BG1 - Integrating genomics and oceanography to understand drivers of microbial diversity and its connection to observed environmental gradients

- Uniting disciplines to discuss how we move towards better predictive capabilities in the response of marine microbes to global change.
- Take home message: There are many forms of diversity in the ocean, taxonomic, trophic and beyond. We are all operating at different scales, yet we are united in our understanding that we don't know the outcome of global change.

field microbes sampling environmental scales given gradients vs important bg data data gradient paramete experimental challenges parameters omics recognised experiments understand n understanding different key need diversity example scale function

Types of gradients

- BG1 recognise that 'environmental gradient' can be a loose term in the oceans as there are many gradients including those below.
- **Spatial**: geochemistry, community structure and organismal/ecosystem function. This includes particle associated microbiomes, free-living and other interactions from the micro to the mesoscale.
- **Temporal**: Microbes can create their own environments hence gradients in each locality. Eddy tracking for example, follows a particular biome over time but is not spatially static. This is logistically difficult, and we recognise the need for autonomous technology. Day-night gradients are another example of temporal variability that can often be larger than spatial gradients.
- Micro-gradients: Certain keystone species with important functionality may exist in low abundance. Would high volume filtration for a given keystone result in many different microbiomes samples and integrated? How do we capture important aspects of metabolism for the functions we are interested in?
- **Experimental**: We often manipulate the natural system in lab or field experiments which can help inform the "rules" running the system. There was broad agreement that a variety of approaches should be considered.

Challenges

- BG1 recognised that there are many grand challenges ahead as we move towards better predictive power, this is both daunting and exciting.
- We discussed different dimensions of diversity and debated the relative importance function vs community composition in predicting outcomes across scales.
- We recognised the importance of standard protocols for sampling and analysis (to a degree) so there can be sharing of resources and data. This is key for the reconciliation of sample sets from different shipboard instruments and samplers.
- A key question arose as to how microbes will change during long filtration procedures and what challenges this posed?
- A pertinent challenge is how we reconcile sampling efforts for omics with that for other environmental parameters (i.e., nutrients). We identified this as another type of gradient that will need to be resolved.

Key Questions

- How do we understand dimensions of diversity, and identify which dimension is most important for predictive power? For example, is there enough functional redundancy and phenotypical plasticity to a fluctuating environment, that ecosystem functions are preserved despite changes in community composition.
- How do we reconcile different gradient scales within BIOGEOSCAPES?
- How should we balance our focus? Large basin-scale scale gradients or is the fine scale just as important to BIOGEOSCAPES? How do we define physical scales? Here, BG1 is divided. We think large scale but are unsure to what extent should we include fine scale studies.
- Do we need to design better field/lab experiments that allow a link to omics and oceanography? Could we take advantage of natural experiments like eddy tracking? Would this help toward a better mechanistic understanding for model outputs?

Key Questions cont...

- In turn, what do models require of experiments, rates, function, time of day/month/year etc? What are the best currencies?
- Lab and field experiments recognised as very important in order to manipulate and test rules. How can we learn from past experimental failures and what can we improve on?
- How important is repeat sampling (time series) of a given location/biogeochemical regime, particularly for modellers? Without repeat sampling, how do we know what the norm is vs an exception. We think that time series (at multiple scales) is key.
- How do we integrate new omics data into existing data sets? How can we connect omics to satellite output, moving towards an understanding beyond pigment derived parameters?
- How do we move away from operational definitions, for example for trace metals (dissolved vs particulate)? Do we need to?

BG1 Hopes for BioGeoSCAPES

- A holistic approach so we know how microbes are interacting with each other, the chemistry, and how processes affect one another.
- Standardised measurements of the chemical-microbes network (omics etc.) and the emergent ecosystem functions we need to model (i.e. primary productivity).
- A key parameter set that can be collected reliably. Intercalibration exercises on suitable parameters.
- Cover diverse biogeographical regions (coastal, surface and deep ocean etc) and diverse gradients
- Collection of lots of different samples, even for archiving, so that we can make use of new technologies as they become available (i.e., no later regrets).
- Sampling at existing time-series and to not be afraid to start new ones

Breaking group #2 Integrating knowledge from genomics networks to predictive models

- bioinformaticians
- the rest?)
- Difficult to be generic: we need specific question to start a real interdisciplinary effort

• Composition of the group#2: 4 modelers, 2 physiologists, 3 biochemists, 2

• Two different modelings (predictive/statistics vs. synthetic) that must talk to each others ==> discover important traits or hypothesis discovery (ignoring

Big questions different contexts in which to dip biogeoscape

- Understanding / predicting Biodiversity
- Mechanisms behind the Carbon Pump and its prediction
- Ecology / community
- Resilience (at different biological scale)
- Implication of adaptation/evolution

Regulation of the ocean systems (different scales & blue operons)

How to address these gaps

- Attract modelers: make the data accessible (RDF and SPARQL) standardization)
- Regular meeting on a « stable » (high profile) case study help creating an interdisciplinary community
- Thinking of new formalization (probabilistic framework?) ahead of data Fundings for analyzing and modeling from existing knowledge

What role will evolution play in the responses of the marine biota to climate change?



The two contrasting focuses of most marine microbial evolution research

Experimental evolution in the lab- single isolate responses

Two co-dominant nitrogen-fixing cyanobacteria demonstrate distinct acclimation and adaptation responses to cope with ocean warming

Ping-Ping Qu, ¹^{*} Fei-Xue Fu,¹ Xin-Wei Wang,² Joshua D. Kling,¹ Mariam Elghazzawy,¹ Megan Huh,³ Qian-Qian Zhou,⁴ Chunguang Wang,⁴

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did not adapt to the three selection temperature regimes during the 2-year evolution experiment, but could instead rapidly and reversibly acclimate to temperature shifts from 20°C to 34°C. In contrast, over the same timeframe apparent thermal adaptation was observed in Crocosphaera, as evidenced by irreversible phenotypic changes as well as whole-genome sequencing and variant analysis. Especially under stressful warming conditions (34°C), 32°C-selected Crocosphaera cells had an advantage in survival and nitrogen fixation over cell lines selected at 22°C and 28°C. The distinct strategies of phenotypic plasticity versus irreversible adaptation in these two sympatric diazotrophs are both viable ways to maintain fitness despite longterm temperature changes, and so could help to stabilize key ocean nitrogen cycle functions under future warming scenarios.

Environmental Microbiology Reports 14 (2022)





Eco-Evolutionary Interaction in Competing Phytoplankton: Nutrient Driven Genotype Sorting Likely Explains Dominance Shift and Species Responses to CO₂

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How ecological and evolutionary processes interact and together determine species and community responses to climate change is poorly understood. We studied longterm dynamics (over approximately 200 asexual generations) in two phytoplankton species, a coccolithophore (*Emiliania huxleyi*), and a diatom (*Chaetoceros affinis*), to increased CO₂ growing alone, or competing with one another in co-occurrence. To

Frontiers in Marine Science 634 (2020)

A glaring gap: lab experimental evolution studies using marine microbes other than phytoplankton are virtually non-existent

- Heterotrophic bacteria
- Ammonia and nitrite oxidizers
- Denitrifiers
- Microzooplankton grazers
- Viruses

The other extreme: Large-scale evolutionary history inferred from 'omics

The role of zinc in the adaptive evolution of polar phytoplankton

Naihao Ye^{1,2,19}, Wentao Han^{1,19}, Andrew Toseland³, Yitao Wang¹, Xiao Fan¹, Dong Xu¹, Cock van Oosterhout³, Sea of Change Consortium^{*}, Igor V. Grigoriev^{4,5}, Alessandro Tagliabue⁶, Jian Zhang¹, Yan Zhang¹, Jian Ma¹, Huan Qiu⁷, Youxun Li⁸, Xiaowen Zhang^{1,2} and Thomas Mock³

Zinc is an essential trace metal for oceanic primary producers with the highest concentrations in polar oceans. However, its role in the biological functioning and adaptive evolution of polar phytoplankton remains enigmatic. Here, we have applied a combination of evolutionary genomics, quantitative proteomics, co-expression analyses and cellular physiology to suggest that model polar phytoplankton species have a higher demand for zinc because of elevated cellular levels of zinc-binding proteins. We propose that adaptive expansion of regulatory zinc-finger protein families, co-expanded and co-expressed zinc-binding proteins families involved in photosynthesis and growth in these microalgal species and their natural communities were identified to be responsible for the higher zinc demand. The expression of their encoding genes in eukaryotic phytoplankton meta-transcriptomes from pole-to-pole was identified to correlate not only with dissolved zinc concentrations in the upper ocean but also with temperature, suggesting that environmental conditions of polar oceans are responsible for an increased demand of zinc. These results suggest that zinc plays an important role in supporting photosynthetic growth in eukaryotic polar phytoplankton and that this has been critical for algal colonization of low-temperature polar oceans.



Annual Review of Marine Science Phytoplankton in the Tara Ocean

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Abstract

Photosynthesis evolved in the ocean more than 2 billion years ago and is now performed by a wide range of evolutionarily distinct organisms, including both prokaryotes and eukaryotes. Our appreciation of their abundance, distributions, and contributions to primary production in the ocean has been increasing since they were first discovered in the seventeenth century and has now been enhanced by data emerging from the *Tara* Oceans project, which performed a comprehensive worldwide sampling of plankton in the upper layers of the ocean between 2009 and 2013. Largely using recent data from *Tara* Oceans, here we review the geographic distributions of phytoplankton in the global ocean and their diversity, abundance, and standing stock biomass. We also discuss how omics-based information can be incorporated into studies of photosynthesis in the ocean and show the likely importance of mixotrophs and photosymbionts.

Annual Review of Marine Science 12 (2020)

Where we haven't really gone yet:

Can we observe rapid evolution in response to global change selection on <u>ecological</u> scales in natural marine environments?

To study evolution *in situ*, the physical context matters a lot...

Drift in ocean currents impacts intergenerational microbial exposure to temperature

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Edited by David M. Karl, University of Hawaii, Honolulu, HI, and approved March 28, 2016 (received for review October 29, 2015)

Microbes are the foundation of marine ecosystems [Falkowski PG, Fenchel T, Delong EF (2008) Science 320(5879):1034-1039]. Until now, the analytical framework for understanding the implications of ocean warming on microbes has not considered thermal exposure during transport in dynamic seascapes, implying that our current view of change for these critical organisms may be inaccurate. Here we show that upper-ocean microbes experience along-trajectory temperature variability up to 10 °C greater than seasonal fluctuations estimated in a static frame, and that this variability depends strongly on location. These findings demonstrate that drift in ocean currents can increase the thermal exposure of microbes and suggests that microbial populations with broad thermal tolerance will survive transport to distant regions of the ocean and invade new habitats. Our findings also suggest that advection has the capacity to influence microbial community assemblies, such that regions with strong currents and large thermal fluctuations select for communities with greatest plasticity and evolvability, and communities with narrow thermal performance are found where ocean currents are weak or along-trajectory temperature variation is low. Given that fluctuating environments select for individual plasticity in microbial lineages, and that physiological plasticity of ancestors can predict the magnitude of evolutionary responses of subsequent generations to environmental change [Schaum CE, Collins S (2014) Proc Biol Soc 281(1793):20141486], our findings suggest that microbial populations in the sub-Antarctic (~40°S), North Pacific, and North Atlantic will have the most capacity to adapt to contemporary ocean warming.

other environmental parameters (8, 10, 13), laboratory investigations that measure performance of microbial ecotypes (thought to be representative of populations) under different conditions (6, 7, 9, 14), and modeling studies that use microbial traits describing resource (e.g., nutrients, light) utilization to estimate fitness and predict future distributions of microbes under projected ocean change (15–17). The limitation of these studies is that microbial traits are assumed to be constant during model runs, so the microbes themselves are not responding to changes in their environment (18). However, there is increasing evidence that photosynthetic microbes are altering their realized niches in response to contemporary changes in ocean temperature and irradiance (19), and that the geographic origin of microbial ecotypes influences their plasticity (capacity for physiological acclimation) (9, 20)—as well as adaptation (21)—at the population level (potentially via increased rate of mitotic mutations) (22), with some ecotypes tolerant of a broad range of temperature and others more thermally specialized (7). Microbes generally experience the ocean as a viscous medium (23), and their motion is therefore predominantly determined by drift with ocean currents (noting that some taxa are motile or regulate their buoyancy) (24). As a result, their habitat temperatures are highly dynamic and cannot be described assuming a fixed location. This means there currently is no clear global estimate of the thermal history of marine microbes, making it difficult to understand their realized thermal niche and relate this to their performance under controlled (typ-

PNAS 113 (2016)

Microbial evolutionary strategies in a dynamic ocean

Nathan G. Walworth 🗅 , Emily J. Zakem, John P. Dunne 🗅 , 🕕 , and Naomi M. Levine 🗅 🎽 Authors Info & Affiliations

Abstract

Marine microbes form the base of ocean food webs and drive ocean biogeochemical cycling. Yet little is known about the ability of microbial populations to adapt as they are advected through changing conditions. Here, we investigated the interplay between physical and biological timescales using a model of adaptation and an eddy-resolving ocean circulation climate model. Two criteria were identified that relate the timing and nature of adaptation to the ratio of physical to biological timescales. Genetic adaptation was impeded in highly variable regimes by nongenetic modifications but was promoted in more stable environments. An evolutionary trade-off emerged where greater short-term nongenetic transgenerational effects (low-y strategy) enabled rapid responses to environmental fluctuations but delayed genetic adaptation, while fewer short-term transgenerational effects (high-y strategy) allowed faster genetic adaptation but inhibited short-term responses. Our results demonstrate that the selective pressures for organisms within a single water mass vary based on differences in generation timescales resulting in different evolutionary strategies being favored. Organisms that experience more variable environments should favor a low-y strategy. Furthermore, faster cell division rates should be a key factor in genetic adaptation in a changing ocean. Understanding and quantifying the relationship between evolutionary and physical

PNAS 117 (2020)

Possible marine ecosystems for Lagrangian in situ evolution investigations

Marine heat wave events

- Boundary currents
- Upwelling plumes

Does the scope of BioGeoSCAPES include adaptive responses of the ocean biota?

Does it include an emphasis on global change processes in the ocean?

Extreme events cause conditions not previously experienced in an organism's evolutionary history – this needs to be added to BioGeoSCAPES

BioGeoSCAPES and similar projects need to respond to societal needs by addressing climate change related impacts such as heat waves, algal blooms, food web shifts, etc

Big issues in microbial evolution:

- Evolutionary mechanisms are still relatively unresolved, but are key to understanding differences in metabolic processes and nutrient cycles
- Need to match evolution to phenotype
- Co-evolution: Symbioses, consortia and community interactions
- Multiple stressor-driven selection- how does it work?
- What are the sources of heritable variation in marine microbes? (mutations, sexual reproduction)

Laboratory experiments are still greatly beneficial and should be used alongside large-scale field operations – but here we are limited by culturing abilities (a culturingfocussed expedition would be greatly beneficial).

- But are model species representative?
- Could omics data benefit our culturing efforts?

Should we focus on a mechanistic approach established in the lab and validated in the ocean? Or an investigative approach starting in the field and validated in the lab? Or a combination? What data do we need to understand evolution?

- Long-read sequencing for better assembly or hybrid short/long read sequencing
- Currently, long-read data is limited in the ocean
- But what is the lifetime of omics data? until better technologies are available?
- Can we bring novel technologies (e.g. from medical fields) to marine evolutionary applications?

Marine microbial evolution take home messages:

- Need to consider global change and societal impacts
- To examine evolutionary processes, we must first understand the key mechanisms across a range of species.
- Supplementary lab experiments can enhance fieldbased research

How to enable basin scale mapping of microbial rates and states

Breakout 4 (Rapporteur Elena García-Martín)





Transcending the scaling issue

Horizontal space length scale (m) Boyd et al. (2016) after Dickey (2003)



Basins

Choosing the key layers to assist basin scale mapping









Scale of observations.

Utilising different ways to map systems and derive the most useful composite map with different layers of information to be able to predict the future.

Choosing the right scale to observe patterns - Basin-scale transects or specific regions?

Latitudinal band vs. provinces which are more likely to change?

Do we focus on the areas where models and observations disagree and try to understand why?

Or shall we focus on regions that they agree on?

The power is in collecting the data. Importance as a community to know where and why we have failed?

Coastal and/or open ocean? They have different threats.

New tools with different capabilities and different sensors integrated which will help us to observe basin scale processes.

Importance of integrating physico-chemical sensors with biological ones.

There is an increasing effort to understand mesoscales and new tools are being used to get data.

However, there is a problem of potential interactive effects between different drivers.

The Precursors Enabling frameworks for basin scale mapping of microbial rates and states

Defining the underlying modes of environmental forcing (Hallberg 2008)

Defining then mapping the biogeochemical province (Cohen et al., 2021)

Characterisation of who is there And in what abundance







WHAT REGULATES THEIR STATES AND RATES???



Community efforts.

Importance of intercalibration and standardization of data, so data are comparable. Follow the example of the cell image community, for example the PACE hyperspectral mission and ITAPINA project.

Importance of proper training, shared technologies, development of low-cost technologies easily applicable by countries with lower capacities.

Importance of networks to measure variables that other countries do not have the capacity of.

Future sampling

Identify key and core parameters to measure.

Which parameters would be catalogued as "core"? It can be beneficial not to be very descriptive as not every country has the ability to measure all parameters.

We know how Temperature and CO2 will change in the future, but there are many other variables that are under debate:

- What will happen with the Fe supply?
- nitrogen, there is no predictive power.
- Include light parameters
- Enzymes are the interface between rates and states. More effort on measuring and understanding enzymes.
- Shall we use mathematical models to extract the environmental drivers which best explain rates and states?

Importance of collecting material and archiving it for future generations to be analysed with upcoming technologies, and make data available to all researchers.

Omics

Can Omics be used to quantify rates? We are often in discovery mode at the initial phase of understanding the data. There was an agreement that more time should be invested. But there are still open questions:

- Does diel omics analysis have the potential of informing us about different rates such as growth, grazing, etc?
- Does it imply that researchers should take their measurements at the same time? Problem: not all processes have a diel cycle, and some processes present diel cycles at specific latitudes.
- Can the omics help with the interpretation of the bio-optical data?

Main knowledge GAPS

Identify the criteria of core parameters

Identify the proper scale of analysis

Context - Who is where at the moment and what are they doing

Relationships between rates and omics: more experiments with cultured and natural populations.

Importance of robust relationship between rates and "easy-to-measure" parameters to be able to incorporate new parameters in models with "simple" parametrizations.

Examples of basin scale mapping of microbial rates and states

Rates NPP from MODIS

Floristics from space – linked with GEOTRACES IDP

Bloom dynamics from floats

Better definitions of oceanic provinces in 4D from satellites and floats



Upscaling from states and rates to basin scale



On the Relationship Between Hydrogen Saturation in the Tropical Atlantic Ocean and Nitrogen Fixation by the Symbiotic Diazotroph UCYN-A

R. M. Moore¹ D, I. Grefe², J. Zorz³, S. Shan¹ D, K. Thompson¹, J. Ratten³, and J. LaRoche³

Key Points:

- Hydrogen supersaturation
- widespread across a tropical
- N. Atlantic transect
- Saturations correlated with UCYNA *nifH* abundance
- High resolution H₂ measurements are capable of illustrating space and time scales of UCYN-A diazotrophy

WHAT ARE THE MOST USEFUL MAP 'OVERLAYS' TO DIRECT FUTURE RESEARCH ON STATES & RATES?

Tools to assist with enabling frameworks



Figure 2. CO_2 flux calculated from Uncrewed Surface Vehicle (USV)measured ΔpCO_2 , sea surface temperature (SST), and salinity (SSS) and CCMP V2 wind speed. Dates and * show the location of the USV with time. Black lines indicate climatological locations of the major fronts from Orsi et al. (1995) as in Figure S1.

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-5

New tools for basin scale mapping of microbial rates and states

Rates P* from nanonutrients

Floristics from space (PACE hyperspectral mission) and floats (UVP6)

Data assimilation from floats (SOSE & B-SOSE)

GEOTRACES IDP - metals and proteins



RATES UPSCALED (MODELS?)

12.09.22 Royal Society Theo Murphy Meeting Marine Microbes in a Changing Climate

Breakout Group 5 Using genomics to help us understand the link between organisms and largescale biogeochemical cycles

Chair: Jamie Becker (jamie.becker@alvernia.edu) Rapporteur: Ben Fisher (ben.fisher@ed.ac.uk)

We asked the following questions at the start of our breakout session. Responses are included below:

- Our community has been doing a good job of using genomics to help us understand links between organisms and large scale biogeochemical cycles. Somewhat agree: 55% Somewhat disagree: 45%
- We need more genomic information derived from **culture-independent** studies to better understand links between organisms and large scale biogeochemical cycles.

Strongly agree: 55%

Somewhat agree: 45%

 We need more genomic information derived from culture-dependent studies to better understand links between organisms and large scale biogeochemical cycles.

Strongly agree: 64% Somewhat agree: 18% Somewhat disagree: 18%

• We need more information derived from biogeochemical models to better understand links between organisms and large scale biogeochemical cycles.

Strongly agree: 36%

Somewhat agree: 36%

Somewhat disagree: 28%

• I have all the skills necessary to make connections between organisms and large scale biogeochemical cycles.

Strongly agree: 9% Somewhat disagree: 9% Strongly disagree: 82%

We then considered our topic in the context of the following two questions (first alone, then in groups of 3, then as a full group of 12):

- 1. What main knowledge gaps hinder progress in predicting responses to global change?
- 2. What future BioGeoSCAPES activities could help address these gaps?

We first discussed the many challenges inherent in making the leap from genomes to biomes and considered where the weakest links may currently exist. We identified a need for increased early communication between all parties (experimentalists, oceanographers, bioinformaticians, & modelers) to holistically design a successful research program. A co-learning and co-planning approach could lead to a common language among these traditionally distinct disciplines.

We then explored the need to discern appropriate levels of specificity given the high degree of intra-genus variability apparent in the literature. Can we identify model genes and organisms that can act as process proxies with fixed transformation functions, or do we consistently need to address dynamic representation? We noted the difficulty in determining which genes matter for rates and states when presenters at the conference indicated genetic changes do not always result in biogeochemical changes.

While exploring activities that BioGeoSCAPES could facilitate, we noted a need to clearly define what the program means by "*predicting responses to global change*". What responses and which changes should be prioritized? We were excited by the opportunity to combine *in-situ* measurements (both chemical and omic) with process studies at sea and back in the lab, which led to a discussion on the importance of cultured isolates for direct measurements of microbial responses to changing environmental conditions. We felt that this approach would help BioGeoSCAPES to move beyond discovery science and toward the aim of understanding metabolic processes. Modelers stressed the need to simplify biological systems to the processes which influence biogeochemical cycling. We assessed a need to move beyond a "measuring every parameter" approach toward a more focused approach driven by clearly defined research questions.

A lengthy discussion of appropriate scales (both spatial and temporal) was had given realistic constraints of limited time & funding. There was strong support for coupling sampling in locations relevant to global change (see earlier comment on clearly defining what is meant by this phrase) with temporal/Lagrangian sampling with less support for a simple "around the world" cruise track with limited temporal assessment. We also noted the need to have good standardization protocols in place to make data from multiple cruises comparable. Other marine microbiology programs have standardization for omics in place - collaboration with these entities could accelerate the project setup.

Our group felt an initial project lifetime of 10-20 years would be appropriate for attracting funding, while continuing to 2050 would help capture the full scale of microbial variability with climate dynamics on course to net zero. Finally, we considered the training and skills required among personnel involved and whether non-traditional skill combinations might be necessary to complete the goal of predicting microbial responses to global change.