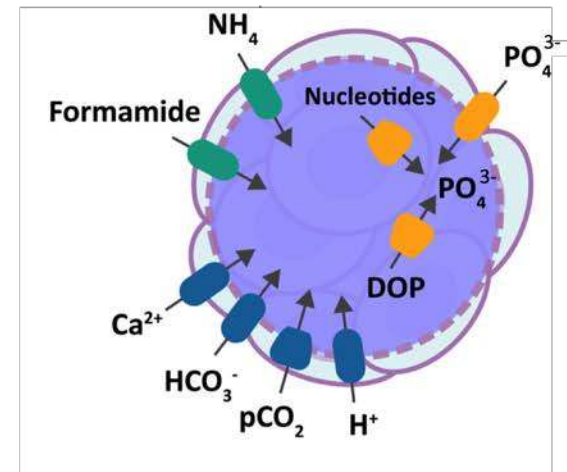


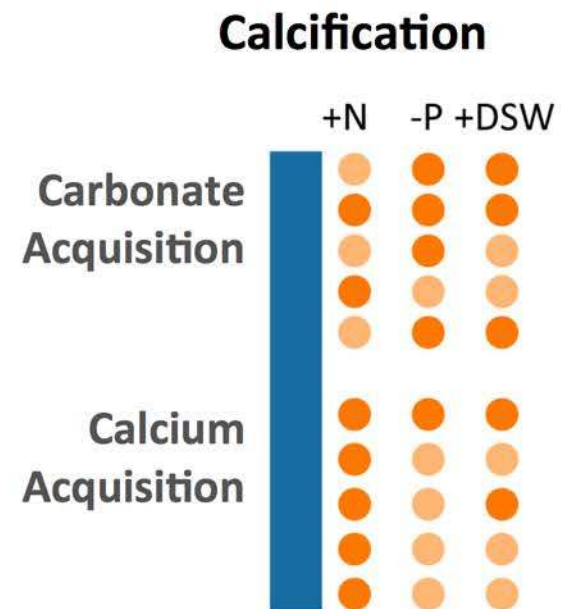
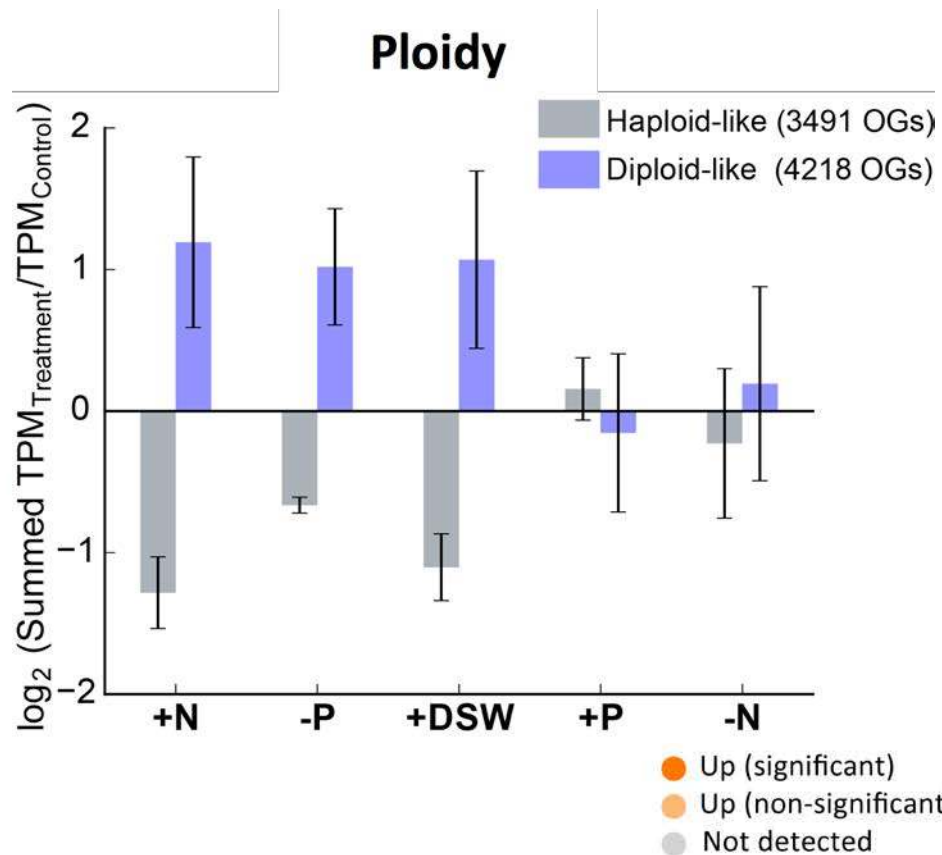
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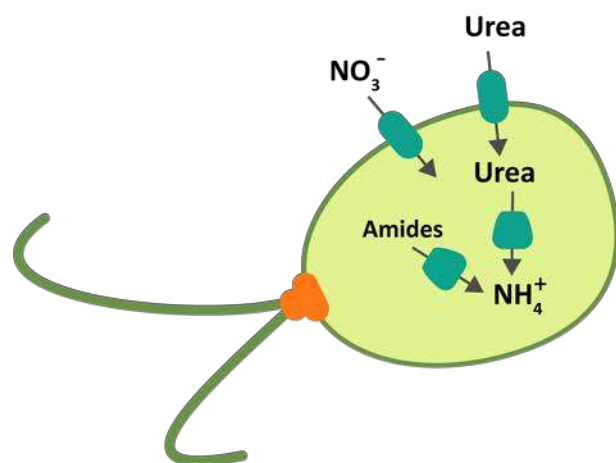
N added

2N, calcifying, P-limited



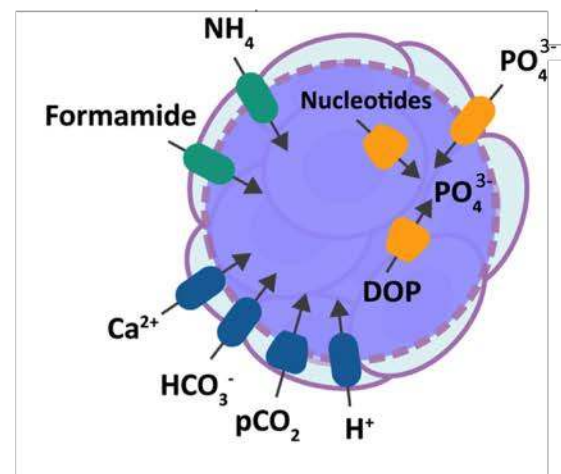


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Does the variable component of the pan-genome underpin
Response to changing environment?

**Collect available
transcriptomes from
E. huxleyi strains**

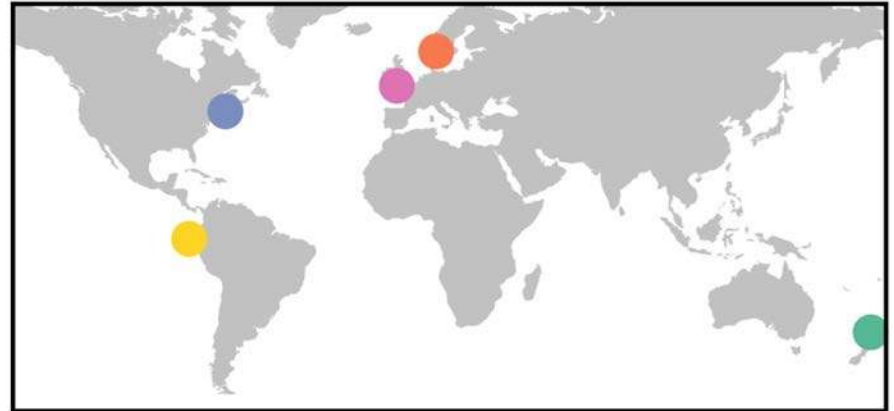


**Cluster transcripts into
orthologous group to
identify core and
variable OGs
(OrthoMCL)**



**Map field data and
examine shifts in core
v. variable expression
in incubations
(RSEM, edgeR)**

- CCMP1516
- CCMP379
- CCMP374
- CCMP370
- PLYM219



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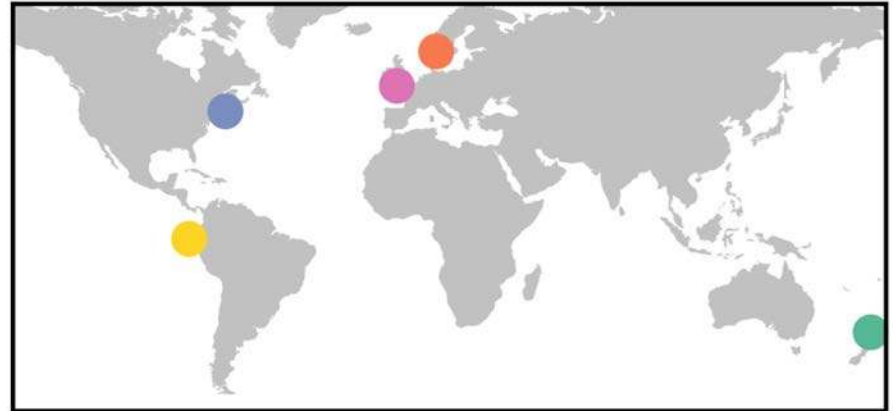


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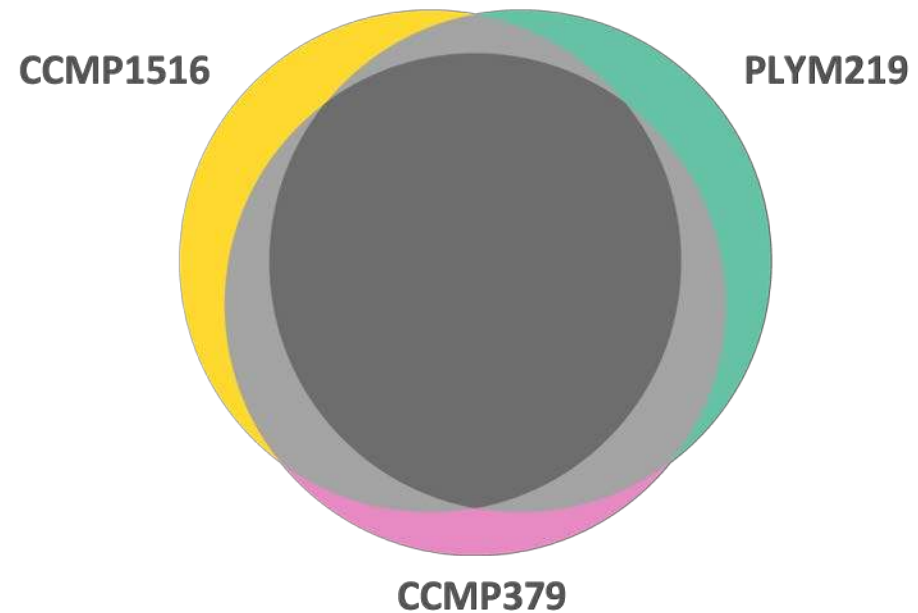


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Gene content of the *E. huxleyi* species complex



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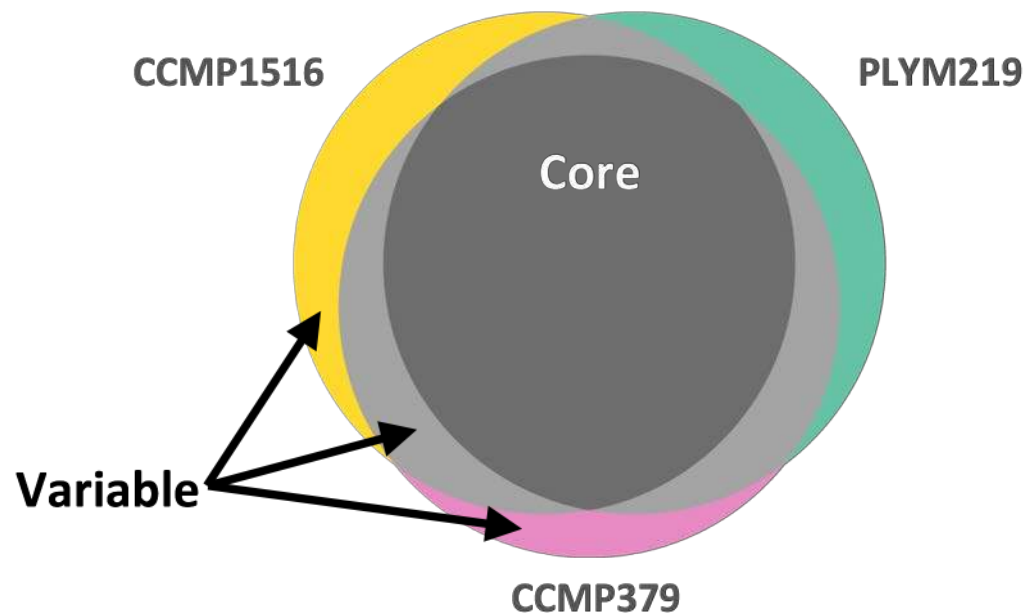


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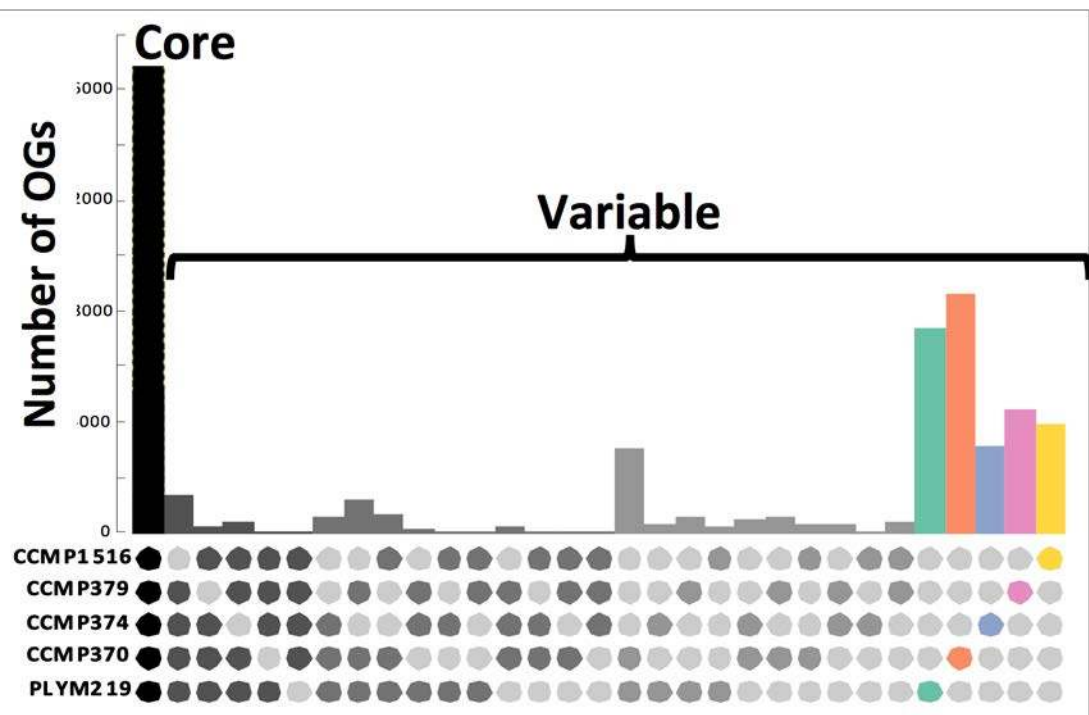


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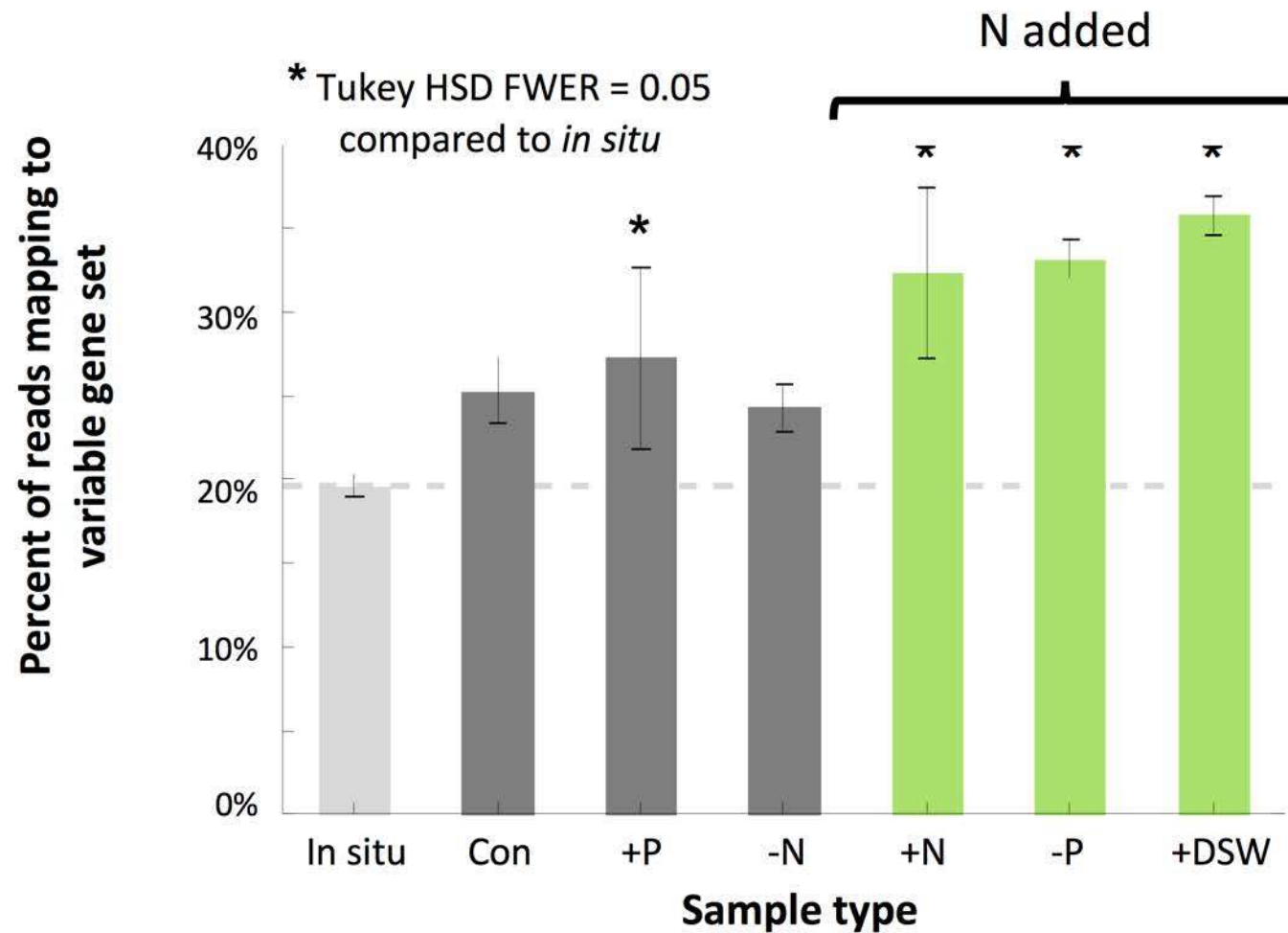


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Expression of the variable portion of the pan-genome

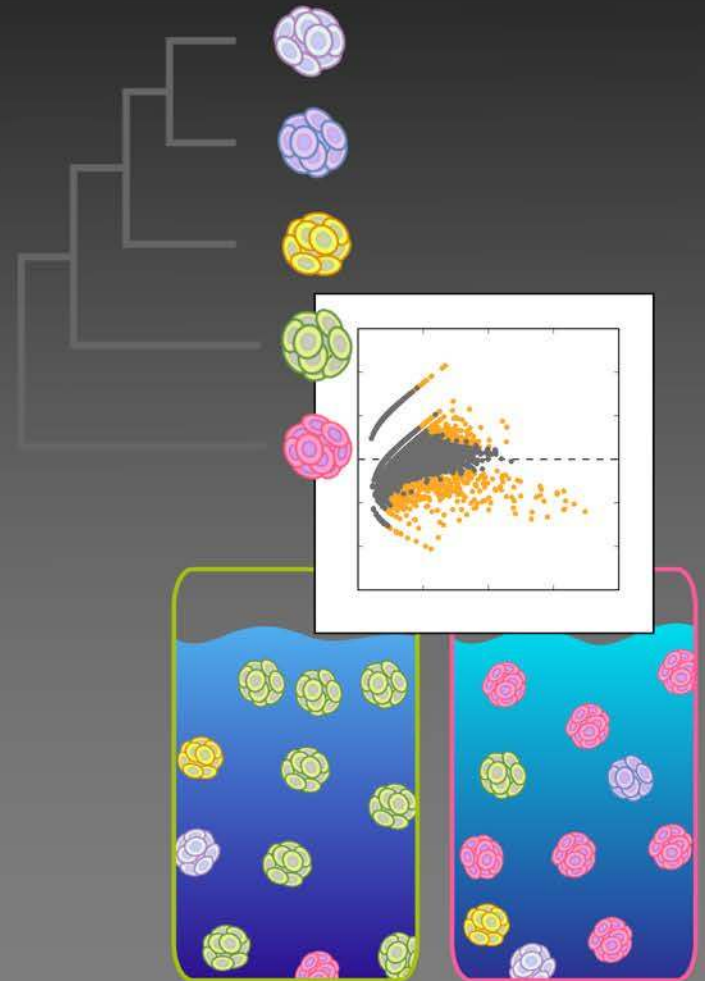


Expression of variable gene set significantly increased following N-addition

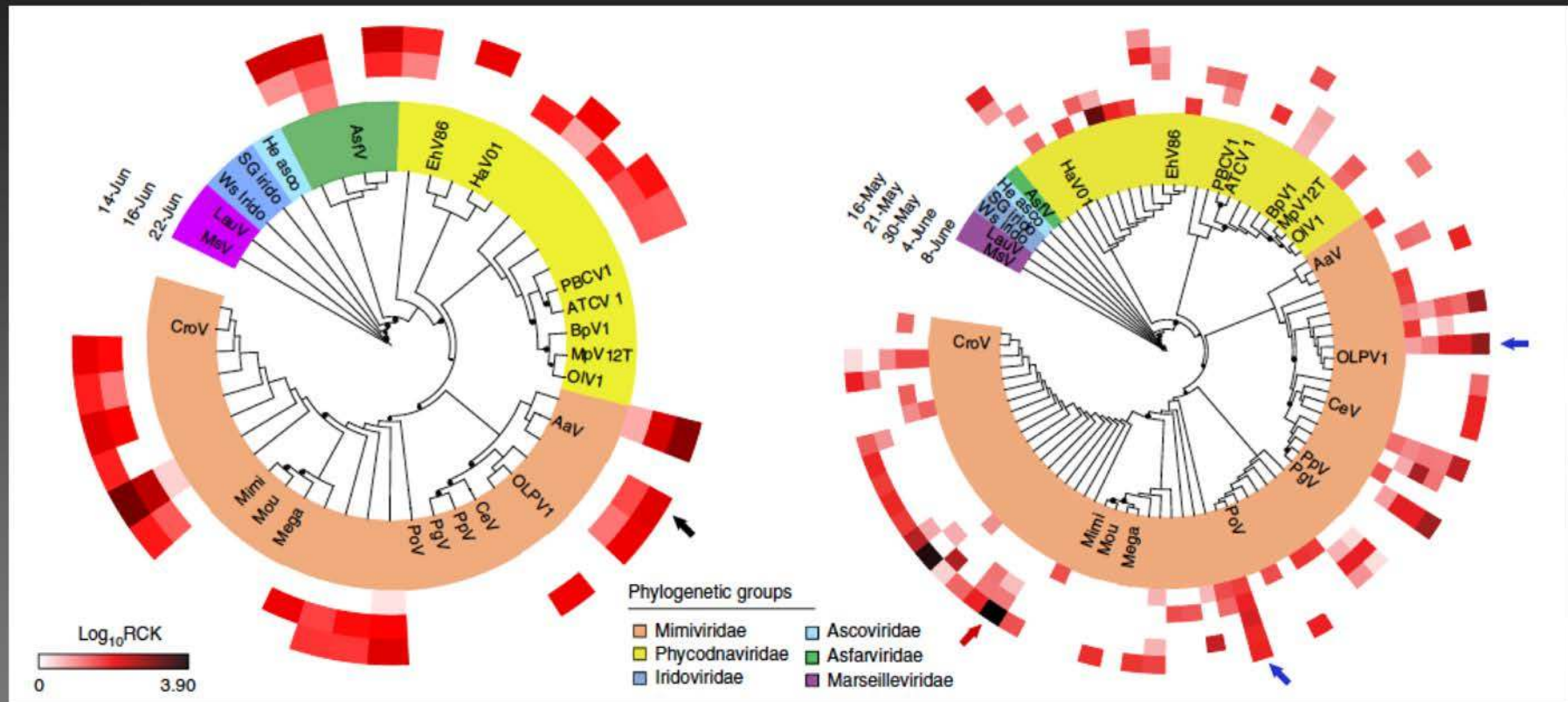
Summary - Metabolic plasticity

What resources drive the physiological ecology of a keystone coccolithophore?

- **Metatranscriptome:** Nitrogen limits coccolithophore activity, and influences shifts in life stage and calcification
- Results support hypothesis by Read et al. (2013) that the genomic variability of the *E. huxleyi* species complex facilitates its ability to thrive in a range of environments
- **Metatranscriptome:** What if you were to keep mining the data even further?
 - Tracking active viral infection of DNA viruses
 - Assemble new RNA viruses



Mining viral expression from metatranscriptomes

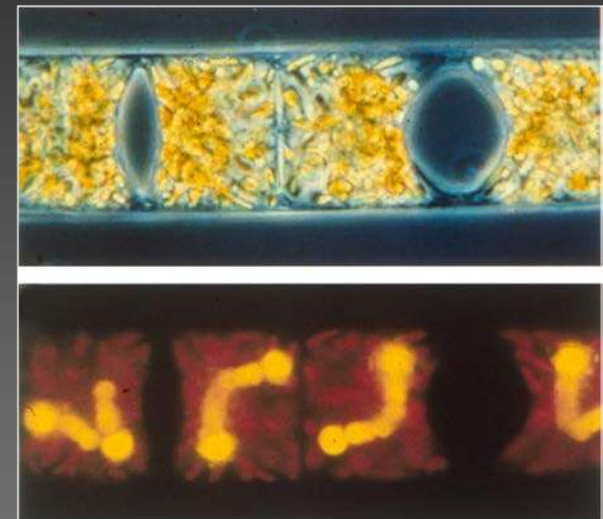


Moniruzzaman et al. (2017) *Nature Comm*

Phylogenetic placement of major capsid protein expression patterns detected in microbial eukaryote samples from two coastal field sites - towards reconstructing viral infection ecology

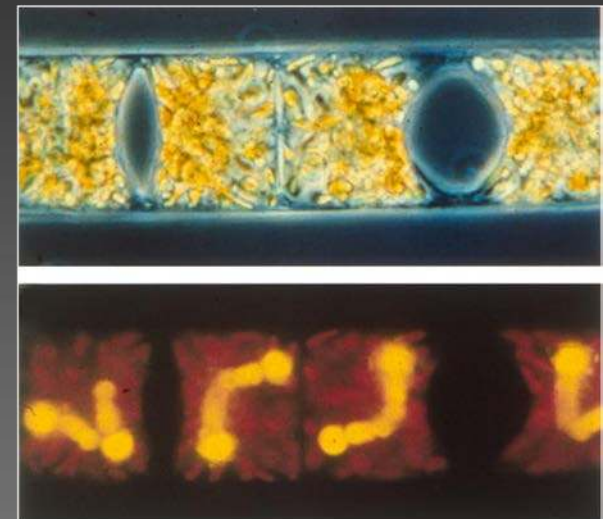
One last story....

- Some of the most important microbial eukaryotes live in symbioses or associations.
- Diatom diazotroph associations (DDAs) drive summer export of carbon to the deep sea, sequestering CO₂.
- Diazotroph supplies fixed N₂ to host.
- There are no long term reference cultures, resulting in limited knowledge about the activities of these symbioses in the field.



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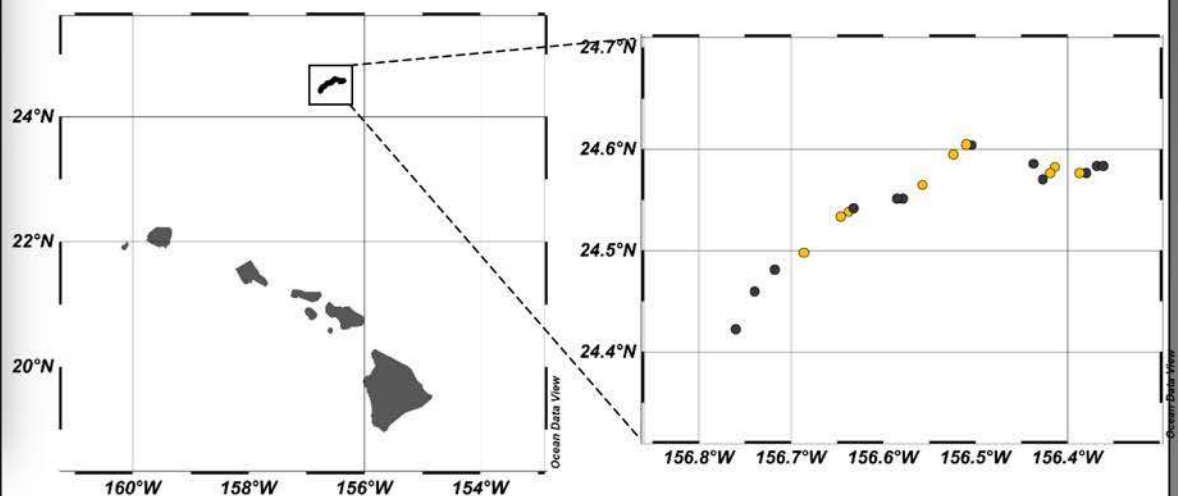
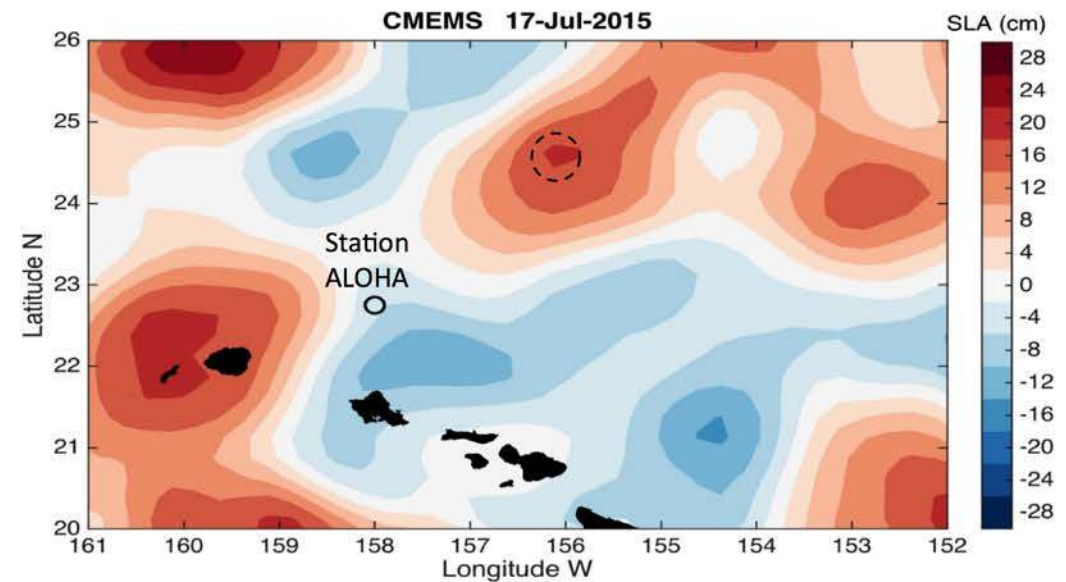
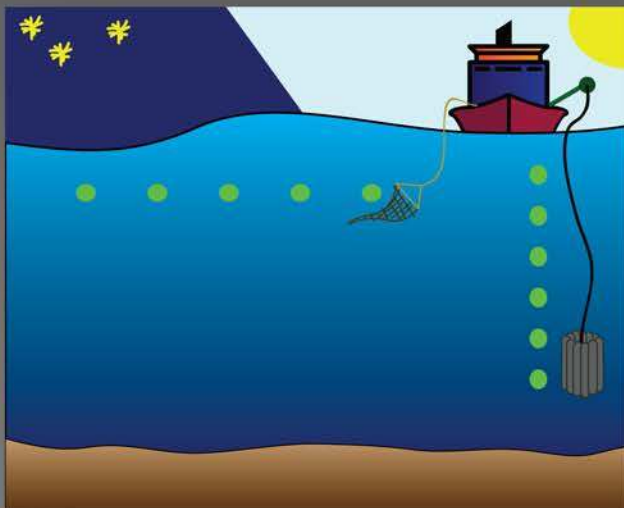


Are there patterns of coordinated expression that underpin host - symbiont physiology?

Sampling the NPSG



R/V Kilo Moana





3x20L from 15m
(21 time points, every 4 h, 3.5 days)

Filter
($>5\mu\text{m}$)

Extract RNA

Selected



Unselected



RAIN and WGCNA



3x20L from 15m
(21 time points, every 4 h, 3.5 days)

Filter
($>5\mu\text{m}$)



Extract RNA

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Unselected



Map to reference
database of MMETSP
diatoms
(Including *Rhizosolenia*)

RAIN and WGCNA



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Unselected



**Map to reference
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Current data set :

- ~ 19 billion reads
- ~ 2 terabytes of data

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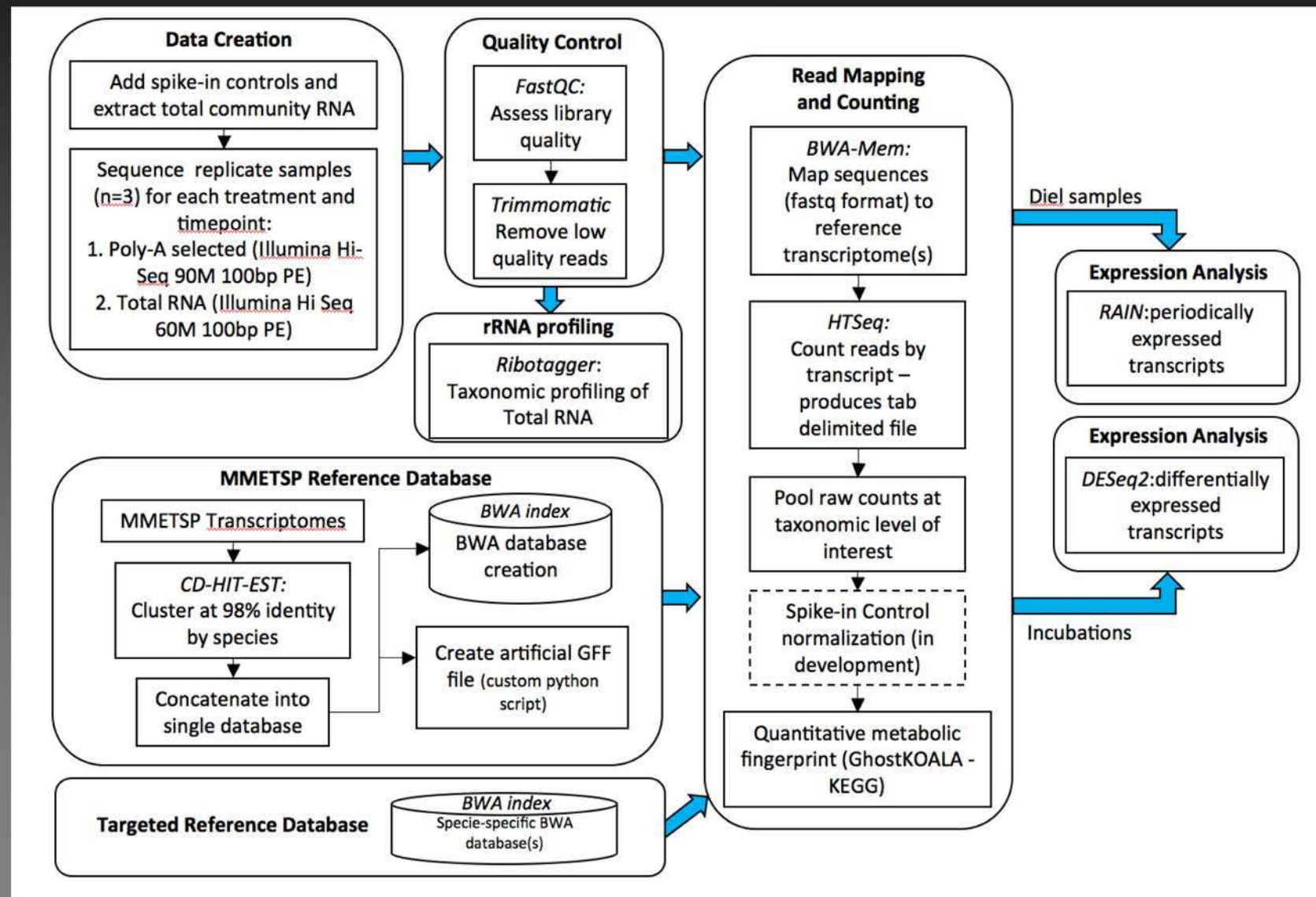
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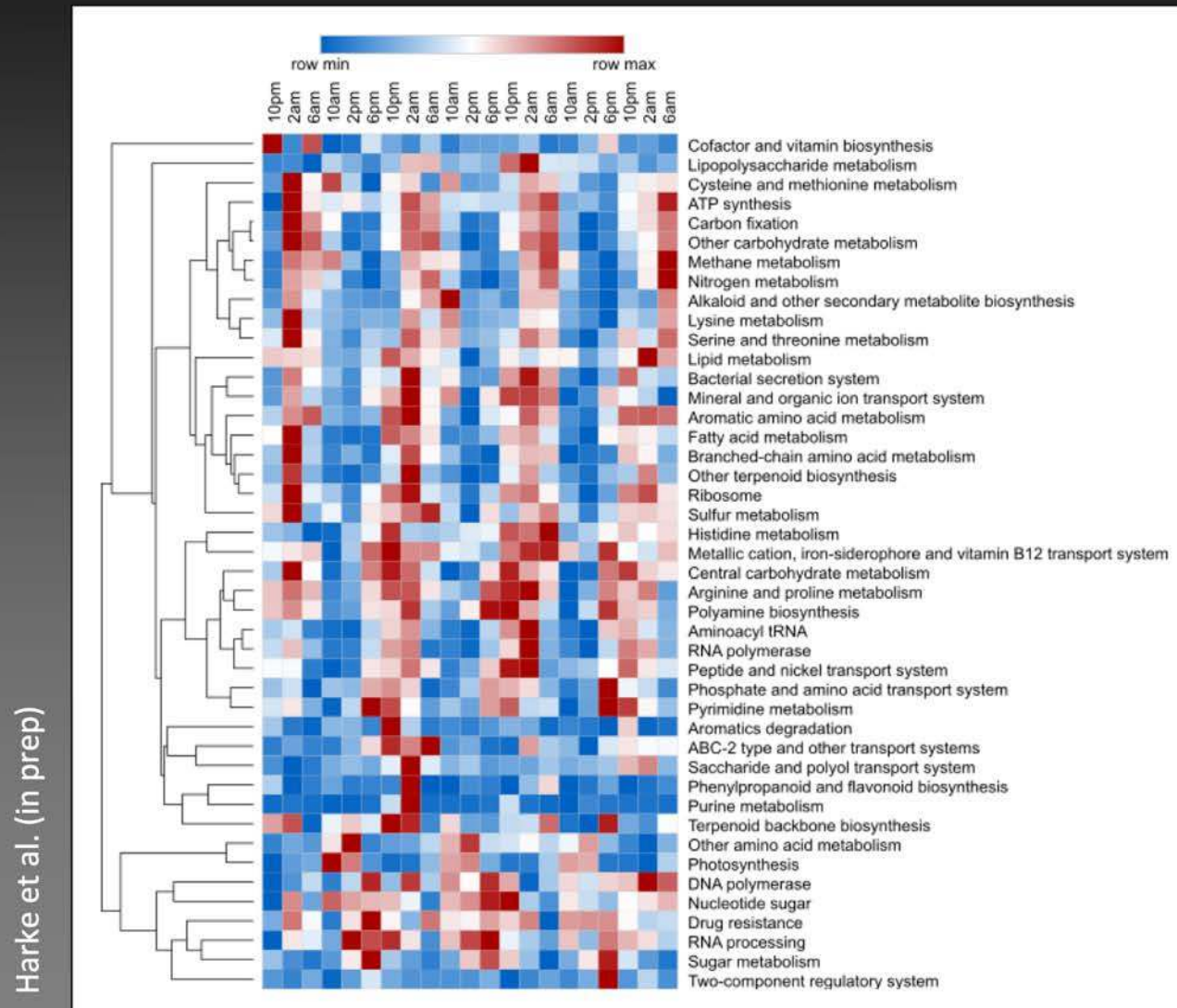
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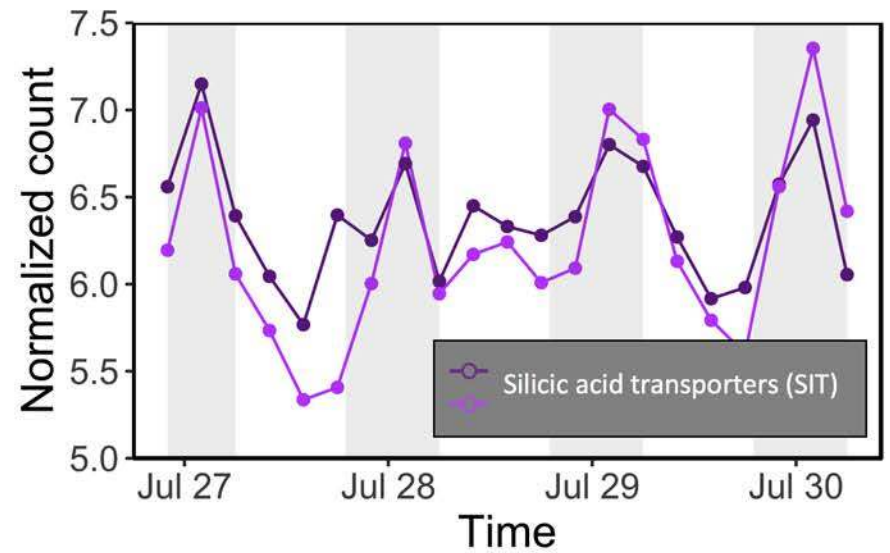
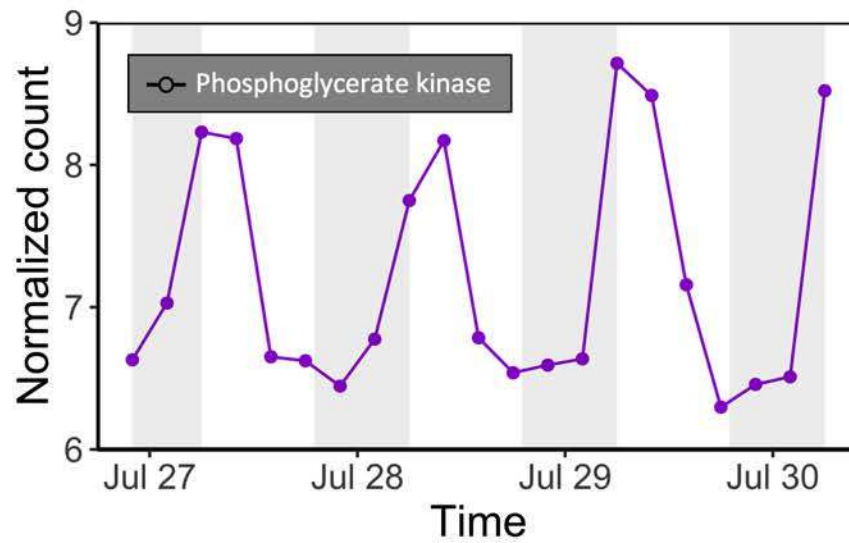
Sequencing and analysis strategy



Diel patterns in *Rhizosolenia* host

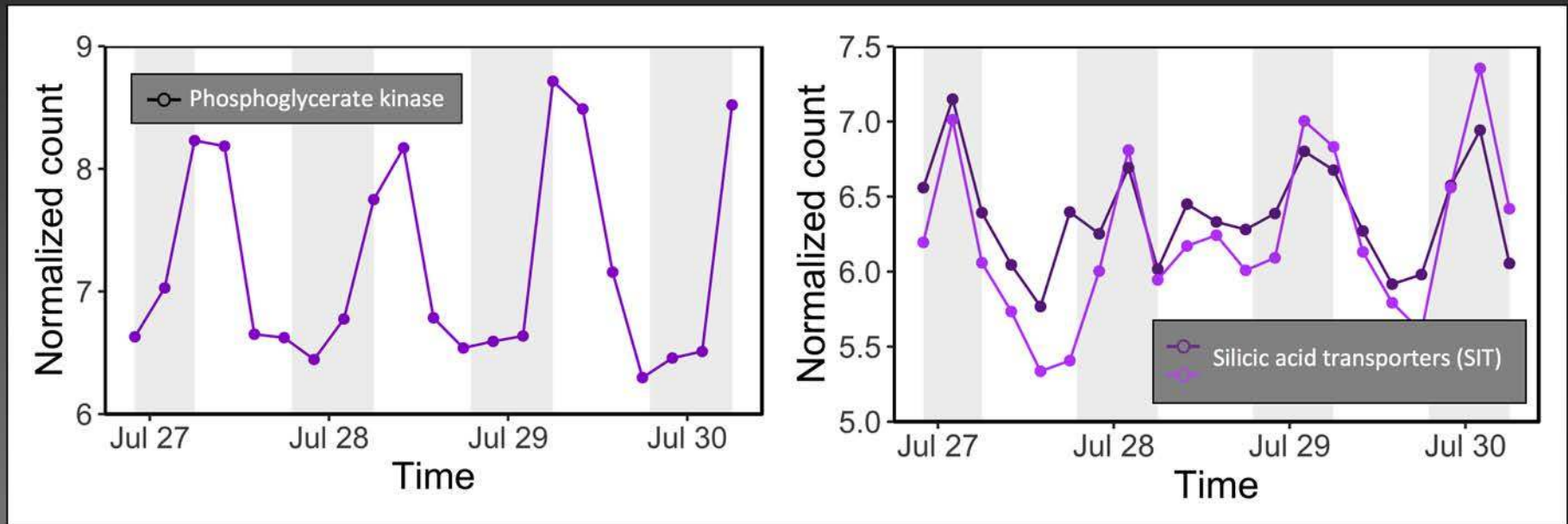


Significantly diel genes in *Rhizosolenia* host



Harke et al. (in prep)

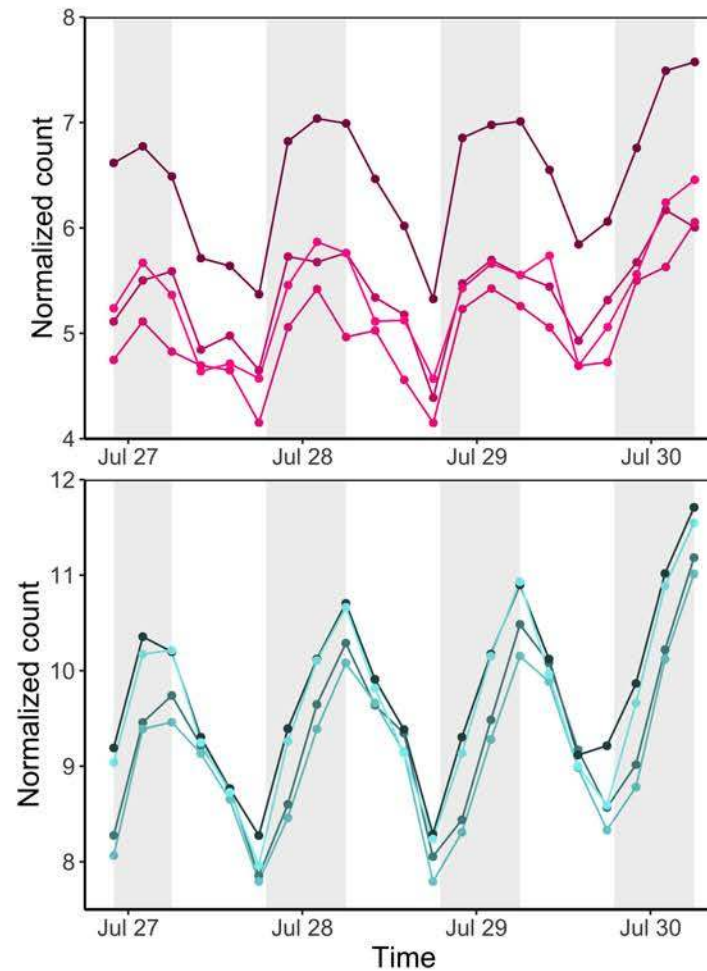
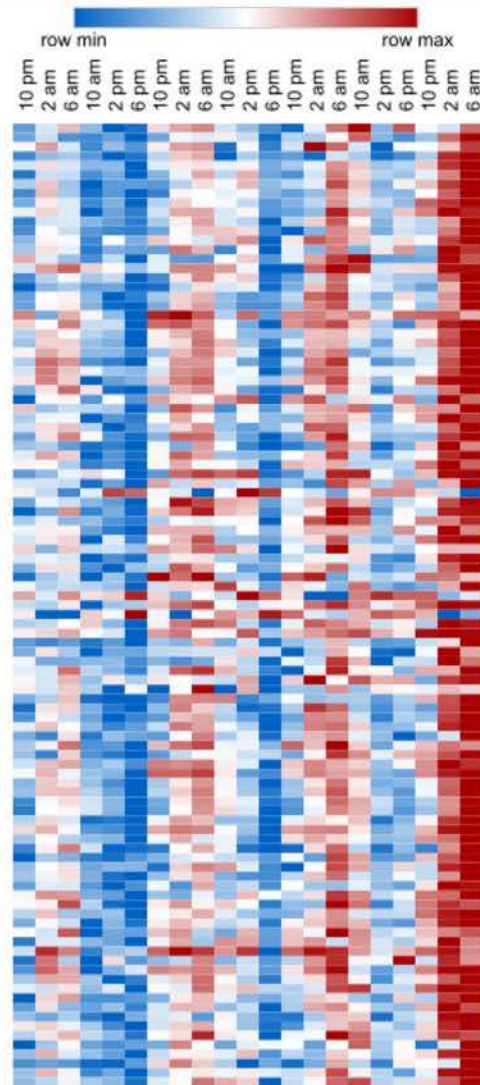
Significantly diel genes in *Rhizosolenia* host



Harke et al. (in prep)

Carbon fixation and growth (Si uptake - cell wall formation) are tightly linked to the light-dark cycle

***Richelia* symbiont has strong diel patterns**

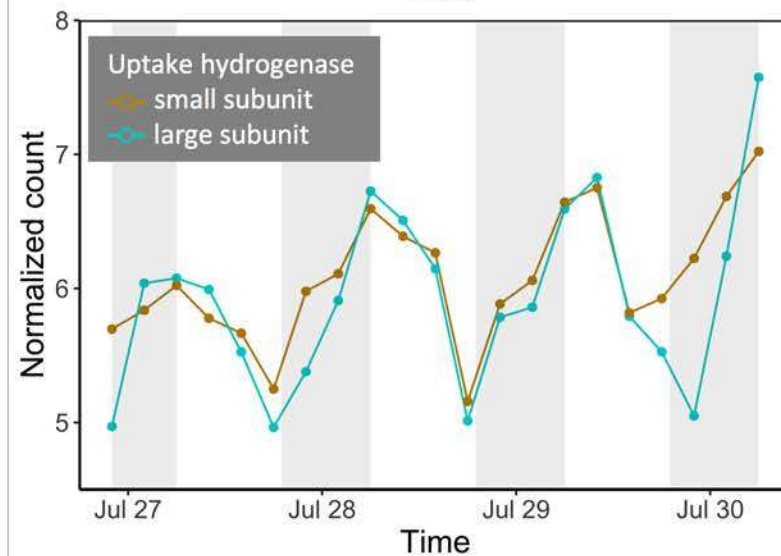
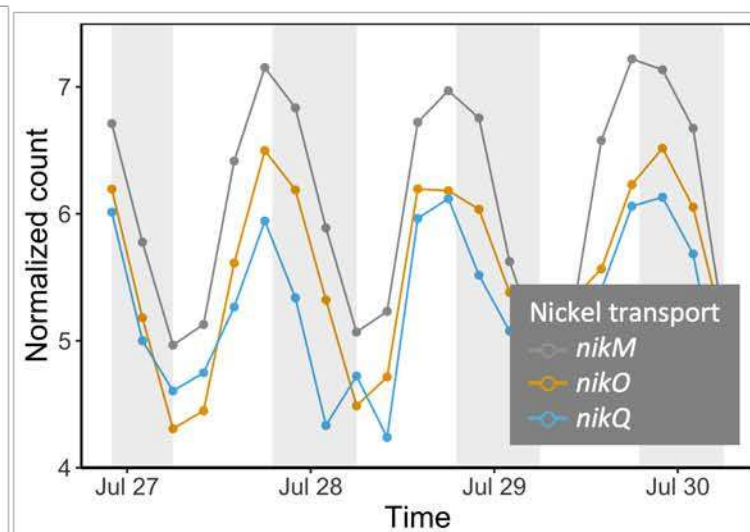
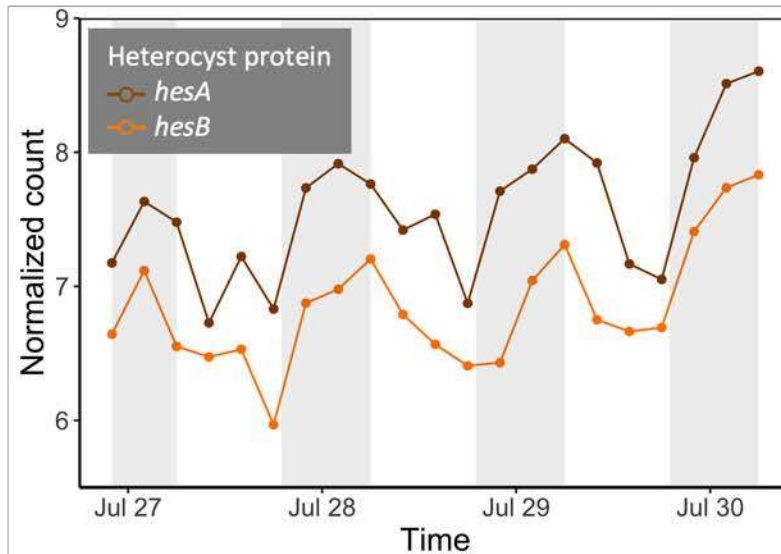


Nitrogenase genes

-  *nifE*
-  *nifT*
-  *nifW*
-  *nifX*
-  *nifD*
-  *nifH*
-  *nifH*
-  *nifK*

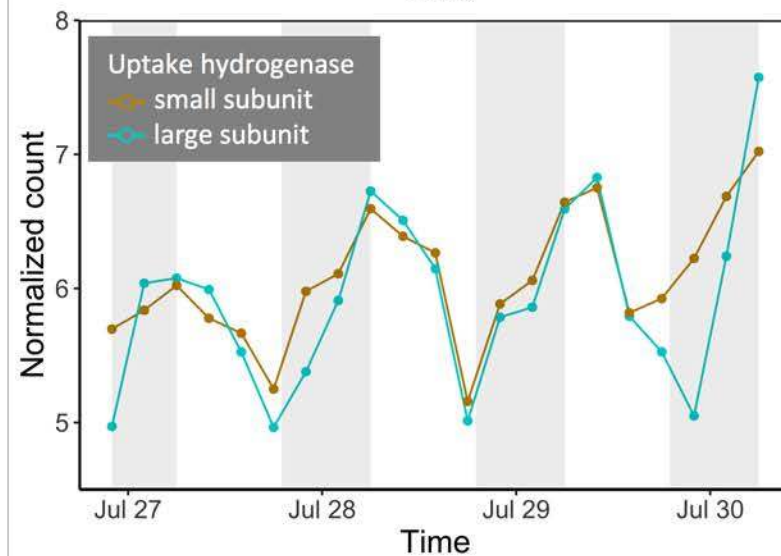
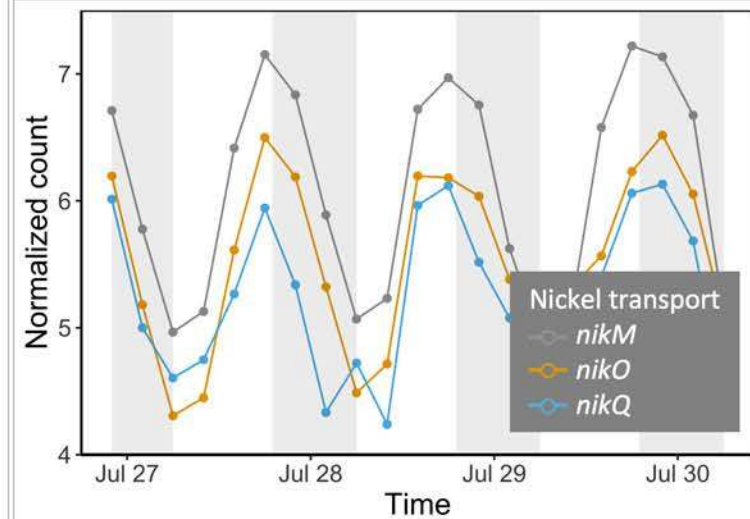
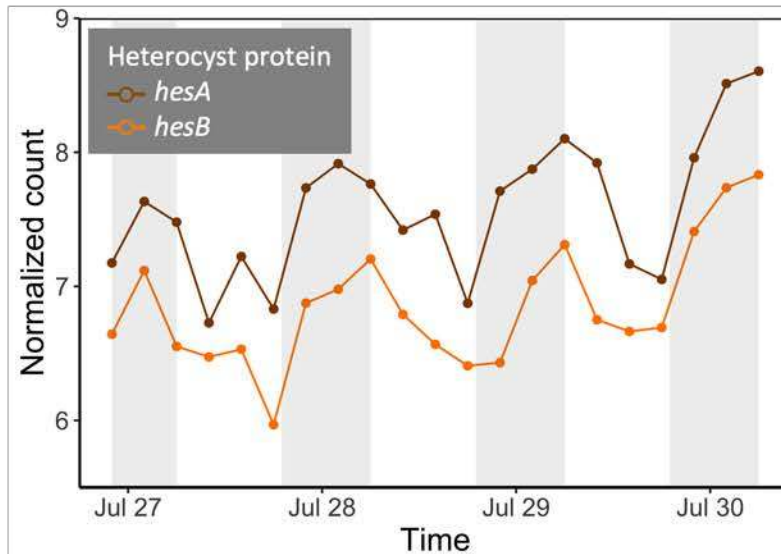
Harke et al. (in prep)

Coordinated expression of genes related to N_2 fixation in *Richelia*



Harke et al. (in prep)

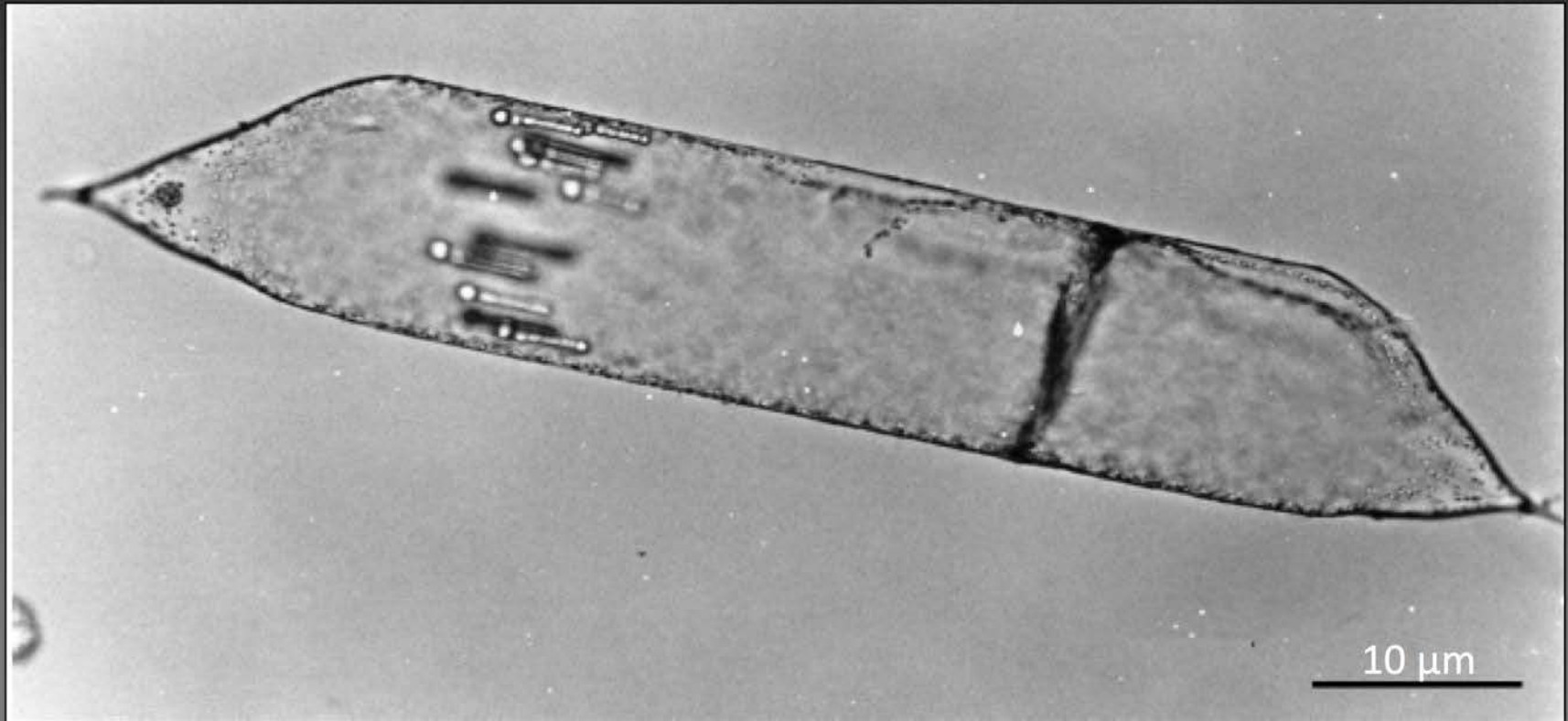
Coordinated expression of genes related to N_2 fixation in *Richelia*



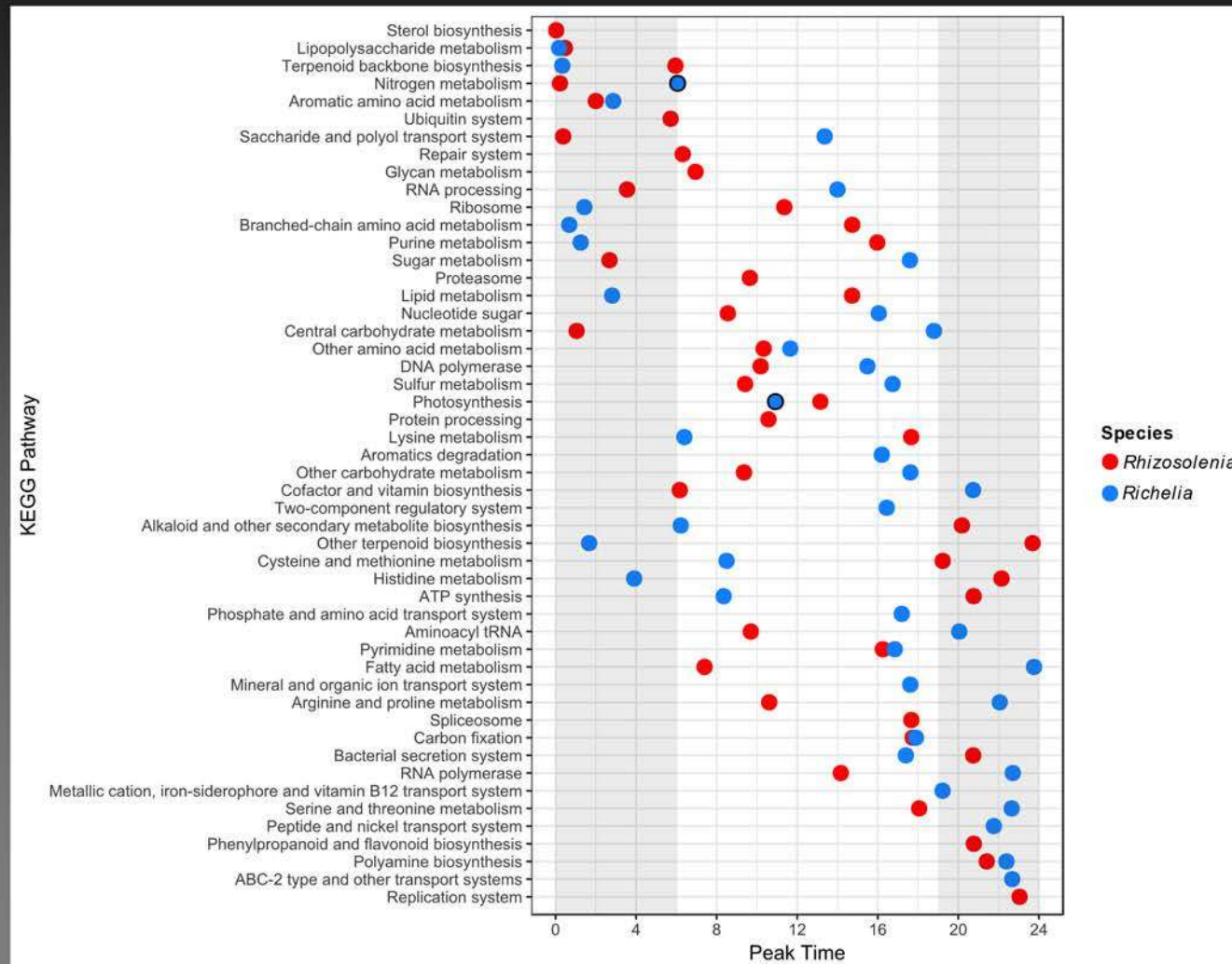
Harke et al. (in prep)

Timing of expression
suggests coordination of
processes supporting N_2
fixation

Coexpression between host and symbiont

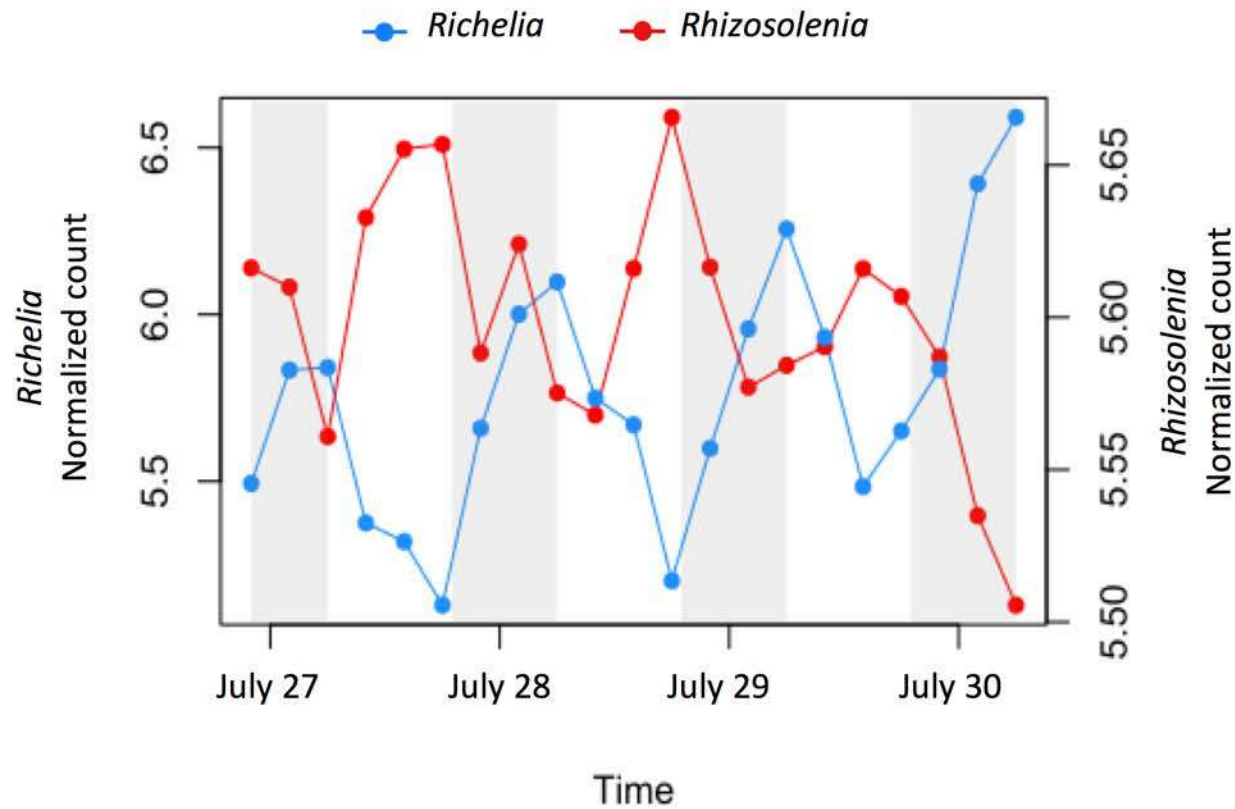


Cascade in metabolic timing between host and symbiont

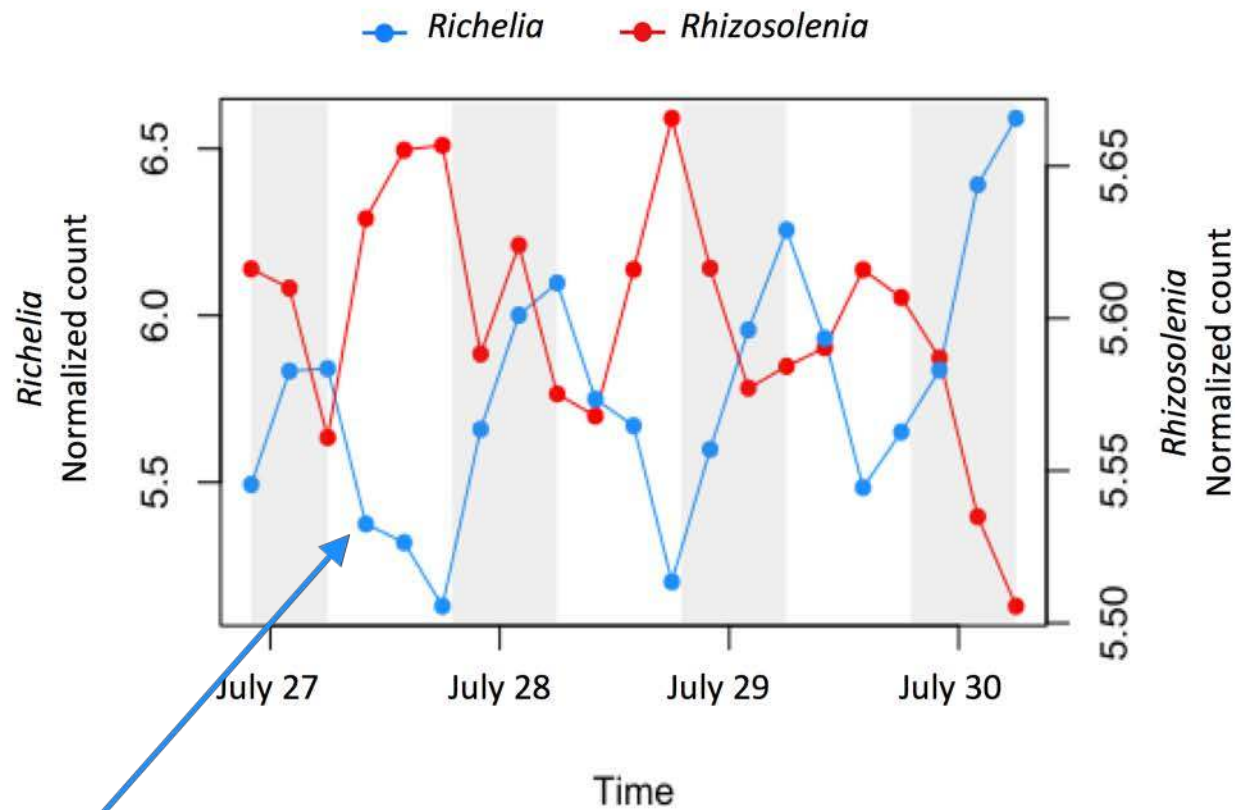


Metabolic offset for many KEGG pathways - although both are photosynthetic, core metabolism is offset

Coordinated expression between host and symbiont in N_2 fixation module

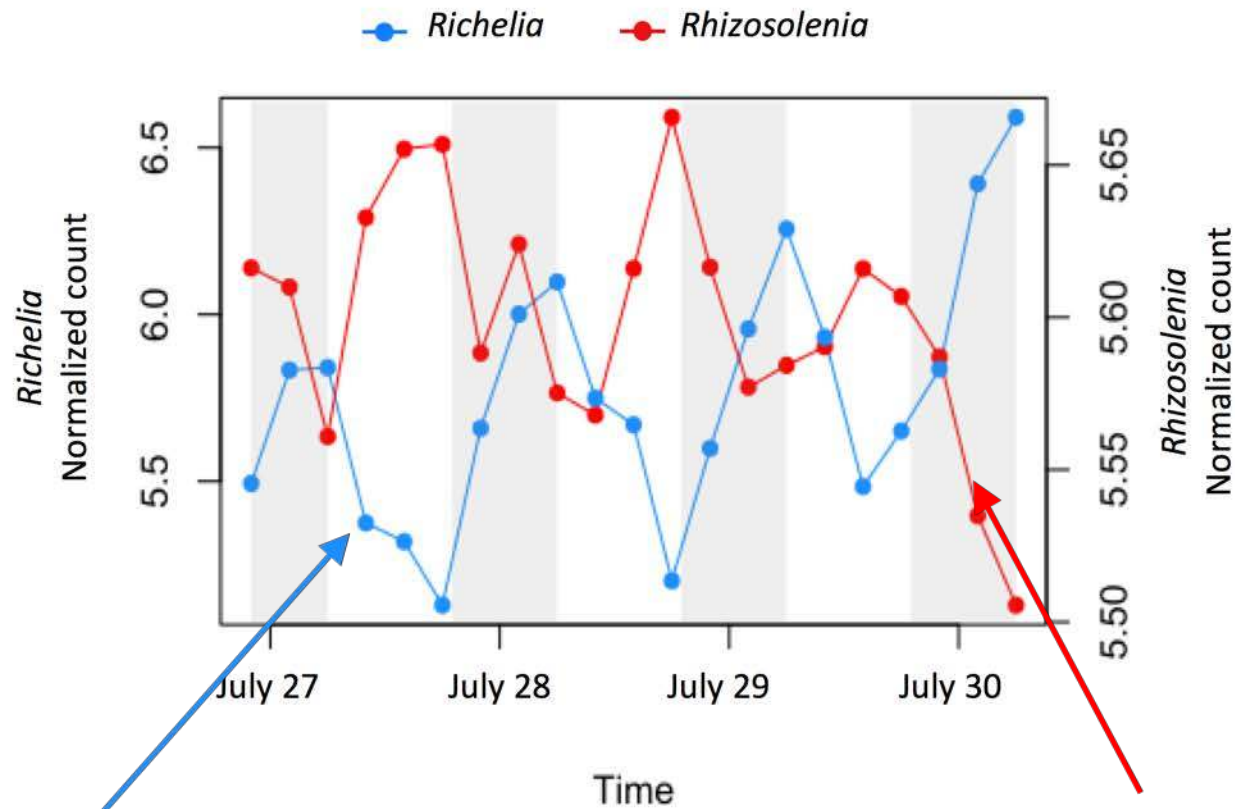


Coordinated expression between host and symbiont in N₂ fixation module



Majority of N₂ fixation genes

Coordinated expression between host and symbiont in N_2 fixation module

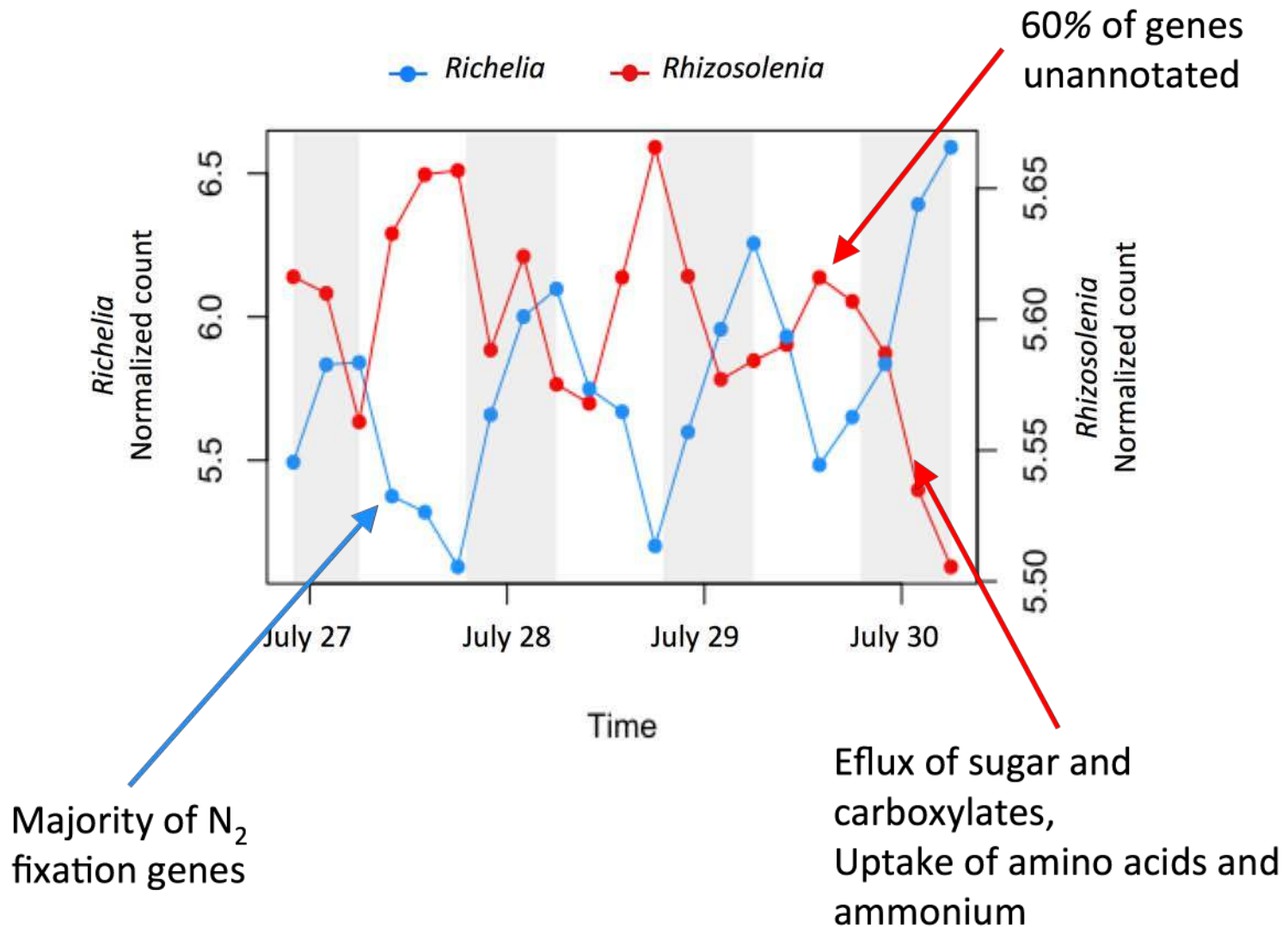


Majority of N_2 fixation genes

Eflux of sugar and carboxylates,
Uptake of amino acids and ammonium

Coordinated expression between host and symbiont in N_2 fixation module

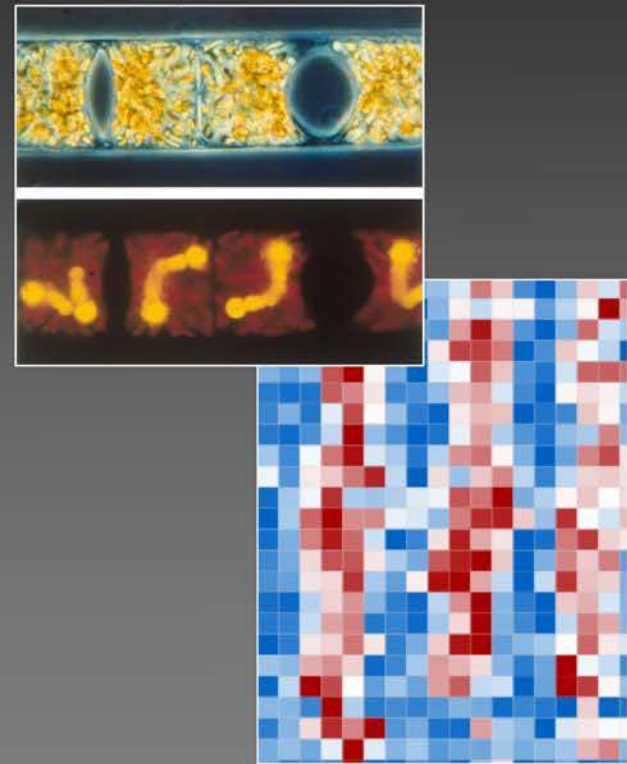
Harke et al. (in prep)



Summary - Coordinated expression in symbioses

Are there patterns of coordinated expression that underpin host - symbiont physiology?

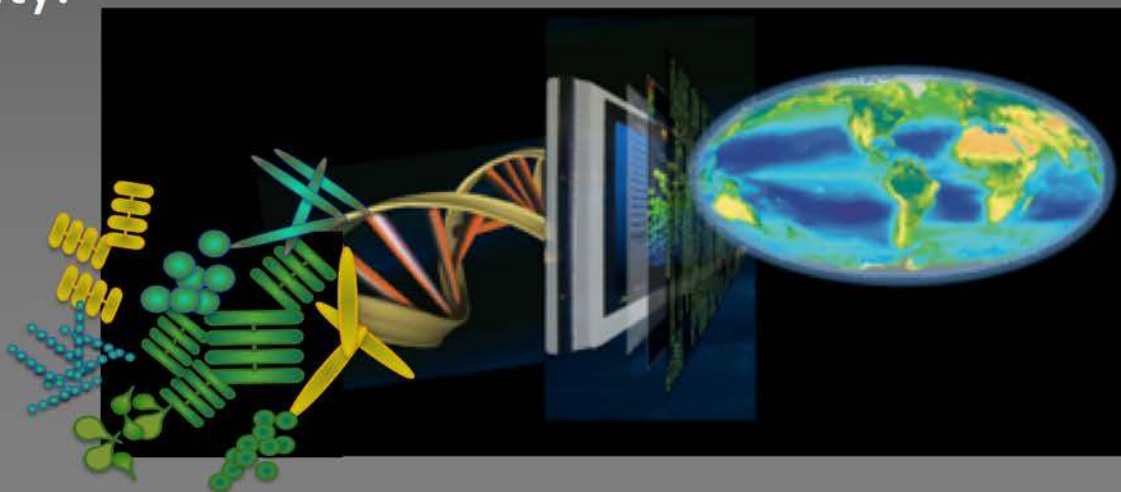
- **Dual Metatranscriptomes:** Light is a strong driver of diel patterns in both host and symbiont, with coordinated patterns that highlight N exchange.



Conclusions

Transcriptome-enabled approaches are providing new tools to identify drivers of bloom formation in keystone eukaryotic phytoplankton.

Lessons learned: We need more reference sequences and to think creatively about how we approach and mine sequence data. Need to sample at the same time of day to avoid diel variability.



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