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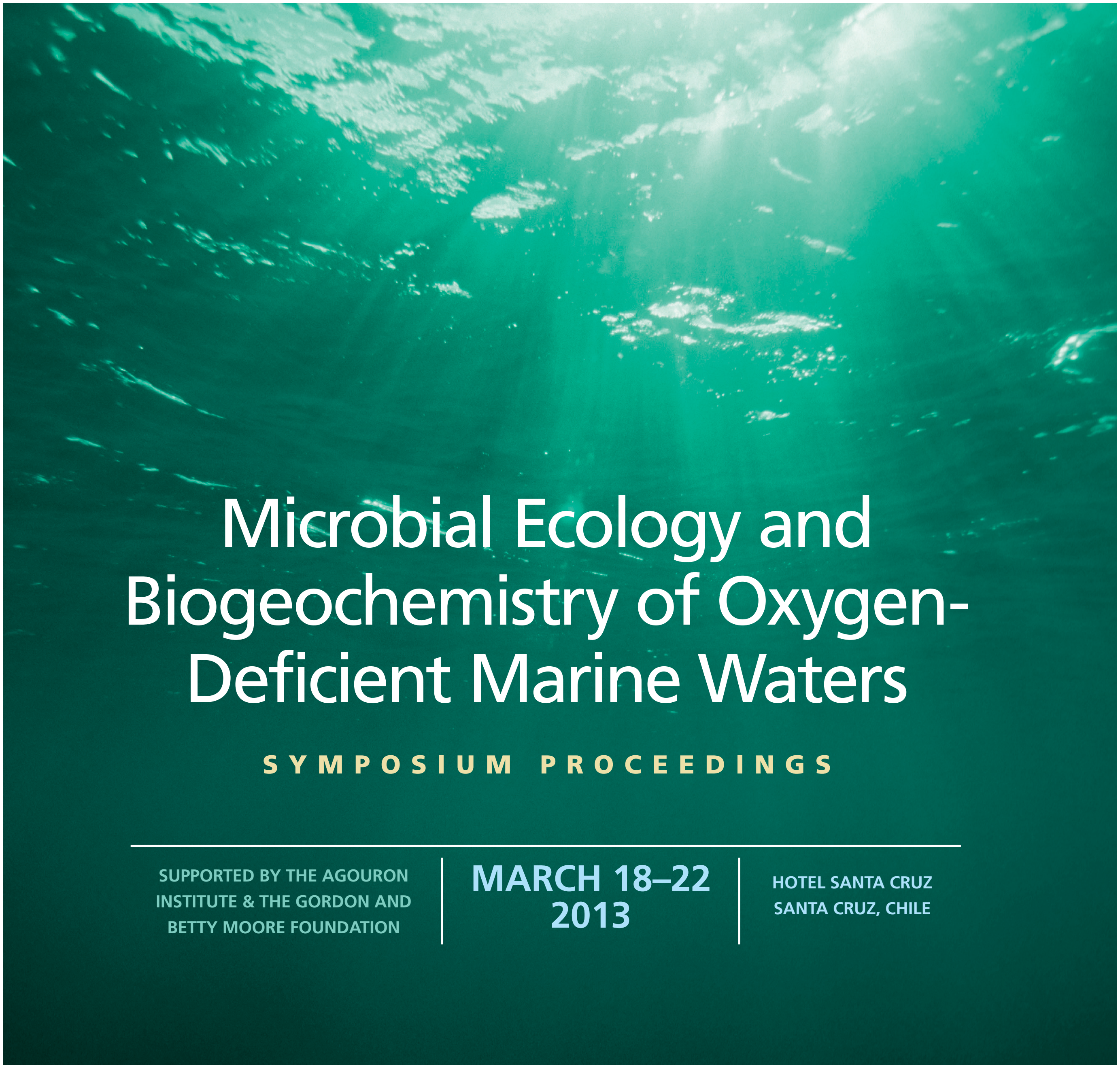

Microbial Ecology and Biogeochemistry of Oxygen-Deficient Marine Waters

SYMPOSIUM PROCEEDINGS

SUPPORTED BY THE AGOURON INSTITUTE & THE GORDON AND BETTY MOORE FOUNDATION

MARCH 18–22 2013

HOTEL SANTA CRUZ
SANTA CRUZ, CHILE

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SYMPOSIUM PROCEEDINGS

1

2

3

4

CONTENTS

Symposium Scope & Goals

Importance

The concentration of dissolved oxygen is a critical organizing variable within marine ecosystems. As oxygen levels decline, energy is diverted away from higher trophic levels into anaerobic microbial pathways, leading to significant chemical changes in the environment, such as the loss of fixed nitrogen and the production of greenhouse gases. These changes are particularly pronounced in severely oxygen-deficient marine environments known as oxygen minimum zones (OMZs; defined here as waters containing $< 20\ \mu mol\ kg^{-1}$ dissolved O_2). At present, global warming–induced ocean deoxygenation and anthropogenic alteration of marine biogeochemical cycles have unconstrained feedbacks on the structure and function of marine microbial communities (the main driver of these cycles) and the climate system. To identify and constrain these feedbacks, current research efforts are defining the metabolic networks underlying nutrient and energy flow patterns within OMZs, generating new insights into coupled biogeochemical processes in the global ocean.

Opportunity

Recently completed and ongoing multi-year field research campaigns to a variety of oxygen-deficient ($< 90\ \mu mol\ kg^{-1}\ O_2$) marine systems are yielding new insights into the functional roles of microbial communities in responding to and shaping marine biogeochemical cycles in these environments. Oxygen-deficient marine systems are diverse (e.g. permanently or seasonally anoxic/sub-oxic/hypoxic; open-ocean or coastal) and are sensitive to perturbations in different ways. This symposium provided an opportunity to discuss and compare the microbial ecology and biogeochemistry of different oxygen-deficient marine systems, including the more extensive permanent OMZs as well as the seasonally oxygen-deficient systems—with an eye toward developing a community-driven framework for data collection and interpretation, knowledge translation, and public engagement.

Themes & Questions for the Symposium

1. *OMZ ecosystem structure and function: What are the key similarities and differences in the physical, biogeochemical, and energy flux properties of different OMZs? How do microbial community structure and biogeochemical cycling vary spatially and temporally as a function of oxygen/redox conditions? What are the roles/relationships between suspended and sinking organic particles? What are the thresholds of oxygen stress that bound aerobic and anaerobic processes?*
2. *OMZ evolution in the context of climate change: What major changes in ocean microbial diversity and biogeochemical cycling associated with OMZs do we expect over the rest of the century? How will these changes impact the global ocean–atmosphere system?*
3. *Identifying critical knowledge gaps: What are the pressing questions and technological needs of OMZ-related research? What would be an appropriate and timely community field experiment or field program?*
4. *Education and recommendations to policy makers: What recommendations can be provided for effective policy development based on scientific evidence (e.g. IPCC synthesis reports)?*

Symposium Goals

1. Compare and contrast the microbial ecology and biogeochemistry of different low-oxygen systems.
2. Consider global assessments and/or predictions based on model outputs on, for example, the impact of OMZ expansion.
3. Identify opportunities for collaboration, including research proposals and cross-training opportunities, among OMZ research teams.
4. Brainstorm about the initial design of a community field experiment, including a clear articulation of the rationale.
5. Develop mechanisms to communicate about, standardize, and/or compare field and experimental protocols.

Executive Summary of Symposium Recommendations

Oxygen minimum zones (OMZs), which play key roles in global biogeochemical cycling and generation of greenhouse gases, are highly sensitive to anthropogenic perturbations and climate change. Therefore, there is an urgent need to develop coordinated research efforts to characterize the metabolic networks underlying nutrient and energy flow patterns within OMZs to predict changes in the biogeochemical cycling of the future ocean. Although significant conceptual and technological advances have helped identify and constrain, to a certain degree, feedback mechanisms between microbial communities, biogeochemical cycles and the climate system, significant gaps remain in our understanding. These gaps include, but are not limited to, the rates and controls of nitrogen fixation in OMZs, the roles of protists and viruses in microbial community structure and biogeochemical function in OMZs, the responses of OMZ microbial communities to perturbation, and the potential importance of particles and their associated microenvironments to microbial diversity and function within the OMZs. In addition, there was consensus among the participants on the critical need to compare methods and develop standardized protocols in order to create comparable datasets describing OMZ microbiology and biogeochemistry across studies and locations. A collaborative cruise or workshop was proposed as a mechanism to develop and agree upon such standardized protocols.

Looking forward, a session on microbial biogeochemistry in oxygen-deficient systems was submitted and accepted for the Association for the Sciences of Limnology and Oceanography (ASLO) Ocean Sciences Meeting in February 2014, and a proposal for a working group on microbial ecology and biogeochemistry of oxygen-deficient marine systems has been submitted to the Scientific Committee on Oceanic Research (SCOR). Finally, a collaborative experiment examining the factors controlling the evolution of microbial community structure and biogeochemistry within a mesoscale eddy is being planned for 2014.

GOALS

SESSION 1:

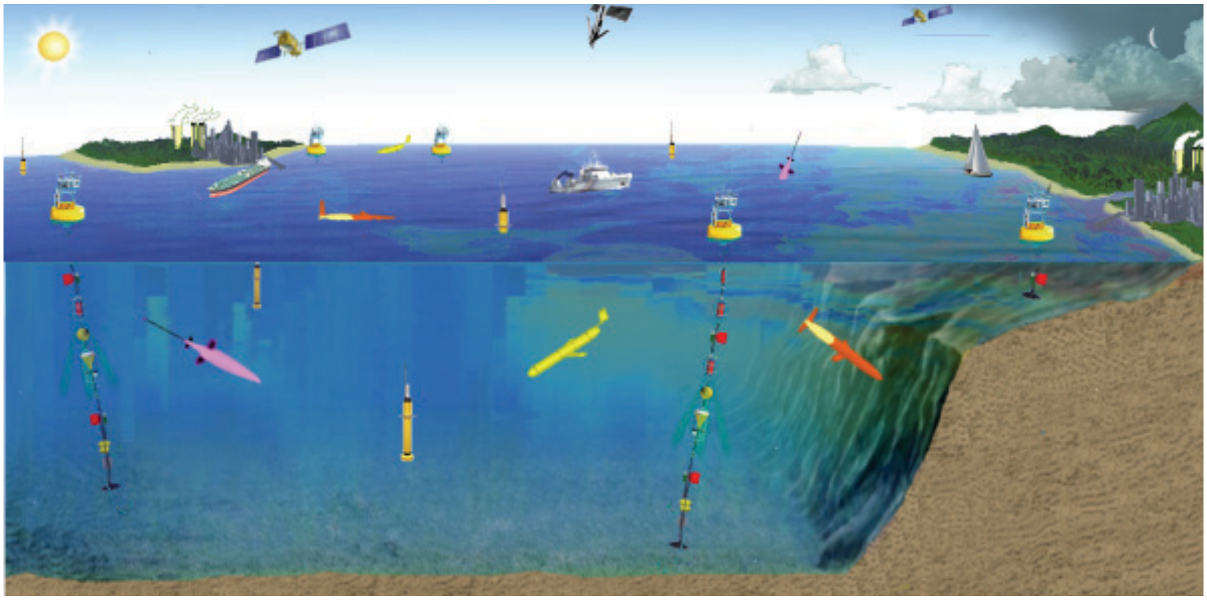
Similarities and differences in microbial ecology and biogeochemistry among different oxygen minimum zones

Chair: Phyllis Lam | University of Southampton, UK

Johannes Karstensen | GEOMAR, Germany

On the physical oceanography of different OMZ regions

Ocean transport processes play a key role in the creation of oxygen-depleted regions in the marine environment, from the large-scale eastern boundary OMZs to the very local and intermittent formation of coastal "dead-zones." Low oxygen concentrations result from the balance between the efficiency of physical processes of oxygen supply and the removal of oxygen by biogeochemical processes. During the presentation some attention was paid to the recent observations of extreme environments created in isolated nonlinear vortices ("eddies"). The extreme eddies originate from the eastern boundary upwelling regions and move westward, into the open ocean. During their westward propagation, the eddy core water is very efficiently isolated from surrounding waters, while productivity and vertical particle fluxes within the eddies are particularly high. As such, the supply/consumption balance that may exist on the large scale is disturbed within these eddies and, as a response to this imbalance, an extreme environment is created. The eddy can be characterized by very low oxygen concentrations, as recently found in the otherwise well-oxygenated eastern tropical North Atlantic Ocean, or by very specific phytoplankton species, as found in the eastern South Pacific Ocean.

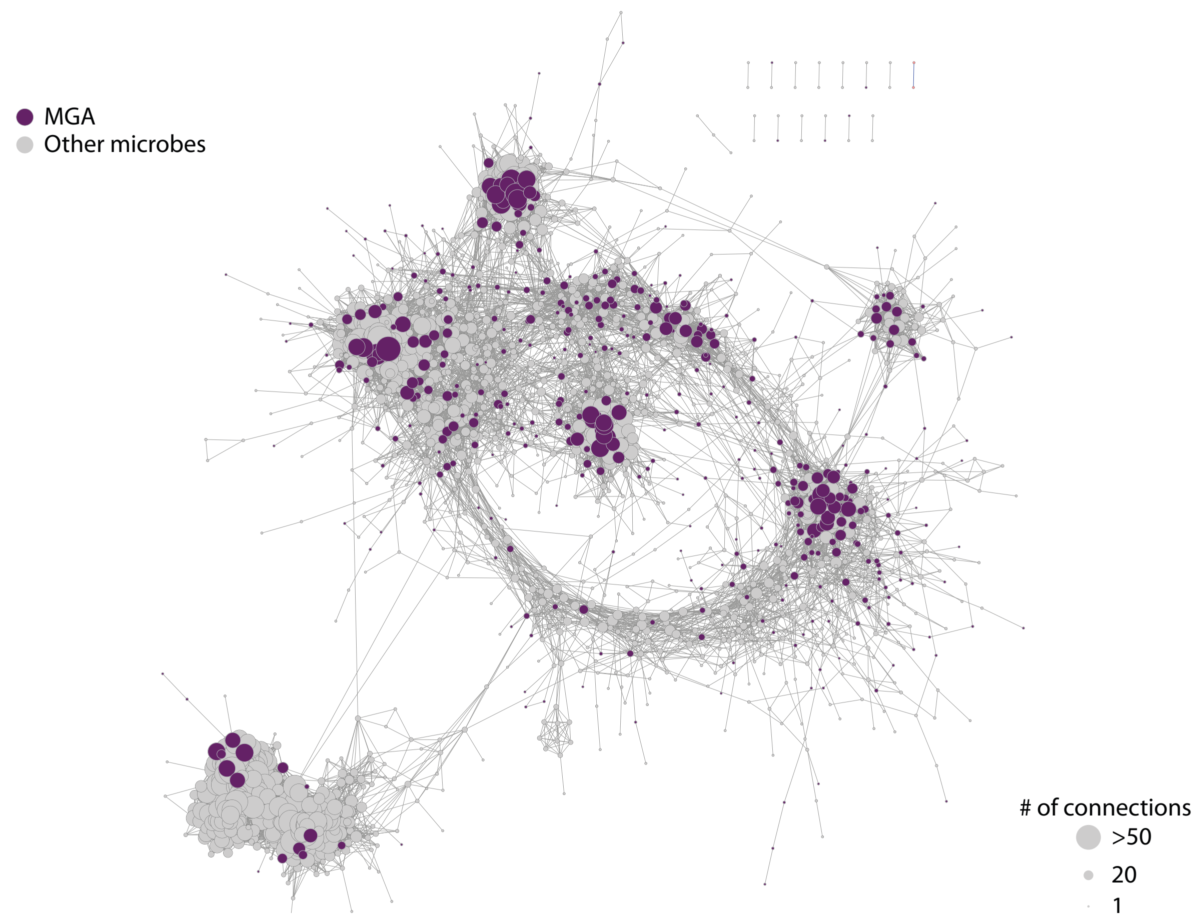


The cornerstone of Johannes' research is the access to the variety of observational data that is routinely collected and distributed through the Global Ocean Observing system (credit: Pierre Testor, LOCEAN, Paris and the GROOM project).

Steven Hallam | University of British Columbia, Canada

Oceans of information: microbial community structure and function across OMZs

Oxygen minimum zones are widespread oceanographic features currently expanding due to global warming. Although inhospitable to metazoan life, OMZs support a thriving microbiota whose combined metabolic activity is intimately connected to nutrient and trace gas cycling within the global ocean. Therefore, OMZ expansion and intensification represents an emerging ecological phenomenon with potentially harmful effects on ocean health and climate balance. To understand, respond to, or mitigate these transitions, studies monitoring and modeling dynamics and systems metabolism of OMZ microbiota in relation to physical and chemical oceanographic parameters are imperative. To this end, we are using environmental genomic approaches to chart microbial community responses to changing levels of water column oxygen-deficiency in the northeastern subarctic Pacific Ocean (NESAP). The NESAP is one of the world's most extensive OMZs and provides an exceptional model system for long-term observation and process-oriented studies of OMZ phenotypes.



Microbial co-occurrence network depicting correlations between bacterial, archaeal, and eukaryotic operational taxonomic units (OTUs) detected in the NESAP. Nodes represent OTUs and links represent a correlation in the presence of those OTUs across samples. Co-occurrence network was generated by calculating pairwise Pearson's correlation coefficients between OTUs detected in 26 samples taken from NESAP waters. Only interactions with strong and significant correlation coefficients ($R > 0.8$, $p < 0.001$) are depicted in the network. Nodes affiliated with the candidate bacterial phylum Marine Group A (MGA), a diverse and abundant group of microbes found in the NESAP OMZ, are highlighted in purple. Nodes are sized based on degree (number of connections to other nodes).

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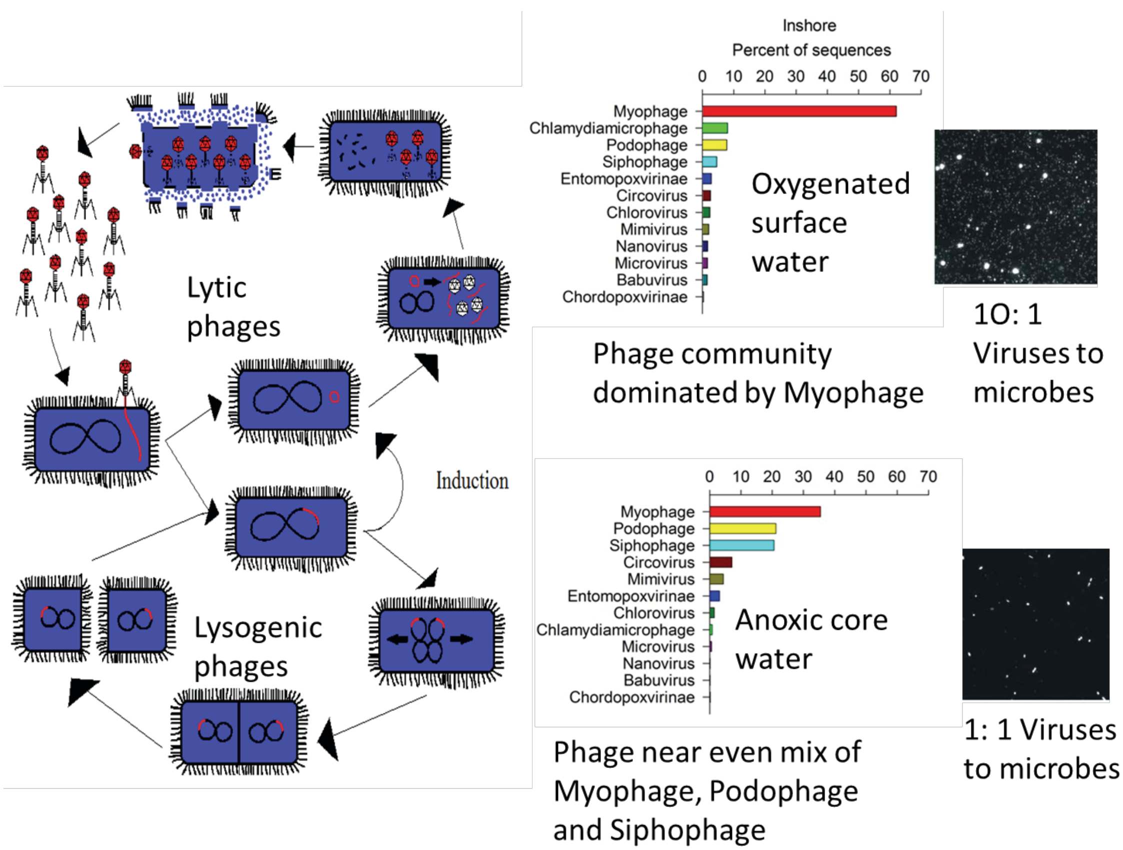
Elizabeth Dinsdale | San Diego State University, USA

Phage and prophage in the marine OMZ off Iquique, Chile

Marine viruses are numerous (~10^7 viruses mL^{-1}) and diverse biological agents that play important roles in shaping microbial community structure and function. However, the viral community of OMZs has remained understudied. We conducted the first study on the abundance and ecological characteristics of the viral communities associated with the permanent Eastern Tropical South Pacific (ETSP) OMZ off Iquique, Chile, and found that both of these characteristics varied with oxygen concentration. The virus-to-microbe ratio (VMR) in the ETSP OMZ fluctuated in the oxycline and declined in the anoxic core to below one on several occasions. The viral community diversity in the ETSP OMZ was extremely low, particularly within the oxycline. Moreover, the viruses detected were novel and showed distinct community structures in the surface, oxycline, and anoxic core. The low viral number and lack of similarity of the sequences in the viral metagenome to the database or microbial community lead us to suggest that lysogeny may be an important viral lifestyle in the anoxic core. To test this hypothesis, prophage metagenomes were constructed. The prophage metagenomes were taxonomically and functionally distinct from the phage metagenomes, suggesting that many prophages were present in the anoxic core.



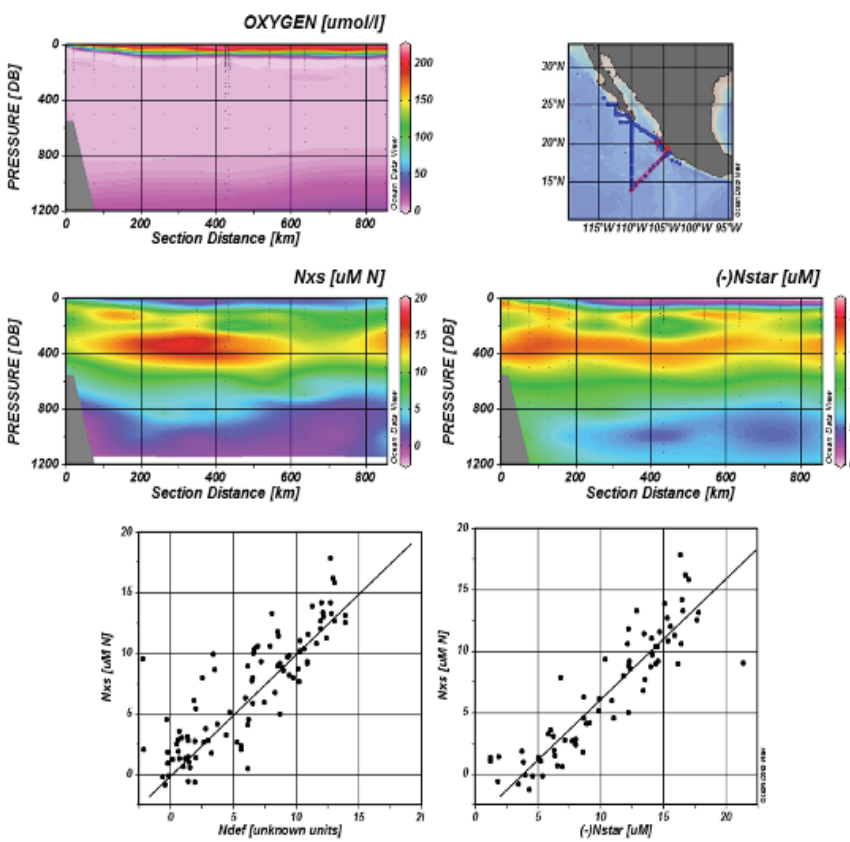
Phage lifestyle shows changes with oxygen condition. The phages in the oxygenated surface water are dominated by myophage and have a VMR of ~10:1, suggesting a more lytic life cycle. In comparison, the viruses in the anoxic core are evenly mixed between three groups (myophage, podophate and siphophate). They have a VMR of 1:1 and appear lysogenic in lifestyle. (Artwork by Noriko Cassman.)

A tetranucleotide analysis showed that the lytic phages had a distinct tetra-meric signature from the microbes, whereas the induced phage show similar tetrameric signature with the microbial community. These results suggest that the lysogeny is an important process in the anoxic core and that the viruses may be sharing important auxiliary genes in this environment.

Allan Devol | University of Washington, USA

Coupling of elemental cycles and constraints in OMZs

Oxygen minimum zones are globally important sites of fixed nitrogen loss (conversion to N_2 gas) by heterotrophic denitrification and anammox. The relative importance of these two processes and how they are coupled to other N cycle processes and other elemental cycles are reviewed. Currently, there appears to be no consensus of these couplings either within a given OMZ or across the three major OMZs. The expanding knowledge of the amount of excess N_2 that is produced by heterotrophic denitrification and anammox in all three major OMZs does, however, provide a strong quantitative constraint on the amount of fixed nitrogen loss and, given an estimate of residence time, the combined rate of loss. Furthermore, the general agreement between N_2 excess, fixed-N deficit and N-star suggests that the overall process follows Redfield stoichiometry and that the majority of fixed-N lost was pre-existing nitrate when the waters entered the OMZ.



The distribution of oxygen (upper left), excess N_2 gas (Nxs, center left) and negative Nstar (center right) along a section roughly perpendicular to the Mexican coast (upper right). Also shown are Nxs vs. Ndef (fixed-N deficit, lower left) and Nxs vs. negative Nstar lower right.

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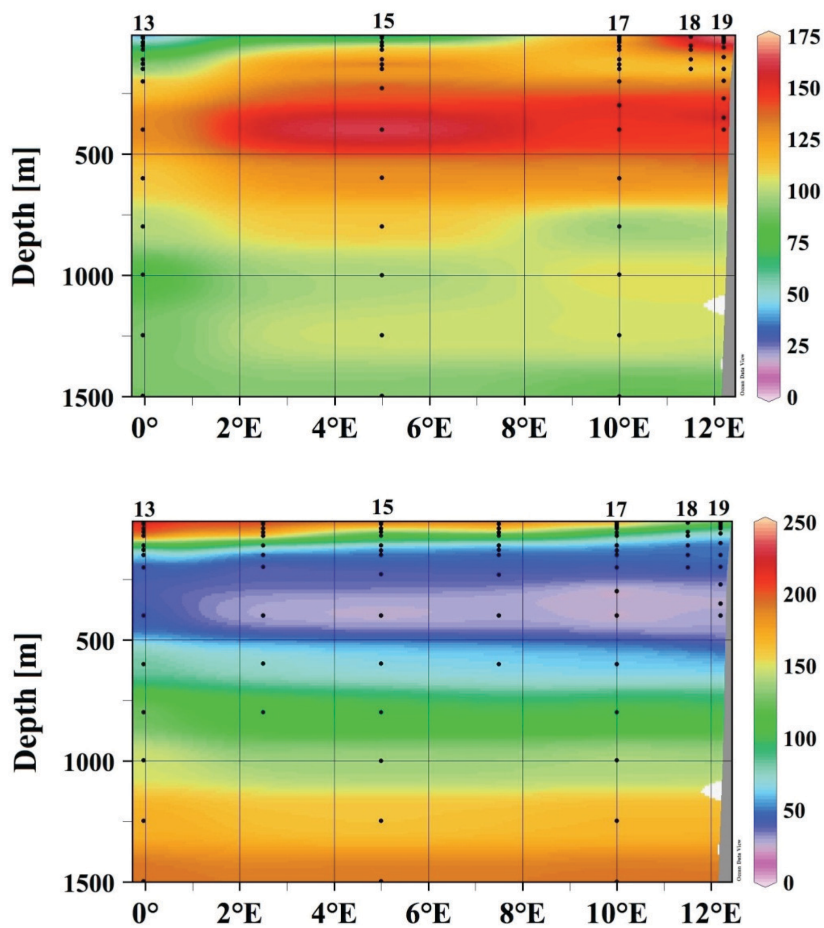
Mak Saito | Woods Hole Oceanographic Institution, USA

The catalytic roles of trace metals in OMZ biogeochemical cycles and considerations for the future

The role of OMZ regions in metal distributions and metalloenzymes is an area of active research. Recent ocean sectional studies reveal that the major OMZ regions are sources of certain metals such as cobalt, iron, and manganese, which implies that their fluxes may increase in the future with increasing ocean deoxygenation. The metalloproteomic approaches are maturing to the extent where key metal-containing enzymes found in OMZ regions can be identified and quantified, allowing their biogeochemical impact to be considered.



In the South Atlantic/Benguela upwelling region (14.5°S to 18.5°S), the distributions of the micronutrient cobalt (total dissolved cobalt measured in pmol L^{-1}, upper plot) were observed to have an inverse correlation with those of the OMZ region (dissolved oxygen measured in µmol kg^{-1}, lower plot), implying an OMZ source for cobalt as well as a reduction in scavenging removal rates within the OMZ. Calculations suggest that at the present rates of deoxygenation, the upper water cobalt inventory could increase by 10% by 2100. From Noble et al., 2011, Limnol. Oceanogr.

SESSION 1 WORKING GROUPS

Group 1 | Chair: Virginia Edgcomb, Woods Hole Oceanographic Institution, USA

How does microbial community structure vary spatially and temporally as a function of oxygen and redox conditions?

This working group discussed the role that mesoscale and other short-lived environmental perturbations may play in structuring OMZ microbial communities. In this context, the group identified the need for a greater effort dedicated towards high frequency sampling of community variability on shorter time scales. High temporal variability (< 1 month) of community structure and function is currently not well constrained. Furthermore, it is necessary to sample and characterize community structure using approaches that are synoptic with key hydrographical events. There is value in a fixed depth sampling approach as well as in sampling of specific water column features (i.e. particle max, isopycnals, chlorophyll max, etc.). "Yo-yo" type sampling could be useful for constraining spatial variability on a vertical scale. Nested temporal sampling would be desirable for determining the appropriate time scale for sampling different types of OMZs.

In addition, this working group highlighted the need to better constrain the distribution of protists and their activities along the redox gradient. Likewise, little is known about the fundamental patterns and consequences of variability in viral abundance, viral types, and viral grazing in OMZs. More research is needed to constrain the effects of viruses on the microbial loop, bacterial production, and DOC production and on biogeochemical cycles in general.

Group 2 | Chair: Laura Bristow, University of Southern Denmark, Denmark

How does biogeochemical cycling vary spatially and temporally as a function of oxygen and redox conditions?

This working group aimed to compare and contrast the two extremes of oxygen-deficient systems, choosing the Black Sea (a permanently anoxic, semi-enclosed basin, with timescales of anoxia of thousands of years), and the Oregon coast (seasonally hypoxic, with timescales of hypoxia of 1 to 6 months) to identify key similarities and differences across oxygen-deficient systems.

Key similarities identified include:

- Enhanced nutrient supply resulting in an increased oxygen demand
- Restricted ventilation
- Presence of redox gradients

Key differences identified include:

- Oxycline versus photic zone depth
- The importance of nitrogen fixation
- Surface productivity
- Nitrite and N_2O gradients
- Accumulation of sulfide

- Variability in oxygen and preformed nutrients in the source water
- Horizontal advection gradients, eddy fluxes
- Benthic fluxes

Key variables that are currently poorly understood in these systems include:
- Rates and regulation of nitrogen fixation
- P cycling – important to note that in systems such as the Black Sea where P cycling is intense, Nstar is no longer a useful variable to assess N loss, highlighting further the value of excess N_2 measurements
- Interactions / coupling of N / P / S / Fe cycles
- Oxygen thresholds for redox transformations
- Role of sinking particles

Group 3 | Chair: Moritz Holtappels, Max Planck Institute for Marine Microbiology, Germany

What are the roles and relationships between suspended and sinking organic particles?

This working group discussed the limits of knowledge related to the contribution of particle-related microbial processes and communities to OMZ biogeochemistry is not fully known. More studies focusing on particles are needed, including the measurement of process rates in combination with molecular studies in samples with and without particles. More molecular studies should include the particulate fraction. There is a need to analyze datasets of OMZ related biogeochemical processes with respect to particulate organic matter (POM) concentration. Little is known about size spectra, associated sinking velocities, and organic composition of particles. Perhaps the particle flux research community could be engaged to perform joint studies in OMZs. With respect to sinking particles, what potential mechanisms allow the maintenance of processes, especially strictly anaerobic processes, in the OMZ boundaries as sinking particles enter and leave the OMZ? What is the role of migration of copepods and fish such as myctophids and physical transport on particle-related microbial processes?

Challenges and unknowns regarding microscale processes occurring on or inside particles include:
- How do microgradients associated with particles affect microbial processes?
- Is there potential for zoning of various processes that are linked to each other (e.g. within the cryptic sulfur cycle)?
- Inside the particle how do microgradients depend on particle size and quality?
- Outside the particle, plumes serve as traces of particles. How can microbes make use of the high concentration of particles in the plumes?

Group 4 | Chairs: Niels Peter Revsbech, Aarhus University, Denmark & Wally Fulweiler, Boston University, USA

What are the thresholds of oxygen stress that bound aerobic and anaerobic processes?

This group discussed the proposition that there is no specific boundary that defines aerobic and anaerobic processes—it depends on the questions being addressed. For each process, K_m and inhibitory values of oxygen (K_s) must be defined. Some of these values are known for the nitrogen cycle. Definition of specific oxygen thresholds will be complicated when systems are not in steady state. In such fluctuating environments, we might see canonically “anaerobic” processes occurring in aerobic environments.

SESSION 2:

Predictions of changes and impacts

Chair: Bess Ward, Princeton University, USA

Sean Crowe | University of British Columbia, Canada

The redox state of Precambrian oceans: an evolving biogeochemical mosaic

The oxygen content of the ocean is a primary regulator of marine life and global biogeochemical cycles. Observations show that the oxygen content of the modern oceans is declining, but oxygen-deficient marine waters are not a new feature of the marine environment. Through most of Earth's history, the oceans contained very little oxygen, and it was only in the last 400–500 million years that they reached their modern, well-oxygenated state. About 3.5 billion years ago, however, oceans were anaerobic and often rich in dissolved ferrous iron—a so-called ferruginous ocean state. Due to their rarity on the modern Earth, ferruginous ecosystems remain very poorly understood in comparison to their oxic and sulfidic counterparts. The understanding of the co-evolution of marine life and Earth surface chemistry through geological time is only possible with detailed contextual knowledge from the ecology of modern ferruginous environments. Ferruginous oceans were also periodically punctuated by intervals during which hydrogen sulfide accumulated to high concentrations over large expanses of the ocean. The duration and extent of these euxinic intervals remain poorly constrained, but they likely occurred at times when sulfate fluxes to the ocean were greater than Fe, primary production was relatively high, and atmospheric oxygen concentrations were relatively low. Though rare relative to ferruginous ocean states, euxinic intervals have likely played an important role in the evolution of marine life during the Precambrian and may have contributed to mass extinction events well into the Phanerozoic. Despite the operation of cryptic sulfur cycles in modern OMZs, sulfide rarely accumulates to routinely detectable concentrations. This is in part due to high-affinity, sulfide uptake systems in anaerobic, nitrate-reducing, sulfide-oxidizing microbes. Indeed, pelagic anaerobic sulfide oxidizers belonging to the SUP05 clade from coastal Chile exhibit half-saturation constants of 85 µmol L^{-1} with threshold sulfide concentrations less than 10 nmol L^{-1}. These uptake kinetics translate to exceptionally high specific affinities for sulfide, which underpin OMZ cryptic sulfur cycling. In addition to the rapid consumption of sulfide produced in OMZs, accumulation of sulfide may also be controlled through a negative feedback that results from fixed nitrogen loss and the ensuing limitation on primary production. Such a negative feedback is supported by models of OMZ biogeochemistry, which suggests that nitrogen fixation in OMZs could replenish nitrogen loss and ultimately lead to enhanced primary production and sulfide accumulation. The currently uncertain role of pelagic sulfur cycling in the modern ocean and its regulation through time stand as important knowledge gaps that need to be filled to constrain and predict the evolution of marine biogeochemical cycling in a time of climate change.

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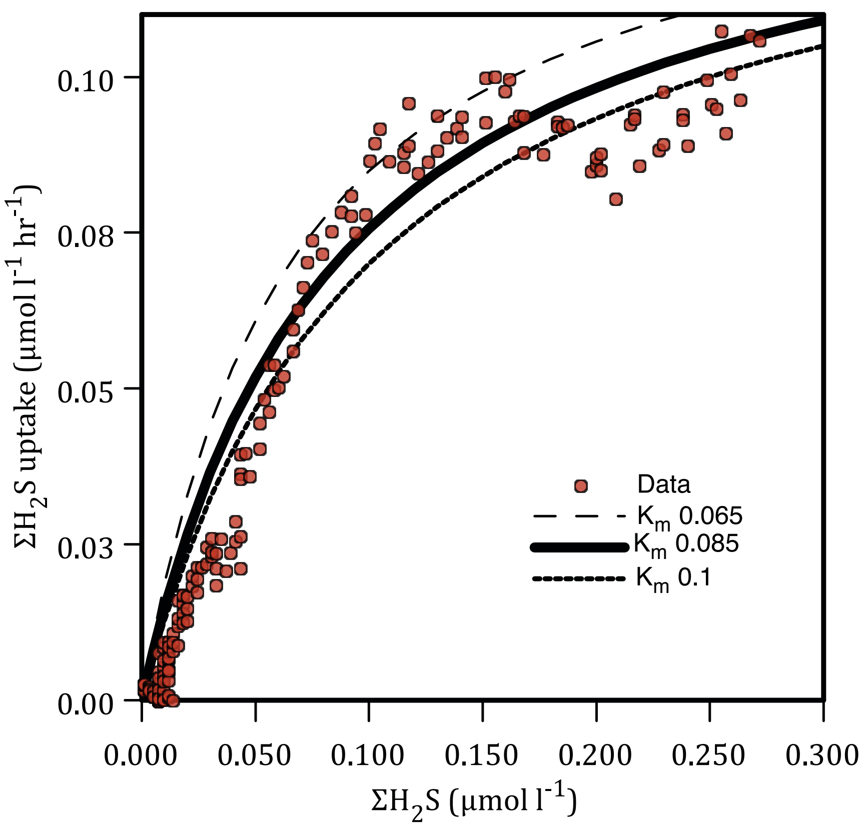
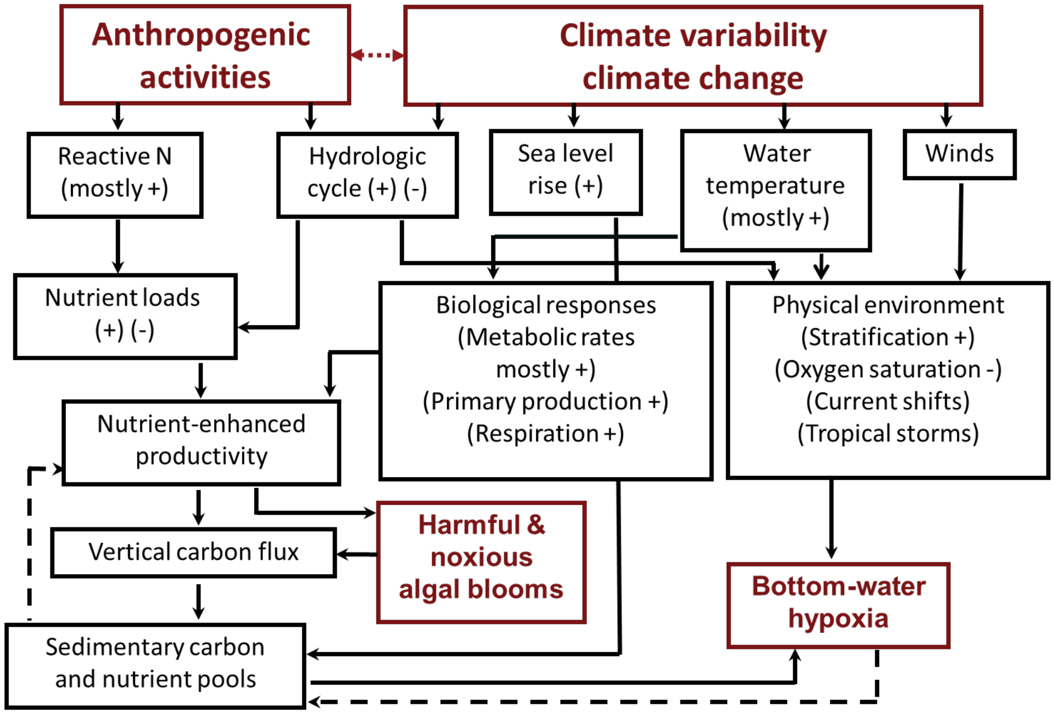


Sulfide uptake kinetics from coastal Chilean water dominated by SUP05 gammaproteobacteria.

Nancy Rabalais | Louisiana Universities Marine Consortium, USA

Will climate change aggravate or alleviate coastal hypoxia?

The cumulative effects of global change, including climate, increased population and more intense industrialization and agribusiness, will likely continue the course of eutrophication in estuarine and coastal waters. As a result, one symptom of eutrophication, the severity of hypoxia (oxygen depletion) will increase. In addition, global climate change will likely result in higher water temperatures, stronger stratification and increased inflows of fresh water and nutrients to coastal environments in many areas of the globe. Both past experience and model forecasts suggest that these changes will



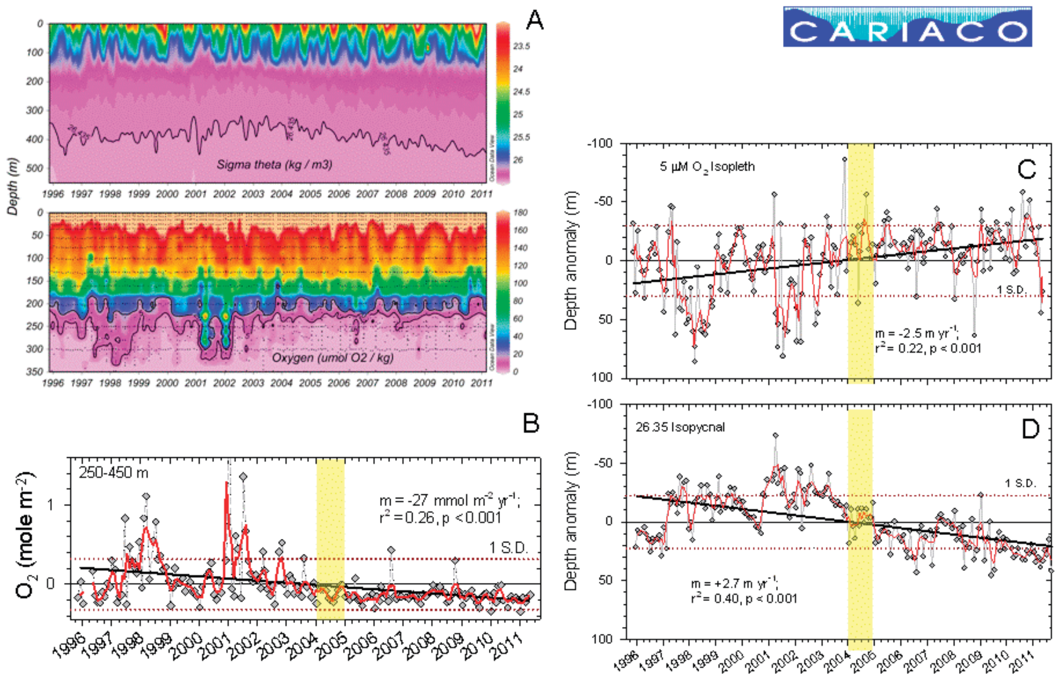
Potential physical and hydrological changes resulting from climate change and their interactions with current and future human activities. The dashed lines represent negative feedback to the system (Rabalais et al., 2010).

lead to enhanced primary production, higher phytoplankton and macroalgal standing stocks, and more frequent or severe hypoxia in coastal waters. The negative consequences of increased nutrient loading and stratification may be partially, but only temporarily, compensated by stronger or more frequent tropical storm activity in low and mid-latitudes. In anticipation of the negative effects of global change, nutrient loadings to coastal waters need to be reduced now so that further water quality degradation is prevented.

Gordon Taylor | Stony Brook University, USA

What does the CARIACO time series tell us about possible changes in OMZs?

CARIACO ocean time-series observations reveal that even this "stable" anoxic end-member is physically and chemically dynamic and presumably so are microbial communities and gene expression. Climatic warming and zonal wind relaxation have amplified stratification thereby inducing an ecosystem state change including: declining surface production, enhanced export production,



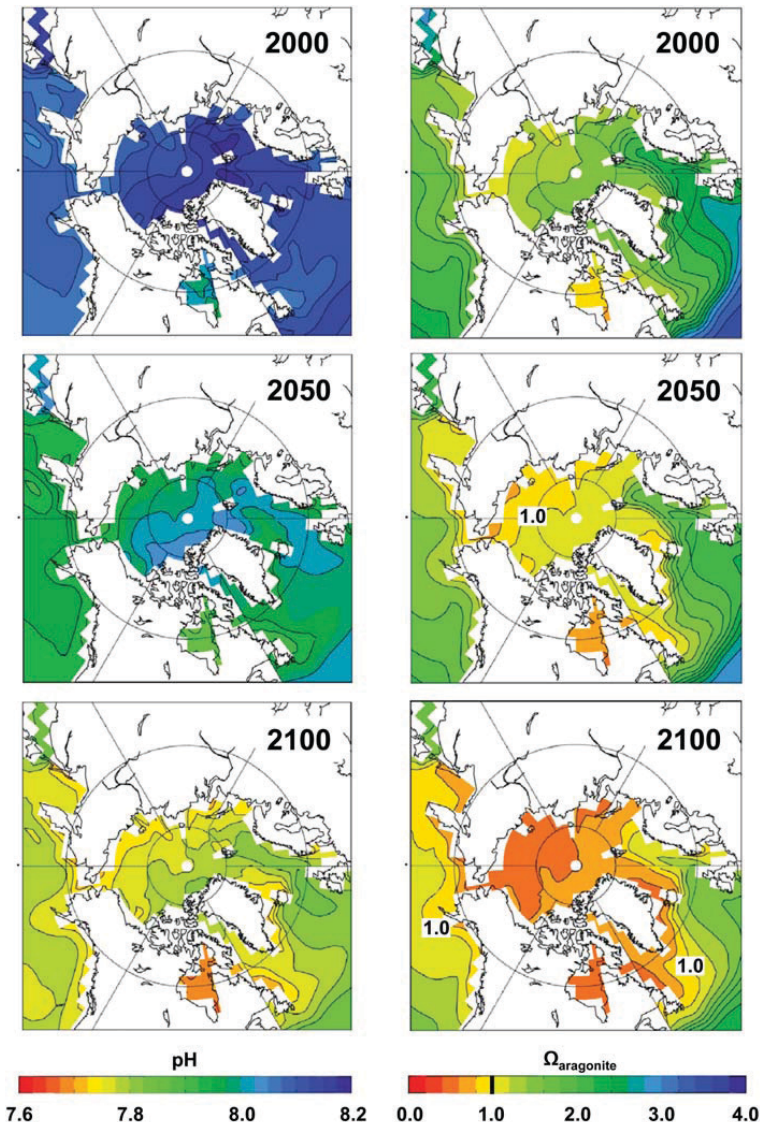
Time-series observations of hydrography and dissolved oxygen (DO) concentrations at Station CARICAO in the southern Caribbean Sea (10.50°N, 64.67°W). Contour plots of sigma-theta in the upper 550 m and DO in the upper 350 m (A). Integrated DO inventory anomalies within the redoxcline determined by removing the mean annual cycle and illustrating DO depletion through time (B). Anomalies in depth of 5 mM DO isopleth determined by interpolations from monthly observations and illustrating shoaling of oxycline through time (C). Anomalies in depth of 26.35 kg m^{-3} isopycnal determined by interpolations from monthly observations and illustrating deepening of buoyant layer and increasing stratification through time (D).

shifting plankton community structure, shoaling anoxia and shoaling of deep-water NH_4^+, PO_4^{3-} and presumably H_2S isopleths (or concentration gradients). Temporal variability within suboxic and anoxic waters and its drivers are poorly understood. Thus, predicting how nitrogen, sulfur and carbon cycling and the microorganisms mediating these processes will respond is difficult. Trends in Cariaco's hydrography and oxygen distributions are consistent with climate change models and OMZ observations.

Kenneth Denman | University of Victoria, Canada

How is the oxygen cycle represented in large-scale ocean models?

Over the last 15 years, a series of global ocean general circulation models has been used to investigate how the ocean oxygen cycle will change as the climate changes. In particular, models provided estimates of how much oxygen will be lost from the ocean to the atmosphere as the climate warms. These models range in complexity from no representation of ecosystems to explicit representation of planktonic ecosystems. Generally, they used a power law expression to represent the flux of organic particles as a function of increasing depth, and fixed ratios between oxygen and a macronutrient (phosphorus or nitrogen) throughout the model. Most models show a loss of oxygen from the oceans over the 21st century in the range of 5–10 µmol kg^{-1} of which a decrease in surface solubility with an increase in temperature accounts for about 25% of the total loss. The other main loss results from a reduction of transport of oxygen downwards into the ocean interior at high latitudes.

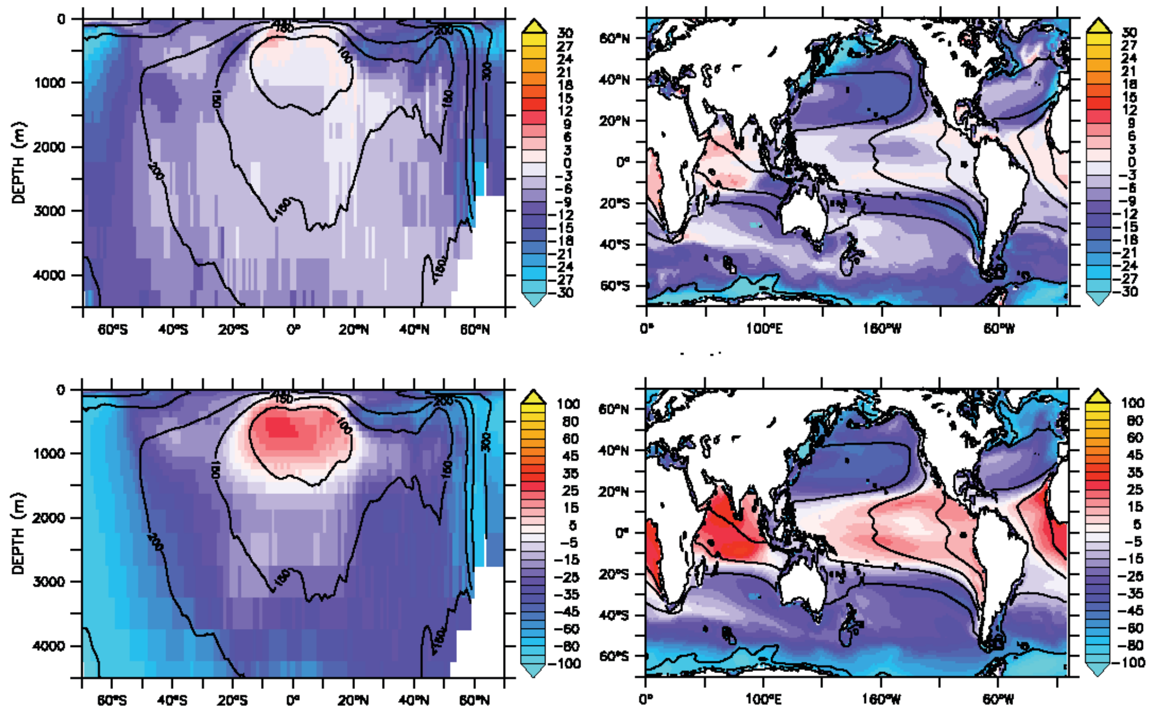


Results for the Arctic Ocean and high latitudes in the North Atlantic and North Pacific oceans, illustrating predicted changes for the A2 scenario in pH (left) and in $\Omega_{aragonite}$ (right), from the Canadian Earth System Model CanESM-1.0 (Christian et al., 2010).

Curtis Deutsch | University of Washington, USA

The future OMZ

A robust prediction of state-of-the-art earth system models is that in the OMZ of the tropical thermocline, oxygen concentrations are relatively stable or even increasing in a warming climate. This counterintuitive stability of tropical O_2 arises because the lower O_2 solubility in warmer water column is closely compensated by a reduced upwelling at the equator, which slows the rate of biological productivity at the surface and the subsurface respiratory oxygen demand. The reduction of nutrient supply to the surface ocean is driven not by stratification but by a weakening of the tropical trade winds. However it can also be viewed as a necessary consequence of the reduced ventilation in mid-latitudes, arising from the conservation of mass and the close coupling of nutrient and oxygen cycles. On centennial time scales, these dynamics are predicted to lead to a reduction of anoxia in the ocean, even while oxygen is steadily declining globally.



Change in oceanic O_2 projected to accompany anthropogenic climate warming. Zonally averaged (a,c) and depth averaged (0–1000 m; b,d) changes in O_2 concentration are differences between the last half of the 21st century (a,b) and the 23rd century (c,d), relative to the last half of the 19th century, for a greenhouse gas emissions scenario reaching a nominal radiative forcing of 8.5 W/m^2 in 2100. The O_2 anomalies are averaged across 5 models with 19 ensemble members for the 21st century, and 3 models with single realizations for the 23rd century.

SESSION 2 WORKING GROUPS

Group 1 | Chair: Julie LaRoche, Dalhousie University, Canada

What major changes in ocean microbial community structure and biogeochemistry associated with OMZs do we expect in the open ocean over the rest of the century?

This working group based their discussion on assuming a future ocean with increased stratification, lower ventilation, and a decrease in oxygen. We would expect a shallower mixed layer depth accompanied by reduced nutrient supply to the euphotic zone. This may result in a decrease in export to sediments, and an increase in metal cycling and dependence on chemosynthetic processes. This may also result in an increased penetration of the euphotic zone into the oxycline, potentially decreasing rates of nitrification due to light inhibition. Additional research is needed to understand the importance of N_2 fixation in present and future OMZs. With respect to changes within the microbial community, we lack an understanding of the adaptive and evolutionary processes acting on these communities at play as a function of imposed selection pressures. As such, it is difficult to predict how the genetic capacity and metabolic function of extant organisms may change in the future and their resulting feedbacks on biogeochemical cycles.

Group 2 | Chair: Jessika Füssel, Max Planck Institute for Marine Microbiology, Germany

What major changes in ocean microbial community structure and biogeochemistry associated with OMZs do we expect in the coastal ocean over the rest of the century?

This working group focused on predicted changes in coastal OMZs, and specifically on predicted changes with the shelf region of these OMZs. In contrast to open-ocean OMZs, these systems are highly variable and dynamic. They are characterized by intense primary production above the OMZ, suboxic (< 5 μM) to anoxic condition in the OMZ, and the direct interaction of the anoxic/suboxic OMZ water with the underlying sediment and biogeochemical processes therein. The low oxygen levels in these zones make them susceptible to even slight changes in the overall oxygen content of the surface ocean (e.g. a 2 μM drop of the average oxygen concentration in the surface ocean would result in a doubling of volume of the coastal OMZs). Hence, the effects of global warming might be more severe on coastal OMZs, where primary production may also be enhanced due to increased inputs of nutrients from land. These coastal areas are particularly important for local communities and economies, and the intensification and extension of OMZs might strongly affect local fisheries, especially if sulfidic conditions emerge.

Microbial communities: Our knowledge of the microbial communities in coastal OMZs is limited. The presence of ammonia oxidizing archaea (AOA) in low-oxygen waters (< 100 μM) and in the oxycline has been demonstrated by metatranscriptomic studies, underlining the importance of nitrification in these hypoxic systems as well as the dominance of AOA over ammonia oxidizing bacteria (AOB) under low-oxygen conditions. The OMZ core is characterised by transcripts indicative of anaerobic processes such as nitrate reduction, nitrite reduction, anammox, and sulfate reduction. The dynamic nature of these

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systems does not permit generalised statements on the microbial community structure of coastal OMZs. Hence, future changes of microbial community structures are more difficult to access.

Biogeochemistry: Regarding the biogeochemistry of coastal OMZs, the cryptic sulfur cycle was discussed as a newly recognized characteristic of OMZs. Sulfidic conditions in coastal OMZs so far only emerge occasionally as outbursts of sulfide from the sediment (e.g. in the Benguela upwelling system). Recently, active sulfate reduction and sulfide oxidation has been found in the water column of the ETSP, indicating the possibility of sulfide build-up in the water column if primary production (e.g. N_2 fixation) increases in the future. However, further research on this topic is needed since, so far, only one study in the ETSP investigated the contribution of such cryptic S cycle in OMZs. Regarding the nitrogen cycle in coastal OMZs, the intensification of anoxia might decrease nitrification while nitrogen loss processes such as anammox and denitrificaton might increase, resulting in an increased net N loss from the system. These changes in the biogeochemistry however are strongly coupled to the hydrographic setting of the system. The influence of local currents and eddies on the ventilation of the water body, the extent of stratification and fertilizer runoff from land are important factors controlling future characteristics of coastal OMZs. Hence, the importance of reliable models for coastal OMZs was discussed. As each coastal OMZ is different, models would have to focus on a specific system. The interaction of the water body with the underlying sediment is an important aspect in this regard, and has to be resolved along with the contribution of N_2 fixation and anthropogenic N inputs to the OMZ. So far, little is known about N_2 fixation in and above OMZs. However, N_2 fixation might mainly be phosphate-limited in these waters. Increasing anoxia in coastal OMZs might result in the release of phosphate from the sediment to the water column, thereby increasing N_2 fixation, while the accelerated N-loss would also likely favor N_2 fixation. This might in turn act as a positive feedback, with increased primary production resulting in enhanced POM export and thus higher remineralization rates. The resulting intensification of anoxia may lead to the accumulation of sulfide in the water column.

Group 3 | Chair: Sam Wilson, University of Hawai'i Manoa, USA

How will changes in microbial community structure and biogeochemistry in the open ocean impact the global ocean–atmosphere system?

This working group identified N_2O, CO_2, CH_4 and DMS, in addition to hydrogen, carbon monoxide and halogenated volatiles, as key climate active trace gases relevant in the open ocean. Microbes may be sources or sinks for these trace gases, and many of the reduced species of trace gases are consumed via microbial processes at the ocean–atmosphere interface with limited escape to the overlying atmosphere. Future changes in microbial community structure and thus in the regulation of trace gas production and consumption may be driven by changes in ocean temperature, pH, trace metal availability, oxygen and sulfide concentration, particle fluxes, or light. At present, it is difficult to predict specific changes in microbial community structure and function that may occur as a result of these chemical and physical changes, however, several possible scenarios were considered:

- The buffering capacity of the microbial community may withstand physical and chemical changes to the ocean environment such that no changes in community structure are evident.
- Microbial community structure may change with limited alteration to community function (i.e. remove one microoganism and another will perform the same activity, known as 'functional redundancy'). There may be some cases where organismal functions are highly specific and thus irreplaceable (e.g. N_2 fixers, anammox bacteria).
- Large changes to both microbial community structure and function, with feedback on trace gas production and consumption (e.g. development of sulfidic conditions altering microbial community structure, leading to inhibition of N_2O production).

Group 4 | Chair: Francis Chan, Oregon State University, USA

How will changes in microbial community structure and biogeochemistry in the coastal ocean impact the global ocean–atmosphere system?

This working group focused on the challenges associated with predicting how future changes in OMZs will manifest, particularly in coastal OMZs, which are highly dynamic on fine spatial and temporal scales. At present, coastal ocean processes are poorly represented in models (e.g. wind variability cannot be accurately reproduced), thus more information needs to be gleaned from observational datasets to feed into physical models and improve assessments of atmospheric forcings. In this context, there is a need for more process studies to develop a better mechanistic understanding of climate active trace gas production and consumption processes (e.g. for N_2O, CH_4, CO_2, and DMS). In particular, further research should focus on assessing fluxes of these gases from ocean to atmosphere in coastal regions with high spatial and temporal resolution. Additional time-series stations are needed in coastal environments, and measurements taken at these stations should be standardized and comparable. High-resolution sampling (i.e. via autonomous observation systems) and sectional cruises extending offshore to study variability along coastal to open ocean gradients would be highly valuable.

SESSION 3:

Pressing questions and technological needs

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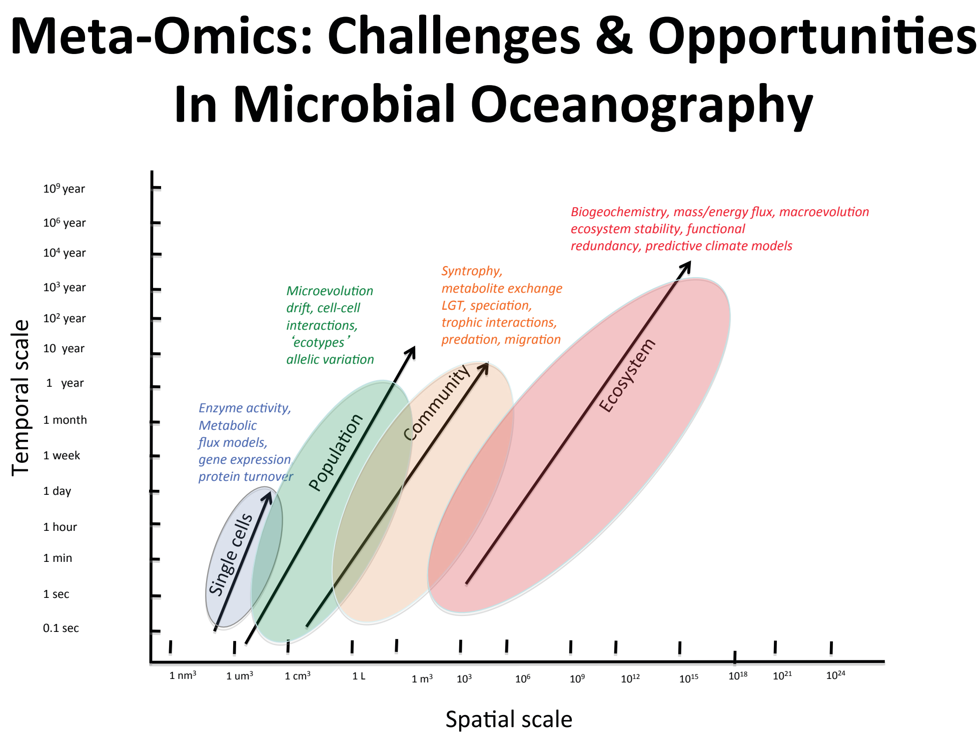
Chair: Steven Hallam, University of British Columbia, Canada

Edward DeLong | Massachusetts Institute of Technology, USA

Lessons and perspectives from the 'omics' era

Oceanic ecosystems, especially OMZs, are dominated by microbes. Yet the population dynamics, metabolic complexity and biological interactions hidden within indigenous marine microbial assemblages still remain largely uncharted. A fuller understanding of how oxygen replete versus oxygen depleted oceanic regions function and evolve requires more than just a 'parts list' of marine microbial taxa and genome sequences. One promising new approach involves characterizing the nature, timing, and responsiveness of expressed genes found in natural microbial communities inhabiting OMZs. Quantifying the variability and kinetics of gene expression in natural assemblages has potential to provide a fundamentally new perspective on microbial community dynamics. Questions that can now be addressed



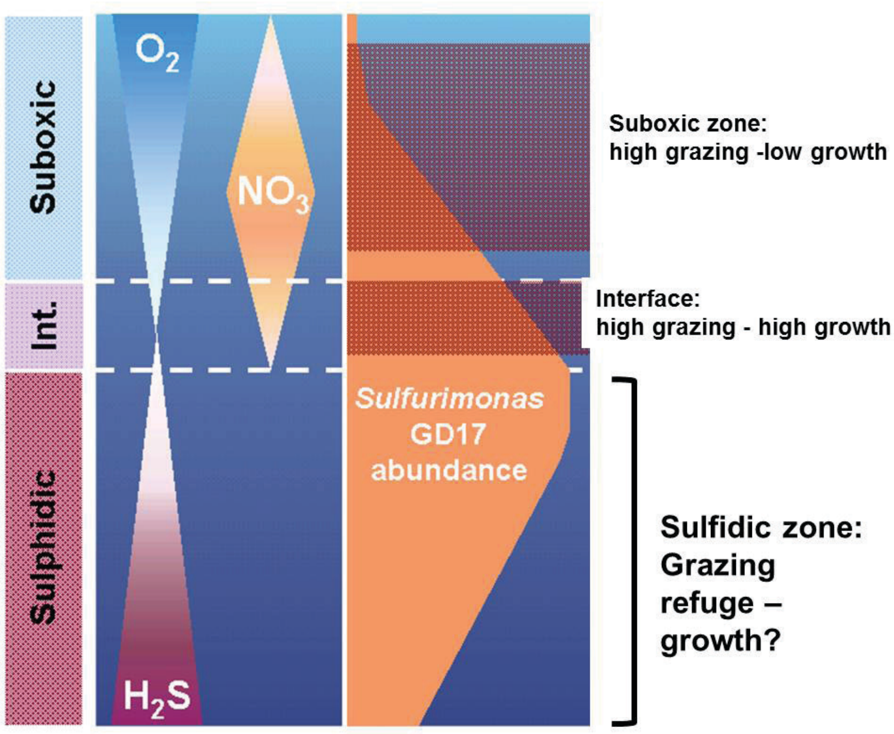
This graphic depicts (in two dimensions) the challenges and opportunities for eco-systems-biology (aka 'omics') approaches applied to microbial communities and processes in the sea. The main point is that different spatial and temporal resolutions and scales need to be addressed, and that different hierarchical levels of biological information flow and transfer (molecular, sub-cellular, single cell, population, community, ecosystem) need to be studied and integrated.

include: Are there fundamental community-wide regulatory responses common to disparate taxa? Are certain taxa or metabolic paths more or less responsive to particular environmental changes? Are specific changes in gene expression indicative of downstream changes in community composition? What taxon or community gene expression patterns can be considered diagnostic, and can these be used as "readouts" of indigenous microbial biosensors?

Klaus Jürgens | Leibniz Institute for Baltic Sea Research, Germany

Lessons and perspectives from culture work: examples from Baltic Sea redoxcline studies

Recent research combining "metaomics" data with process rate measurements has provided new insights into coupled biogeochemical cycling in different types of oxygen-deficient marine waters and revealed general patterns in global distributions of microbial biodiversity. However, there remain many open questions in our understanding of microbially driven elemental cycling, microbial adaptations and interactions, which are difficult to answer without studying isolated organisms or communities in experimental approaches. While there are many examples of microbial isolates from oxygen-deficient



Scheme of the distribution of Sulfurimonas GD17 group around the oxic–anoxic interface in the central Baltic Sea based and major selective forces. Data on growth and grazing losses in Anderson et al. (2013).

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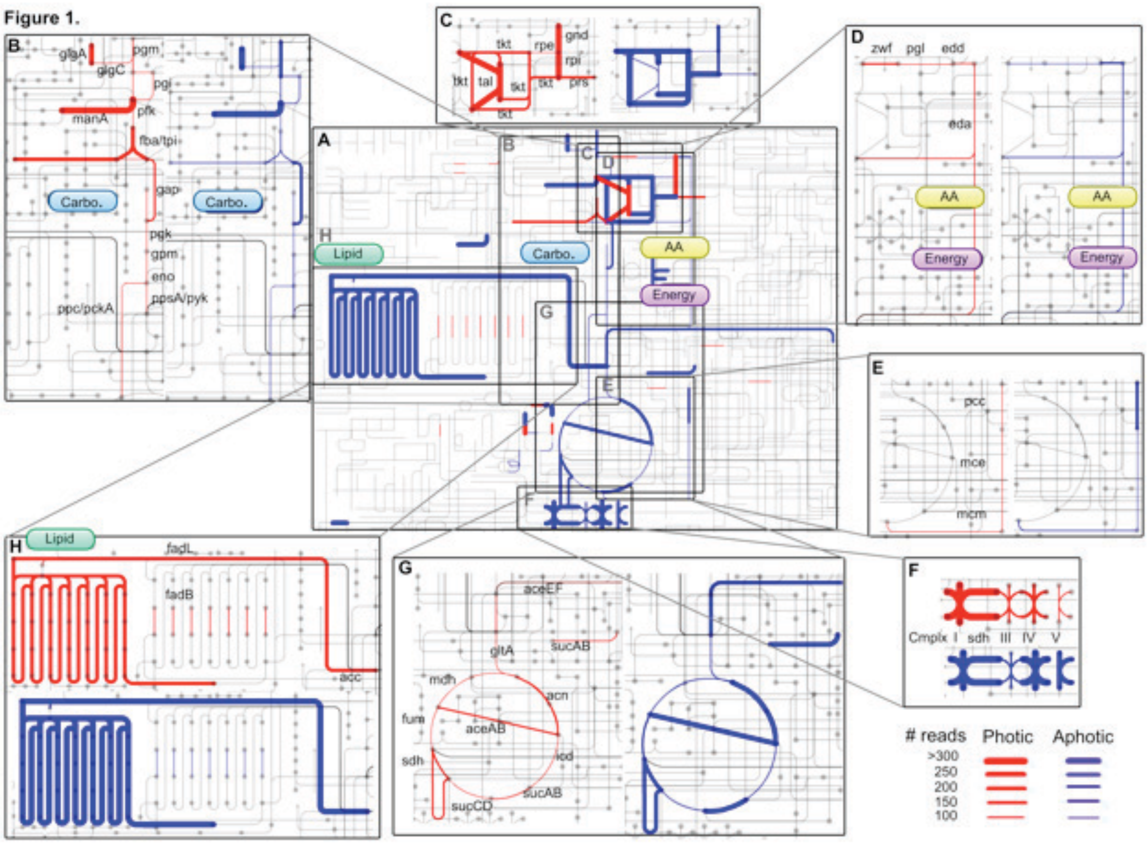
systems, only very few have been proven as representative key players in terms of abundance and function in the environment. Our studies on the anoxic basins of the central Baltic Sea revealed that the microbial community of the pelagic oxic–anoxic interface is dominated by chemolithoautotrophic microorganisms. Several groups can be considered as key players for distinct biogeochemical processes. These include ammonia-oxidizing Thaumarchaeota, chemoautotrophic denitrifying Epsilonproteobacteria (e.g. *Sulfurimonas* sp.) and potentially sulfur-oxidizing Gammaproteobacteria (e.g. SUP05 cluster). Accounting for up to one fourth of total cell counts in their respective redox zones, these organisms link the carbon, nitrogen and sulfur cycles, and their chemoautotrophic production is the basis of a microbial food web. Close relatives of these groups have been found in marine OMZs worldwide. As such, the Baltic Sea represents an ideal model system for an in-depth understanding of the structure and regulating mechanisms of the biogeochemistry and microbiology of marine pelagic anoxia. The successful isolation of "*Sulfurimonas gotlandica* GD1" allowed a combination of genetic, physiological and ecological investigations, which revealed a comprehensive understanding on the adaptations of this organism to pelagic redoxclines with sulfidic conditions. Four other key players studied with enrichments provided valuable information as well. However, more cultivation-based studies are required to cover the most important microorganisms and their microdiversity in the different oxygen-deficient systems.

Matthew Sullivan | University of Arizona, USA

Emerging challenges and opportunities in environmental virology

Marine ecosystems exert a profound influence on the operating conditions for life on Earth, and marine ecosystem function is largely determined by matter and energy transformations flowing through microbial interaction networks. Viral infection modulates network properties through mortality, gene transfer and metabolic reprogramming. In the case of metabolic reprogramming, bacterial viruses (phages) obtain genes from their hosts (termed "auxiliary metabolic genes," AMGs) and maintain them to bolster host metabolism during infection. For example, cyanobacterial viruses (cyanophages) harbor and express core photosynthesis genes that are modeled to improve phage fitness and impact the evolutionary trajectory of globally distributed host-encoded alleles. Recent studies suggest that viruses abundant in OMZs impact metabolic reprogramming of central carbon metabolism during infection. Reactions of central metabolic pathways are strongly influenced by viral infection because viral replication requires energy and materials for synthesis of macromolecules including proteins, nucleic acids and sometimes lipids. Emerging evidence supports a general model of viral reprogramming in which perturbations in glycolysis, pentose phosphate

Figure 1.



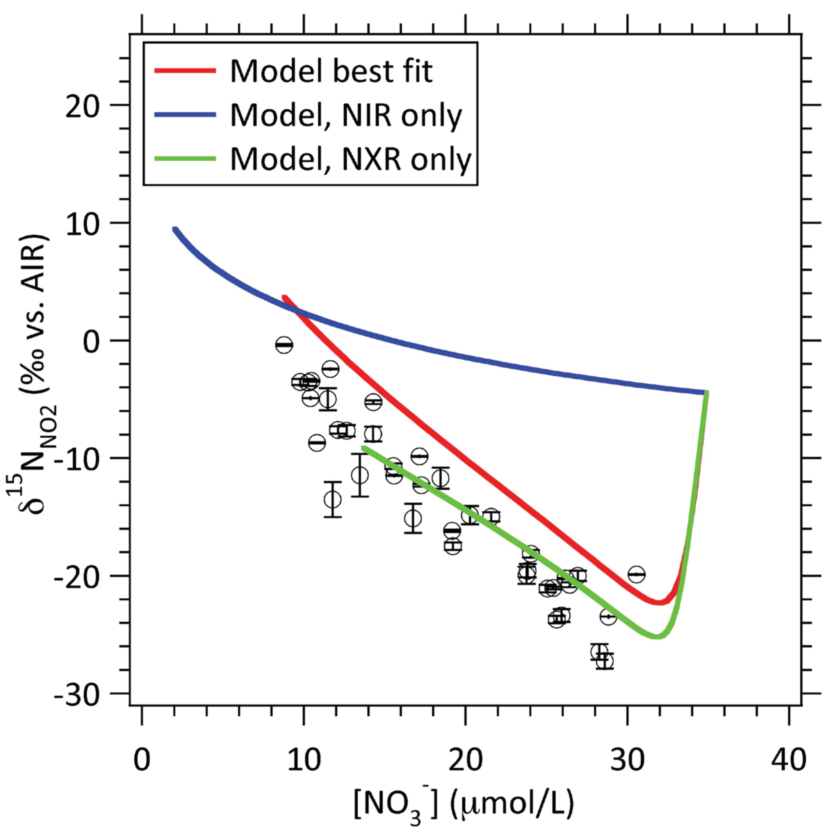
Metabolic map of viral-encoded carbon metabolism host genes from 30 viral metagenomes in sunlit and dark Pacific Ocean waters including permanent OMZs along the line P transect of the northeast subarctic Pacific Ocean. Red lines represent genes encoded in the photic zone and blue in the aphotic zone. The width of the lines corresponds to the normalized read abundance as shown in the legend. (A) Overview of viral encoded host genes in carbon metabolic pathways based on most abundant read count in the sunlit or dark ocean. Photic and aphotic encoded host genes in (B) glycolysis; (C) the pentose phosphate pathway; (D) the Entner–Doudoroff pathway; (E) components of the 3-hydroxypropionate cycle; (F) electron transport chain; (G) TCA cycle; and (H) and fatty acid metabolism. Figure from Hurwitz et al. (2013) in review.

pathway (PPP), and tricarboxylic acid cycle (TCA) alter host cell metabolic flux and energy homoestasis in support of viral replication and propagation at different stages of infection. The challenge now is to combine ‘gene ecology’ style surveys of OMZs with emerging and to-be-developed technologies and theory to more fully map who infects whom in the genomic context necessary to more comprehensively understand and model the metabolic reprogramming capabilities of OMZ-associated viruses.

Karen Casciotti | Stanford University, USA

Perspectives from natural abundance NO_3^- and NO_2^- isotope ratio measurements

Oceanic OMZs are important regions for N_2O production and the marine N budget. Stable isotopes of nitrate and nitrite integrate the effects of a complex suite of processes occurring in these regions. We examined the distributions of nitrate $\delta^{15}N$ and $\delta^{18}O$ and nitrite $\delta^{15}N$ in the Peruvian OMZ. Our data reveal elevated nitrate $\delta^{15}N$ and $\delta^{18}O$ values, particularly after correcting for the isotopic contribution of nitrite. Moreover, the isotopic composition of nitrite, a central intermediate in the marine N cycle, provides an additional constraint on the processes occurring in the Peru OMZ. A simple finite difference model is used to interpret the mechanisms and relative rates of N transformation in the waters sampled off the coast of Peru. Nitrite oxidation is found to be an important sink for nitrite, in many cases exceeding the rate of nitrite reduction.



Distribution of $\delta^{15}NO_2$ as a function of NO_3 in the Peruvian OMZ. The red line shows results from the best Nfit model, the blue line shows results from the model case excluding nitrite oxidation, and the green line shows results from the model simulation excluding nitrite reduction (Casciotti et al. 2013).

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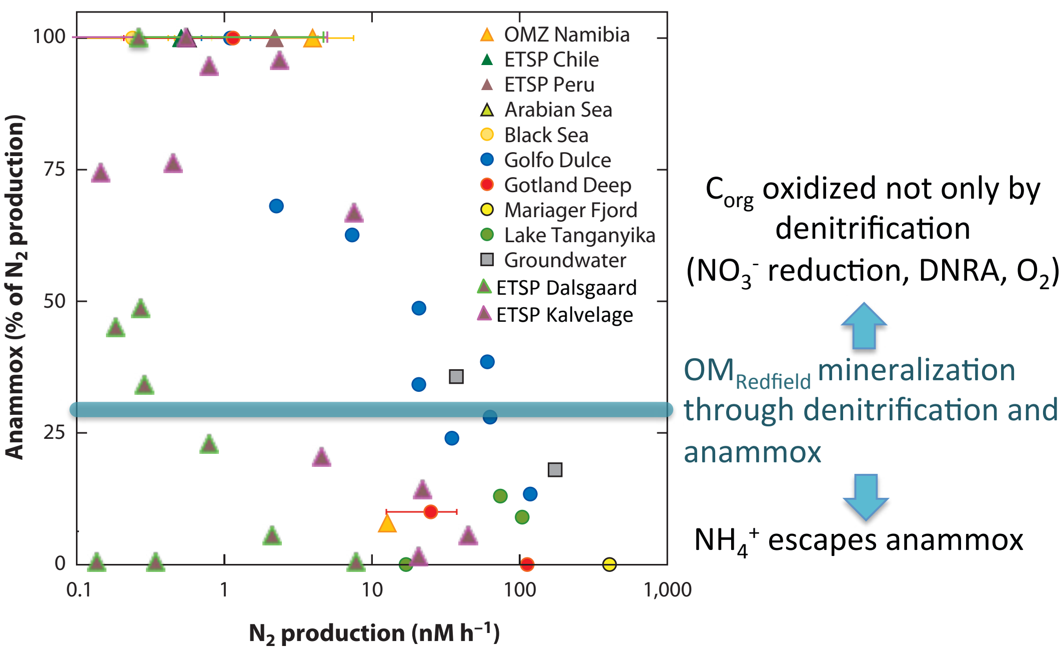
Bo Thamdrup | University of Southern Denmark, Denmark

Lessons and perspectives from perturbation and process rate experiments

Experimental studies are essential for understanding the complex web of microbial transformations in OMZs, yet all batch experiments in themselves represent perturbations of the in situ conditions. Most importantly for oxygen-depleted waters, substantial oxygen contamination is associated with the existing techniques for water sampling and with commonly used incubation methods, which are intended to maintain anoxic conditions. Poorly understood "bottle effects" further influence results during longer incubations. The recent development of highly sensitive oxygen sensors enables us to assess oxygen contamination in the nanomolar range and, more importantly, to investigate the response of both aerobic and anaerobic microbial metabolisms to such oxygen levels. Ongoing investigations point to a high sensitivity of denitrification and anammox in OMZ waters to oxygen levels below 1 µmol L^{-1} but also to substantial regional variation in this sensitivity. Consistent with the high oxygen sensitivity, profiling at high spatial resolution across the oxic–anoxic boundary in the OMZ off northern Chile shows a sharp zonation of processes with N_2 production restricted to anoxic depths except when disturbances move waters from



Compilation showing the large variation in rates and relative importance of denitrification and anammox for N_2 production in oxygen-depleted waters as determined in experimental incubations. The relative contribution of anammox to N_2 production (denitrification + anammox) is plotted as a function of the total N_2 production rate. Oxygen minimum zones are indicated by triangles, anoxic, sulfidic basins by circles, and groundwater by squares. The horizontal bar indicates the 29% contribution of anammox predicted for the complete oxidation of Redfield-type organic matter coupled to denitrification and anammox. For waters where anammox accounted for all N_2 production in a large number of samples, only the mean is shown with error bars indicating the range in rates. Redrawn from Thamdrup (2012) Annu. Rev. Ecol. Evol. Syst. 43:407 with additional data from the eastern tropical South Pacific from Dalsgaard et al. (2012) Limnol. Oceanogr. 57:1331 and Kalvelage et al. (2013) Nature Geosci. 6:228.

the anoxic core into the lower oxycline. Despite such advances, there is as yet no general understanding of the distribution and regulation of nitrogen metabolisms in the OMZs, and different recent surveys reach widely different conclusions regarding the dominant microbial pathways for the removal of reactive nitrogen. Important approaches and issues for improving our understanding include:

- Rate determinations at high spatial and temporal resolution in combination with transcript/proteomic analyses and environmental data
- Focus on particle-associated processes, gradients within particles, process dynamics with respect to oxygen
- Analysis of temporal dynamics of processes and communities associated with mixing across the oxic–anoxic interface
- The role of population dynamics of slow-growing clades in controlling community metabolism
- Comparisons across systems

Andreas Oschlies | GEOMAR, Germany

Lessons and perspectives from large interdisciplinary research in OMZs

The scientific aims and management concepts of the Collaborative Research Centre "Climate–Biogeochemistry Interactions in the Tropical Oceans" (SFB 754), funded by the German Research Foundation since 2008, were described. The main scientific questions addressed by the SFB 754 are:

- How does subsurface dissolved oxygen in the tropical ocean respond to variability in ocean circulation and ventilation?
- What are the sensitivities and feedbacks linking low or variable oxygen levels and key nutrient source sink mechanisms?
- What are the magnitudes and time scales of past, present and likely future variations in oceanic oxygen and nutrient levels?

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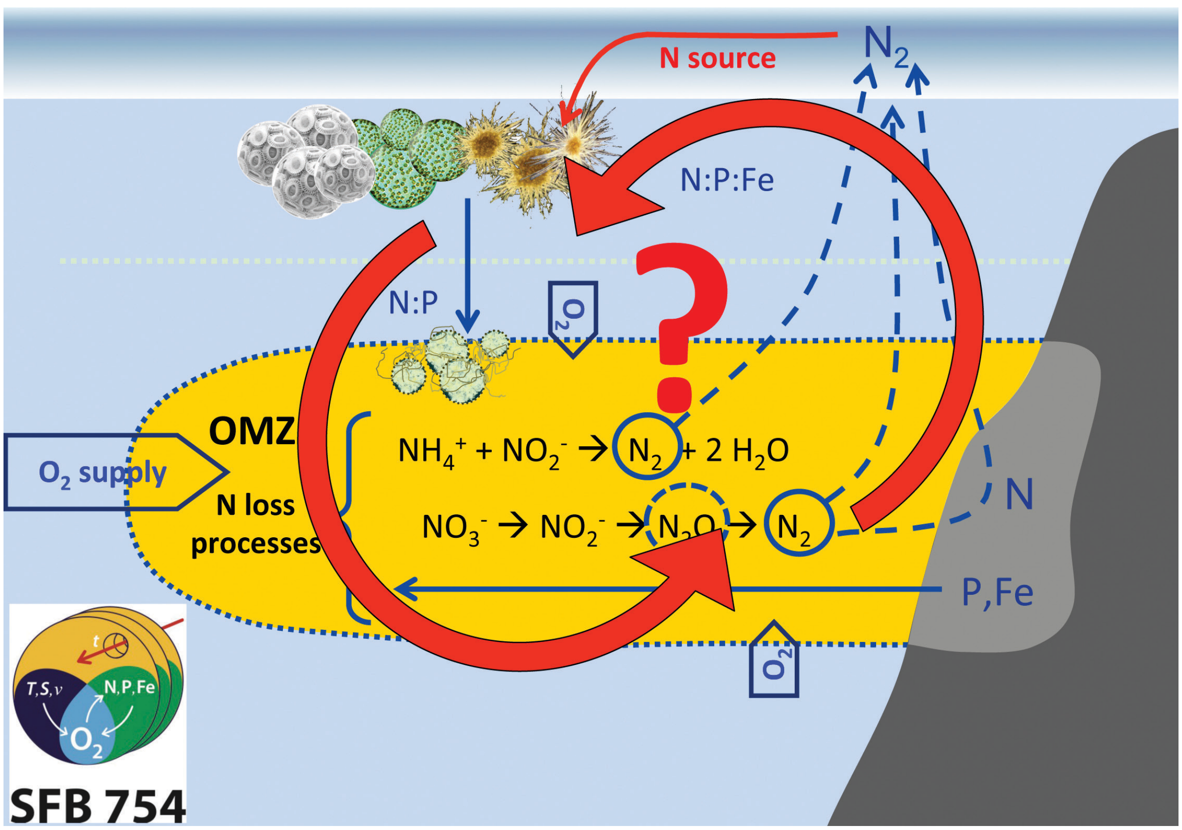
More than 100 scientists, most of them based at Kiel and from various disciplines, collaborate within the SFB 754. Networking and encouraging exchange of information among the PhD students and PIs is of critical importance for the success of the collaborative research centre. A data policy that ensures mutual access to all data among the participants while protecting intellectual property has been set up and helped to encourage active sharing of data and other information.

Recent scientific findings of SFB 754 include identification of a vicious cycle that, at least in numerical models, can link nitrogen loss processes and nitrogen fixation in a runaway nitrogen loss cycle (Landolfi et al., 2013). Newly identified but poorly understood transport processes in the equatorial oceans (Brandt et al., 2012) as well as turbulent mixing events associated with on-shore propagating internal waves have been found to be of prime importance for the supply of nutrients and oxygen. These processes could successfully be studied in comprehensive way thanks to the interdisciplinary team involved in the field and modeling work.



Scientific questions addressed by the Collaborative Research Center SFB754 www.sfb754.de, funded by the German National Research Foundation (DFG) center around the coupling of tropical climate variability and circulation with biogeochemical feedbacks in OMZs.

SESSION 4:

Final working groups

Chair: Jonathan Kaye, Gordon and Betty Moore Foundation, USA

Group 1 | Members: Elizabeth Dinsdale, David Karl, Raquel Vaquer-Sunyer, Francis Chan, Ellery Ingall, Alyse Hawley

For open-ocean low-oxygen and permanently/seasonally hypoxic systems, identify a pressing research question and design a lab / microcosm / mesocosm research plan

OVERARCHING QUESTIONS

- What are the oxygen thresholds for regulating microbial (including viruses) community, biogeochemical cycles, and upper trophic level dynamics? (For systems that don't reach zero dissolved oxygen, are the dynamics as we approach zero important?)
- How do these thresholds vary across systems? Are they modulated by system-specific physiological acclimation, community-shifts, adaptation, as well as interactions with other environmental factors such as warming and inorganic carbon system changes?

RESEARCH DIRECTIONS

- Comparative ecosystem studies (with mechanistic studies to assess dynamics of change).
- Particulate flux, respiration and maintenance of OMZs.
- *In situ* experiments to manipulate dissolved oxygen (and dissolved inorganic carbon).
- Ecosystem scale experiments, taking advantage of industrial artificial upwelling operations to test the controlling factors in the evolution of biogeochemical cycles and microbial communities.

Group 2 | Members: Alejandro Murillo, Klaus Jürgens, Annie Bourbonnais, Alexander Galán, Anil Pratihary, Steven Hallam, Alyse Hawley

For permanent and seasonally anoxic ecosystems, identify a pressing research question and design a lab / microcosm / mesocosm research plan

Overarching questions

- Ecosystem functions: What are the rates and underlying regulating factors for coupled biogeochemical processes and element cycles (N, C, S, trace metals) and what factors determine differences in microbial community metabolism in contrasting low oxygen ecosystems?

4

- Ecosystem service: How do microbial communities modify fluxes of elements and matter (export) from anoxic waters to surface communities and sediment communities and what are the ecological consequences of these transport or buffering processes (sulfide, P, trace metals, etc.)?
- Microbial community responses: How do microbial community interaction networks change as a function of water column gradients and external forcing (climate change, eutrophication, etc.)?

RESEARCH DIRECTIONS

- Focus on seasonal anoxia and upwelling events in four different ecosystems across four different time points.
- Conduct *in situ* process rate measurements in conjunction with molecular analyses (community structure and gene expression) using common sampling, screening and information standards.
- Conduct *in situ* mesocosm experiments using a matrix of organic matter, sulfide and oxygen perturbations to determine network rates.
- Long-term: construct human engineered experimental mesocosm system for joint laboratory experiments at one location.

Group 3 | Members: Niels Peter Revsbech, Bess Ward, Moritz Holtappels, Bo Thamdrup, Frank Stewart

Identify a technological or methodological need and develop an action plan to address it

Goal: Develop instrumentation for *in situ* experimentation under low-oxygen conditions

SAMPLING CAPABILITIES

- Coupled process rate measurements and sample collection for DNA/RNA/proteomics across multiple size fractions (for particle sampling). Will require in situ pumping and preservation.
- Water collection and preservation for microscopy (especially important for protists).
- Metal or glass bottles/chambers for *in situ* process rate measurements across multiple replicates. Chambers should be equipped with injection ports/syringes for tracer and substrate additions.

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- Sensing capability for high-sensitivity measurements of oxygen (optodes, STOX sensors), nutrients (ideally including nitrite), temp, pH, etc.

SYSTEM FEATURES

- System should be scalable to multiple volumes (milliliters to liters) and enable mixing of incubation volumes during experimentation.
- System should enable responsive sampling (i.e. detect oxygen change, collect an RNA sample).
- Equipped with imaging/video systems or *in situ* visualization of microscale environment, including particle flux (and potentially protists). Holographic cameras may be an option.

ACTION PLAN

- May involve a proposal to modify instrumentation or to build new system from scratch.
- Identify core working group.
- Develop/modify list of OMZ-specific modifications to instrumentation (see above).
- Approach users and designers of existing technology to inquire about routes/recommendations to modify/develop technology.
- Determine feasibility and technical requirements for prototype development and testing.
- Determine funding options (e.g. instrumentation grant, foundation funding).
- Submit proposal.

INSTRUMENTATION AND METHODOLOGY IMPROVEMENTS TO THE BROADER USER COMMUNITY

- Yo-Yo profilers to measure high frequency variation.
- Expanded instrumentation for assessing physical oceanography across OMZ boundaries (e.g. ADCPs).
- Pump cast systems for collecting water through oxygen-impermeable tubing.
- Non-plastic sampling bottles made of metal (or glass, ceramics, Kevlar bags).
- Identify "core" sampling objectives and protocols to facilitate cross-comparison. What should be the common measurement set?
- Develop a robust, fast-responding nitrite sensor.
- Minimize bottle effects during incubations (systematic exploration of the causes of bottle effects is needed).
- Improve techniques for sampling protists (desperately needed!). For example, how do we get good in situ grazing rates?
- Expand use of high-sensitivity oxygen sensors. Great options already exist but need to become more widely implementable.

Group 4 | Members: Jack Barth, Sean Crowe, Veronique Garçon, Johannes Karstensen, Andreas Oschlies, Oscar Pizarro, Nancy Rabalais, Osvaldo Ulloa, Sam Wilson

Design a field experiment or a global international field effort (location, methods, analysis, and approach to synthesis)

OVERARCHING QUESTION

- What are the factors controlling the evolution of microbial community structure and biogeochemistry within a mesoscale eddy?

RATIONALE

- An open-ocean experiment rather than a closed system experiment (e.g. Saanich Inlet) is proposed, as we do not think it is possible to extrapolate from closed systems that have defined seasonal cycles.
- Mesoscale eddies represent a natural environmental perturbation.
- Goal is to follow a mesoscale eddy as it is preferable to understand the eddy physics from a Lagrangian perspective rather than at a fixed position.
- Eddy formation is predictable (with some degree of certainty) off Mauritania in August, eddies reach Cape Verde in February, and then persist for 3–4 additional months.
- Compare Atlantic with Pacific eddies, which should have different characteristics and processes. The possibility of comparing selected/targeted measurements with closed systems (e.g. Saanich Inlet) was also suggested.

BACKGROUND AND GENERAL QUESTIONS

- Eddies have a diameter of ~130 km and a depth of ~400 m. 1 km vertical distribution should be considered.
- One issue is ship time if this project has an inherent waiting time or unpredictable nature associated with eddies.
- What are the potential controlling factors in the evolution of microbial community structure and biogeochemistry?
  - Primary productivity
  - Nitrogen fixation
  - Particle flux
  - Respiration (across the various trophic levels)
  - Physical forcings—atmospheric stresses (wind), sub-mesoscale processes (vertical diffusivity)
  - Initial microbial community structure—to what extent is eddy influenced by / influences microbial community structure from source area?
  - With many/most of these factors, there is a spatial aspect as well. i.e. the vertical distribution of primary productivity, or particle flux.

PROPOSED METHODS

- Overall 2–3 visits to the eddy are required, which can be focused on preliminary characterization, halfway through its lifetime, and then close to termination (for example).
- Initial detection of eddy using satellite-derived SLA.
- Glider/AUV required to characterize the type of eddy.
- Float with CTD, backscatter, NO_3^-, oxygen, pH (might not be required if AUV is available?).
- Need to characterize the conditions (metals, microbial community structure) of the eddy when it is just formed, but it should also be possible to use the general boundary environment to obtain this.
- Shipboard measurements to include:
  - Primary productivity
  - Nitrogen fixation
  - Particle flux (rotating trap to float with the eddy, and multiple depths during the cruises)
- Natural tracers, i.e. isotopic composition of NO_3^-, oxygen, N_2O.
- Tracer required to determine dilution of eddy—probably not a good idea to add a dye, so need to consider natural tracers.
- 'Omics, grazing (zooplankton), UV-P, low oxygen sensor, FCM, sulfate reduction, POM, PON.

FURTHER WORK NEEDED

- It should be possible to plan this project within 1–2 years. A meeting in Kiel in September has been proposed to move ahead with project planning. Team leaders identified include Johannes Karstensen, Jack Barth and Osvaldo Ulloa.

OTHER COMMENTS / QUESTIONS

- How many times would you have to repeat to consider if this is representative?
- Should we go to one place and everybody comes to sample collectively or build a kit around what you might measure and these kits could be deployed in different places by different teams—still needs to be decided.
- At least 3 visits close to initial source location are recommended, looking at transformation towards more anoxic conditions vs. towards more oxic conditions as the system recovers.

Group 5 | Members: Daniel Conley, Ricardo Letelier, Virginia Edgcomb, Julie LaRoche, Mak Saito, Jessika Füssel, Phyllis Lam, Wally Fulweiler, Edward DeLong

Articulate a question only addressable by comparing systems and prioritize the methods and approaches that need to be standardized to perform such a study

OVERARCHING QUESTION

- To predict the impact of changing OMZ volume and intensity on biogeochemical cycles, food web structure, economy and human health, we need to understand how community structure and function are organized across redox gradients.

PROPOSED APPROACH

- Develop a comparative study program across redox and geographic regions.

REQUIREMENTS

- Intercalibrate among different methods either in the lab or field so everyone has a benchmark while allowing methods to develop and move forward without restricting the community to particular methods.

CORE MEASUREMENTS TO BE STANDARDIZED

- Hydrography: T, S, oxygen (high sensitivity STOX), light, chlorophyll, turbidity, DIC, pH, alkalinity, nutrients, POM, DOM, stable isotopes, (CH_4, N_2O).
- Process: C transformation rates (C fixation, C oxidation), N transformation rates (N fixation, nitrification, denitrification, anammox).
- Microbial community: total cell counts, rRNA tag sequencing, targeted gene expression.

Summary and Recommendations

1 A mesoscale eddy project (similar to that described in Session 4, Working Group 4) will be moving ahead, led by Johannes Karstensen. Attendees discussed the possibility of a follow-up meeting to plan this project in September 2013 in Kiel. Anyone interested in participating in this project should contact Johannes at jkarstensen@geomar.de.

2 The need for standardization of methods and protocols to create comparable datasets across studies and regions was raised on multiple occasions by attendees at this symposium. A future workshop or group cruise for learning a standardized set of methods was proposed.

3 There is a strong desire to develop instrumentation that combines sampling and *in situ* experimentation capabilities. Some work is already being done to develop in situ incubation systems to reduce problems associated with oxygen contamination.

4 Several key topics requiring further study were raised repeatedly during the symposium:

- Rates and importance of nitrogen fixation within OMZs.
- Community structure and role of protists in OMZs, in addition to impact of protist grazing on microbial community structure and function in OMZs.
- Community structure of viruses in OMZs and impact of viral infection on microbial community structure and function in OMZs.

5 A proposal for a session on microbial biogeochemistry was submitted by Klaus Jürgens and Steven Hallam and accepted for the ASLO Ocean Sciences Meeting meeting in February 2014. Symposium attendees are encouraged to apply to this session (#111).

6 The possibility of compiling a journal special issue (for example, in *PLoS*) on microbial ecology and biogeochemistry of oxygen-deficient marine systems was discussed. In this special OMZ issue, each regional OMZ would be described independently and a series of synthesis papers could be developed that include protein clusters, comparative community ecology, systems ecology, and biogeochemistry. Steven Hallam has agreed to follow up on this possibility and contact symposium attendees if an appropriate opportunity arises.

7 A summer school for working in anoxic systems to train future generations of scientists was proposed. This program could be coupled with an existing summer school, or development as a separate program. Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) was proposed as an organization that could be solicited regarding an interest in sponsoring or being involved with such a training program. Alternatively, a summer workshop would be useful during which researchers would get together to standardize techniques and methodologies.

8 A group of workshop attendees agreed to compile and submit a Scientific Committee on Oceanic Research (SCOR) proposal for a working group on microbial ecology and biogeochemistry of oxygen-deficient marine systems. A SCOR proposal was submitted in May 2013, led by Sean Crowe and Steven Hallam, shortly after the OMZ workshop. This SCOR proposal will be reviewed in November 2013 at the SCOR Executive Committee Meeting in New Zealand. The summary and objectives for this working group can be found online at: http://www.scor-int.org/2013EC/Microbial_Communities.pdf.

9 A session on life and processes in redox gradients, co-chaired by Sean Crowe and Steven Hallam, was accepted for the colloquim "Low oxygen environments in marine, estuarine and fresh waters" at the University of Liège, Belgium from May 5–9, 2014. The summary and objectives for this working group can be found online at: http://modb.oce.ulg.ac.be/colloquium/. Symposium attendees are encouraged to apply to this session.

Participants

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Conley, Daniel	Lund University
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Denman, Kenneth	University of Victoria
Deutsch, Curtis	University of Washington
Devol, Allan	University of Washington
Dinsdale, Elizabeth	San Diego State University
Edgcomb, Virginia	Woods Hole Oceanographic Institution
Farías, Laura	Universidad de Concepción
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Karen is an assistant professor in the Department of Environmental Earth System Science at Stanford University. Her background is in marine biogeochemistry from Princeton University, where she worked with Professors Bess Ward and Daniel Sigman. Her research interests include using a combination of molecular and stable isotopic techniques to understand how nitrogen is cycled in marine oxygen-deficient zones, as well as the sources of marine nitrous oxide.

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Elizabeth Dinsdale is an assistant professor at San Diego State University and conducts research in ecological genomics, particularly addressing the role of microbes in coral reef and kelp forest health. She has developed a new course in ecological metagenomics which has revolutionized the training of undergraduates in microbial ecology. The course provides students with hands-on experience of next-generation DNA sequencing and analyzing the data. To date the students have sequenced 30 microbial genomes, 60 metagenomes, and the genome of the California Sea Lion.

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Steven Hallam is an associate professor in the Department of Microbiology and Immunology at UBC and Canada Research Chair in Environmental Genomics. He received his PhD from the University of California, Santa Cruz where he studied developmental regulation of neuronal asymmetry and synaptic remodeling in the model nematode Caenorhabditis elegans. Motivated by this experience in complex networks he became a postdoctoral researcher at the Monterey Bay Aquarium Research Institute and later Massachusetts Institute of Technology where he studied various aspects of marine microbiology and environmental genomics. His current research interests include microbial ecology, genetics and bioinformatics with specific emphasis on the creation of computational tools and combined workflows for taxonomic and functional binning, population genome assembly, and metabolic pathway reconstruction.

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Klaus studied Biology at the University of Konstanz, Germany. He completed his PhD in Limnology at the Max Planck Institute in Plön and at the University of Kiel, working on microbial food webs in planktonic systems. After a post-doc at the National Environmental Research Institute in Silkeborg, Denmark, he continued at the MPI in Plön, studying microbial predator–prey interactions. Since 2003 he is Professor for Biological Oceanography at the Leibniz Institute for Baltic Sea Research and at the University of Rostock. His group is conducting studies on microbial diversity and function in salinity and redox gradients.

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His thesis was on a quantification of the processes responsible for the ventilation of the Indian Ocean thermocline. As a postdoctoral researcher at the Lamont–Doherty Earth Observatory of Columbia University, USA, and in the Programa Regional de Oceanografía Física y Clima at the Universidad de Concepción, Chile, Johannes has been working on different aspects of ocean ventilation in the Nordic Sea and the eastern South Pacific, respectively. Johannes is currently employed as a Senior Scientist at the GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany. His main scientific interests include large scale ocean circulation, mixing and transformation of water masses and the physical control on biogeochemical cycling in the ocean.

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Gordon Taylor is a microbiological oceanographer specializing in microbial ecology and biogeochemistry of hypoxic/anoxic and other stratified ecosystems. Joining the faculty of Stony Brook University in 1990, he has been a full professor since 2005. Prior to this, he was associate research professor at the University of Hawaii, starting there as a postdoctoral associate under Dr. David M. Karl working in the VERTEX, ADIOS, Guaymas Basin, and RACER programs. He received his Ph.D. in Biological Sciences from the University of Southern California in 1983 under Dr. C.W. Sullivan's direction. He received his undergraduate training in Biology at SUNY Binghamton.

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Recommended Reading

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