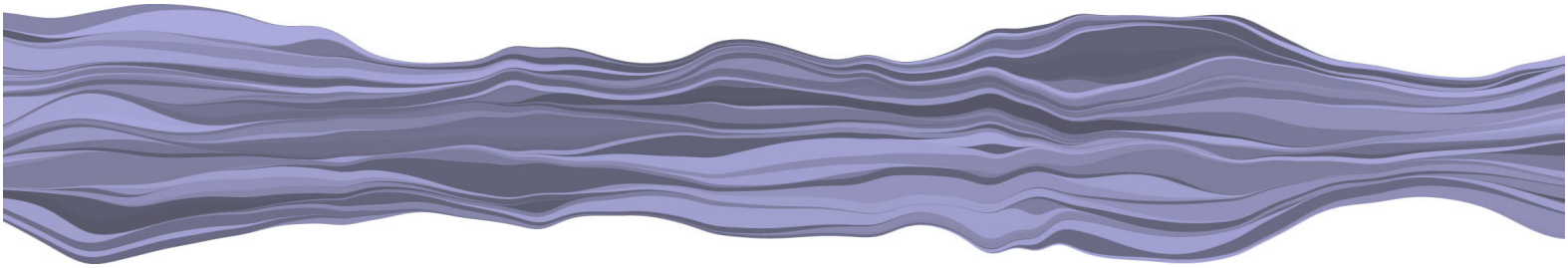
Report on the "Trait-based Approaches to Ocean Life" Scoping Workshop



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Waterville Valley, NH, USA

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Executive Summary

Marine ecosystems are rich and biodiverse, often populated by thousands of competing and interacting species with a vast range of behaviors, forms, and life histories. This great ecological complexity presents a formidable challenge to understanding how marine ecosystems are structured and controlled, but also how they respond to natural and anthropogenic changes. The *trait-based approach to ocean life* is emerging as a novel framework for understanding the complexity, structure, and dynamics of marine ecosystems, but also their broader significance. Rather than considering species individually, organisms are characterized by essential traits that capture key aspects of diversity. Trait distributions in the ocean emerge through evolution and natural selection, and are mediated by the environment, biological interactions, anthropogenic drivers, and organism behavior. Because trait variations within and across communities lead to variation in the rates of crucial ecosystem functions such as carbon export, this mechanistic approach sheds light on how variability in the environment, including climate change, impacts marine ecosystems, biogeochemical cycles, and associated feedbacks to climate and society.

89 scientists, including 18 students, 22 postdoctoral scholars, scientists, program managers, and foundation representatives, convened for the "Trait-based Approaches to Ocean Life" workshop in Waterville Valley, NH, USA on October 5-8, 2015. The participants covered many disciplines, including theoreticians, numerical modelers, experimentalists, satellite oceanographers, and microbial biologists, with many participants spanning multiple disciplines. Organisms from marine viruses, bacteria, plankton, jellyfish, and fish were represented. Invited speakers shared recent developments in trait-based science from terrestrial systems (Professor Hans Cornelissen, Vrije Universiteit Amsterdam), marine fisheries (Professor Simon Jennings, Centre for Environment, Fisheries and Aquaculture Science, and University of East Anglia), zooplankton (Professor Thomas Kiørboe, Technical University of Denmark), phytoplankton (Professor Elena Litchman, Michigan State University), and molecular ecology (Professor Sonya Dyhrman, Columbia University). Contributed talks and plenary discussions centered on coherent themes:

- *Measuring and detecting traits*
- *Biogeography of traits*
- *Linking observations and models*
- *Size as a master trait*
- *Role of physics on setting and linking traits*
- *Contributions to cross-cutting principles in marine ecosystems*
- *Contributions to climate science and biogeochemical cycles*
- *Contributions to policy*
- *From the gene to the ecosystem*

In addition to the plenary program (www.whoi.edu/workshop/traitworkshop2015/program) and linked poster sessions (www.whoi.edu/workshop/traitworkshop2015/posters), numerous small group discussions and informal "chalk talks" (informal lab-group style presentations) were held to maximize participant interaction.

The workshop showcased abundant examples of how the trait-based approach to ocean life provides a powerful, reductive framework for understanding the complexity and dynamics of marine ecosystems, and pinpointed areas for further development in the coming years. It also highlighted the inherent multi-disciplinary nature of the trait-based approach, encompassing species

groups from bacteria to fish, as well as diverse methodological approaches. The workshop encouraged the development of meaningful interactions between modelers/theorists and scientists making or aggregating fundamental trait observations. These new lines of communication between methodological perspectives have helped to facilitate the development of a common "trait" language.

The workshop highlighted the need for robust investment in making and aggregating individual lab-, field-, or satellite measured trait observations. Such meta-analyses provide a powerful tool to unveil relationships between traits and their environment. Trait-based models and theory readily incorporate this meta-analytical perspective to develop global representations of species biogeography and formulate testable hypotheses that link traits to ecosystem structure, function, and fundamental controlling mechanisms. Improved cyber infrastructure (e.g., data and model repositories) and a culture of data sharing, curation, and stewardship will produce more effective linkages throughout the field and across methodological perspectives.

The need for a forum for a growing number of researchers working on trait-based approaches was obvious from the very successful 1st International Workshop on "Trait-based Approaches to Ocean Life" held in Copenhagen in August 2013, organized by Thomas Kiørboe (Technical University of Denmark) and committee. This 2nd workshop provided a venue to continue the discussions and development of a strong research community. Numerous requests from participants to continue the momentum have led to plans for a 3rd workshop to be held in Bergen Norway in 2017. Øyvind Fiksen (University of Bergen) has volunteered to be the lead organizer.

In addition to building a strong interdisciplinary network for scientists studying trait-based approaches to ocean life, numerous tangible workshop outcomes are forthcoming. Firstly, this workshop summary report, with recommendations for future directions, will be shared with OCB and the broader scientific community. Secondly, the workshop served as an incubator for several review and synthesis papers, for example a review of the roles of ocean circulation on setting trait distributions, a synthesis of marine ecosystem model techniques, and a perspective on trait-based modeling of viruses. Lastly, several new data and model stewardship efforts were proposed, including a global plankton trait database (to be linked to Encyclopedia of Life and World Register of Marine Species) and trait-based model repository and inter-comparison project.

The organizers thank the Ocean Carbon and Biogeochemistry (OCB) Program (with funding from the National Science Foundation and National Aeronautics and Space Administration), the Simons Foundation, and the Gordon and Betty Moore Foundation for their support and encouragement.

Introduction

Scientific Rationale

Marine ecosystems perform central roles in global biogeochemical cycles and the climate system by facilitating the transport, trophic transfer, and transformation of carbon and other key elements in the ocean. Their structure—including their diversity, relative abundance of species, and rates of biological interactions—controls, to a large extent, the quantity and quality of biological carbon export from the ocean surface. Despite their importance to biogeochemical cycles, understanding of the fundamental processes structuring marine ecosystems remains limited. To date, we do not have a complete understanding of how environmental change affects marine ecosystems, and how this change imprints on their biogeochemical roles. This uncertainty is particularly acute when we consider anthropogenic climate change; not only will environmental conditions change markedly, with the potential to reassemble and move marine ecosystems, but organisms themselves may adapt in response to changing conditions.

The trait-based approach to ocean life has great and, as yet, unrealized potential in reducing the uncertainties in understanding the regulation of ecosystem structure and their susceptibility to change. A trait is any quantitative organism characteristic that affects growth, reproduction or survival, and includes, for example, resource acquisition and growth rates in microbes, but also development time and generation length in multicellular organisms such as zooplankton and fish. A trait is usually measured at the individual level and can be used to compare across species (McGill et al. 2006). The fitness of different organisms along environmental or biological gradients is tied mechanistically to their functional traits. Whereas historically ecologists and biogeochemical modelers typically considered the population dynamics and biogeochemical signatures of species or groups of species (for example plankton functional type modeling), in the trait-based approach diversity is resolved by variations among key traits. Thus, important diversity within and between species is resolved or interpreted in a relatively simple, mechanistic manner. Interactions between marine organisms, including predation and resulting flows of carbon and energy, may be similarly represented and understood through interaction of traits, such as prey size preference or prey ingestion rate.

Trait distributions in the ocean emerge through competition, natural selection, and evolution, and are mediated by the environment, biological interactions, and organism behavior. Because trait variations within and across communities lead to variation in the rates of crucial ecosystem functions, such as carbon export and nitrogen fixation or productivity of higher trophic levels, this mechanistic approach sheds light on how variability in the environment, including climate change, impacts communities of ocean life and marine biogeochemical cycles. The trait-based approach to ocean life is a powerful and reductive ecological framework for understanding the complexity, structure, and dynamics of marine ecosystems and the ecological basis of ecosystem functions.

An essential aspect of the trait-based approach to ocean life is abundant and accurate data on organism traits. In terrestrial plant ecology, researchers have long recognized the necessity of accumulating, curating, and sharing trait data from a wide range of traits, locations, and taxa (Kattge et al. 2011). However, our ability to observe traits in open water marine systems, especially on a global scale, is limited. For the plankton, traditional tools such as lab cultures, microscopy, HPLC, and flow cytometers can provide important details on plankton traits, but are conducted under controlled and perhaps unrealistic lab conditions or, in the case of field measurements, only over limited regions covered by shipboard and other sampling programs.

Genome and transcriptome data offer promising avenues to identify and examine *in situ* physiological traits on large numbers of samples. Satellite ocean color data offer a unique opportunity to observe large-scale patterns of traits in the surface ocean, particularly at the phytoplankton level (see IOCCG report 15, 2014). For metazoans, trait measurements often rely on collection and enumeration of organisms, but there are promising new acoustic, optical, and imaging technologies that could facilitate the rapid collection of trait data.

Trait-based perspectives have in recent decades spurred significant advances in terrestrial plant ecology (Westoby & Wright 2006; Kattge et al. 2011), but are less advanced in marine ecology (Litchman & Klausmeier 2008). However, trait-based approaches are rapidly developing in the marine realm through extensive modeling (Follows et al. 2007; Ward et al. 2012) and empirical efforts (Thomas et al. 2012; Barton et al. 2013). Building a research community with the tools to understand how functional traits can scale upwards to global biogeochemical cycles and climate will require significant and ongoing support and organizational effort. Building this research community, determining the most important questions, and providing a forum to develop a vocabulary were the rationale for this workshop.

Workshop Goals and Format

This 2nd international "Trait-based Approaches to Ocean Life" workshop was held October 5-8, 2015 at the Waterville Valley Resort in Waterville Valley, NH USA. The goals of this workshop were to:

1) Synthesize the state of the trait-based approach to ocean life by sharing noteworthy research successes and identifying key knowledge gaps

2) Advance the science by forging new collaborations and solidifying a nucleus of researchers working on trait-based approaches to ocean life.

This highly interdisciplinary international workshop brought together 89 participants (Appendix III), including biologists, ecologists, chemists, mathematicians, and physicists working on different aspects of trait-based descriptions of life in the oceans across all trophic levels and scales, from viruses to top predators and from fine-scale turbulence to global-scale processes. Five talks by invited speakers covered recent developments in trait-based approaches from terrestrial systems, marine fisheries, zooplankton, phytoplankton, and molecular ecology. The meeting included formal plenary presentations to set the stage for more interactive activities such as moderated panel discussions done in plenary and smaller group discussions. Additional interactive formats such as poster sessions and "chalk talks" facilitated exchange of ideas, vetting of new and unpublished research, and potential new collaborations. The meeting agenda is included in Appendix I, and the list of posters is included in Appendix II. Most presentations listed below are hyperlinked to the workshop website: www.whoi.edu/workshop/traitworkshop2015/program. Posters are available at: www.whoi.edu/workshop/traitworkshop2015/posters.

Day 1. Getting a Handle on Traits

Trait-based perspectives have been in use longer and more widely in terrestrial ecology than in marine systems, but marine scientists are rapidly adopting this approach. The workshop program began with an invited presentation by Hans Cornelissen bringing insight from the plant trait-based community. His invitation and presentation reflects the increasing flow of information between

marine and terrestrial ecologists, and was titled: *Plant traits and biochemical cycling on land: parallels with marine ecosystems?*

Session 1: Measuring and Detecting Traits

This session focused on novel methodologies for measuring traits in the field, including morphological (size) and physiological (growth, nutrient uptake) traits, as well as the ecological implications of these traits. The link between phylogeny and traits was also discussed. Plenary presentations were given by:

Heidi Sosik: *Plankton traits from flow cytometry and imaging-in-flow cytometry*
Adam Martiny: *Microbiomes in light of traits: a phylogenetic perspective*
Harriet Alexander: *Functional group specific traits drive ecosystem state shift in the oligotrophic ocean*

Session 2: Biogeography of Traits

This session focused on the distribution of traits in space and time in the ocean, and the underlying ecological and physical processes that lead to these patterns. Speakers in this session discussed organisms ranging from viruses to mesozooplankton, and included both observational and modeling perspectives. Plenary presentations were given by:

David Talmy: *The influence of viral reproduction strategies on marine microbial community dynamics*
Tim Moore /Colleen Mouw: *Approaches for detecting phytoplankton composition from space-based sensors*
Fi Prowe: *Effects of trade-off based zooplankton feeding in a global ocean ecosystem model*

Session 3: Linking Observations and Models

This session consisted of a plenary discussion (led by Anna Hickman) that focused on how well observations and models interface in modern trait-based science. Despite notable successes, such as meta-analyses of plankton growth and uptake rates that are routinely built into trait-based models, additional progress could be made by improved dialogue between empirical- and model-focused researchers. This discussion was stimulated by the question:
How well do models include observations, and what needs to be done better?

Discussion Summary:

- Participants agreed that as a community we could make a better distinction in what we mean by 'model'. A model can be a simulation, a theoretical framework (e.g., Margalef's Mandala), or even an algorithm.
- There needs to be more communication between empirical scientists and modelers from the beginning: share ideas, find questions of mutual interest, and write proposals together.
- Models and observations should be used in an iterative way, with dynamic back and forth, rather than one after another.
- One important concern that participants raised was that in a competitive funding environment, it is difficult to obtain funding for the less novel but nonetheless important long-term measurements needed to support modeling work.

Day 2. Frontiers of Trait-Based Ecology in the Ocean

Session 4: Size as a Master Trait

Organism size is often considered to be a "master trait" because of its importance to many vital rates (e.g., growth, metabolism), predator-prey interactions, life-history strategies, and behaviors. Speakers in this session explored how body size shapes ecological dynamics in the ocean, as well as the biogeochemical ramifications of body size. Invited and plenary presentations were given by:

Elena Litchman, **invited**: *Trait-based approaches to microbial ecology and evolution*
Karen Stamieszkin: *Changes in North Atlantic copepod community size structure and fecal pellet carbon flux over 55 years*
Subhendu Chakraborty: *Correlation between organism size and trophic strategies*
Kathy Mills: *Using size structure and metabolic theory to forecast fish community characteristics in a changing climate*

After these presentations, Ken H. Andersen led a plenary discussion based on the question:
What can and cannot be described by body size?

Discussion Summary:

- "Size as a nuisance". In many cases we now know the main scaling rules with size for many rates, processes, and parameters (e.g., metabolism and photosynthetic rate). The field is therefore moving towards examining the causes of variation around the size-scaling rule. In this case the size scaling has to be subtracted from the data, and it can therefore be referred to as a "nuisance" that has to be dealt with before the interesting work can begin. This is a positive development that highlights the maturity of the research area.
- Size can refer to many things and it is important to distinguish what is meant, whether "size" refers to body mass, body volume, or body surface.
- Size may be determined by one metric (e.g., equivalent spherical diameter) for one process (e.g., nutrient uptake), while another metric (e.g., length) maybe a more appropriate for another process (e.g., potential for predation). See, for instance, talk by Heidi Sosik.
- When is size not very useful? Simple relationships with size often fail to emerge when a small variation in body size is considered. In such cases the variation around the size relation will be larger than the size relation itself. Sometimes specific species break size-scaling rules. An example given was the prices of landed fish — some small species take home high prices (e.g., shrimp).

Session 5: Role of Physics in Setting and Linking Traits

This session explored the significant role of the physical environment in setting the distribution of traits in the ocean, community structure, and biodiversity. Physical processes not only impact the light, temperature, and resource conditions experienced by marine organisms, but also mediate dispersal, nutrient acquisition rates, predator-prey encounter rates, and reproduction. Invited and plenary presentations were given by:

Thomas Kiørboe, **invited**: *How traits are interrelated through tradeoffs in zooplankton*
Lan Smith: *Trait-based modeling of phytoplankton under realistic sub-scale variability*
Marina Levy: *The dynamical landscape of marine phytoplankton diversity*

Bror Jonsson: *The effect of advection on temperature adaptation by phytoplankton communities in the global ocean*

After these presentations a plenary discussion (led by Stephanie Dutkiewicz) considered the following questions:
What spatial and temporal scales are important for setting traits? How do these scales relate to organisms?

Discussion Summary:

- A recurring theme from the talks and discussions was that: "Things in the ocean move a lot!"
- There are many different scales on which physics can affect organisms:
    - Large-scale circulation (important in issues of connectivity of populations).
    - Meso- and sub-mesoscale (including eddies, filaments) controlling community structure (e.g., talk by Marina Levy), not just productivity.
    - Small-scale turbulence, especially important at the scale of the organism (see invited talk and shared movies by Thomas Kiørboe).
    - Organisms can make their own "physics" by jumping, feeding currents etc. (see invited talk and shared movies by Thomas Kiørboe).
- We tried to summarize the two questions in a "Stommel-like" diagram to link traits in a space/time plane. This would be difficult across all organisms, though might work better for certain sized organisms. A better axis than "time" might be "number of generations"; in which case things like selection, migration, and sexual reproduction could be put onto the axes. The "space" axis could then also be translated to "body length." All diagrams drawn in the session had linear aspect (going from small size/short time to large size/large time). This brought up the compelling question of whether this is necessarily true of all traits.

Day 3. Broader Contributions of Trait-based Approach

Session 6: Contributions to Cross-Cutting Principles in Marine Ecosystems

This session focused on combining trait-based perspectives to make inferences about marine communities and whole ecosystems, building upon research covered in previous sessions. Invited and plenary talks were given by:

Simon Jennings, **invited**: *Size- and trait-based structures and processes in marine ecosystems*
Stephanie Dutkiewicz: *Combining phytoplankton size and functional traits in a global ocean ecosystem model*
Jorn Bruggeman: *Traits of benthic fauna: from observations to community models*
Susanne Menden-Deuer: *The role of intra-specific trait variability in plankton biodiversity: a gametheoretic and model examination*
Selina Våge: *Combining internal and external pelagic prokaryote community control links biodiversity to ecosystem function*

A plenary discussion, facilitated by Øyvind Fiksen, focused on the questions:
What is the usefulness of taking a trait-based approach? What are the strengths and weaknesses? Which directions should we take in the future?

Discussion Summary:

- A trait-based approach has an important integrative aspect. The marine sciences have a long but detached history in which oceanography, fisheries science, and marine biology have developed at separate institutions, meetings, and sessions, often with little interaction and collaboration.
- A trait-based approach is facilitating a common language in understanding the broader picture of the trade-offs faced by organisms and the evolved solutions and ramifications of these.
- A trait-based approach simplifies the vast diversity among species, and provides a tool to organize models and data while not focusing on species.
- The aim of models need not be to fit a particular dataset, but can also be a tool to explore uncertainty in parameter space or model formulations and identify which areas of research are most needed. Uncertainty within models needs to be explicitly addressed.
- Many at the meeting were interested in behavioral traits and processes, and these are often key traits in zooplankton and fish. The attention is now directed to foraging modes, as a parallel to the focus on nutrient uptake in phytoplankton, but there are a range of other behavioral traits that may also have a bearing on the structure of marine food webs. For instance, diet selection in zooplankton can be important to the size-structure in phytoplankton and consequently the productivity of oceans.

Session 7: Contributions to Climate Science and Biogeochemical Cycles

This session consisted of a plenary discussion (moderated by Stephanie Dutkiewicz) focused on how trait-based perspectives have influenced research on biogeochemical cycles and their feedbacks with climate. To date, trait-based approaches have been influential in marine ecology but less so on biogeochemical cycles. However, the potential is large, and there have been some notable successes, for example in understanding the ecology of marine nitrogen fixers and mixotrophs. The discussion focused on the following questions:

What are the most important traits for biogeochemistry and climate studies? Are there biogeochemically important traits that we have not yet included in trait-based approaches?

Discussion Summary:

- When it comes to understanding drivers of biogenic fluxes, we can use traits to characterize the food webs that coincide with export events. Singular traits may not offer as much as the ensemble of traits that describe entire biological communities. Further, the coincidence and covariance of particular traits within a community may likely reveal more about the functioning of a food web and its impact on biogeochemical cycles.
- Specifically, traits important for biogenic fluxes include: Size (see poster by Colleen Mouw and talk by Karen Stamieszkin), density, calcification/silicification, biological controls on sinking/floating (e.g., salps), the ratio of what is taken up to what is excreted (e.g., food quality), and those that control uptake of labile DOC and production of refractory DOC.
- From the biogeochemical point of view, it is useful to separate into community level traits (i.e., not single species), traits that encompass feedbacks (e.g., metabolism and connection to temperature), "after life" or effect traits (see Hans Cornelissen invited talk).

- Can we use trait-based methods to put the biology back into biogeochemistry? Discussion noted that there were examples of this in the presentations (e.g., poster by Emily Zakem and talk by Victoria Coles). It was also suggested that established paradigms linking traits (e.g., size) to export and transfer efficiency do not appear correct when considering shifts in composition over the annual cycle.

Session 8: Contributions to Policy

This discussion session (facilitated by Nick Record and Andrew Pershing) focused on what trait-based approaches to ocean life have to offer the management of marine resources. Though to date, trait-based approaches have not been widely applied in this way, the perspective provides an appealing lens for simplifying the dynamics and management of complex communities, ecosystems, and marine resources. The discussion was based on the question:
How can the trait-based approach to ocean science inform policy and/or management?

Discussion Summary:

- Fisheries science is increasingly recognizing the important role of fish size in the policy and management decision-making processes.
- A trait-based approach provides a lens for simplifying the management of complex communities of fish.
- Traits can help to organize and measure the value (ecologically and economically) of different managed species.
- The trait-based contribution to understanding global biogeochemical cycles has a role in climate policy.
- There is a need for improved dialogue between scientific communities and public/policy communities. A tight-knit and small but globally networked group like the one represented at this workshop could be well positioned to engage in dialogues with outside groups.

Day 4. New Directions for Trait-Based Ocean Science

Session 9: From the Gene to the Ecosystem

This session focused on novel research linking genes to organism traits that shape population and community dynamics. The genetic basis of traits, the maintenance of a diversity of traits within a species, and the ecological implications of this diversity were also discussed. Invited and plenary presentations were given by:

Sonya Dyhrman**, invited:** *Linking 'omic approaches to a trait-based view of ocean life: using transcripts to define microbial traits*
Frederic Maps: Blurred lines between species in trait-based numerical approaches. A case study of *Calanus* hybrid
Elizabeth Harvey: Linking individual movement to population-level dynamics: strain-specific behaviors of *Heterosigma akashiwo*
Victoria Coles: *Emergent patterns of genes, transcripts and community structure in the GENOME model*

A plenary discussion (moderated by Nick Record and Bethany Jenkins) addressed the question: ***What are the big questions and unknowns at different scales between "gene" and "global system"?***

Discussion Summary:

- GENES: We still need to understand mechanisms, rates, and how to extrapolate to ecosystems. What are the key traits and tradeoffs? How do we scale variability that is occurring over space and time? Phenotype is important.
- TRAIT: A key challenge is identifying tradeoffs that correspond to traits. Tradeoffs are often assumed in models without hard evidence to support them. Traits are better defined but it is often hard to clearly delineate between traits considered and those that are not. Defining variability around a given trait or multiple traits is important and challenging. Genetic level data are easier to integrate with microbial traits but much more challenging for larger eukaryotes where it may be easier to connect phenotypes with traits. New studies are looking at how genes describe traits (for example, genes or expressed genes) that correlate with spawning time in the same species of fish. There are efforts to map traits onto genes in other fields; we should look to these for guidance.
- POPULATION: How do we link from the liter/meter scale to the kilometer scale?
- COMMUNITY: What information do we need to predict the structure of the community? How to link community to global ecosystem and other levels of organization? What are the functions of the community? What is the biogeography of community structure?
- ECOSYSTEM: How to do the actual scaling up from level to level via trait aggregation across organisms to understand and predict community outcomes and biogeochemical cycling from gene or cell to ocean, at multiple locations? At each scaling step the essential aspects of the lower scale have to be summarized for such aggregation, which involves decisions about which details at lower scale are important enough to feed the one above. To do this, trait trade-offs need to be defined to delimit the potential multi-trait space occupied. We need to know how feeding-related traits determine trophic structure and food webs in oceanic ecosystems.
- GLOBE: How can we use trait-based approaches at global scales to understand the response of biogeography and biogeochemistry to climate variability and change? Meta-analyses and emphasis on observational, experimental and model uncertainty. How can we span spatial and temporal scales in models and observations?

Figure 1. *"From genes to global system". Workshop participants arranged by the scale at which their work fit on the spectrum, from gene to global ecosystem.*

Session 10: Summary and Wrap-Up

The focus question for the final plenary discussion (led by Andrew Barton) was:
What have we done well at this workshop, and what might we improve upon next time?

Discussion Summary:

- Participants were positive overall about the workshop experience and there is considerable interest in a follow-on meeting in 2 years. Øyvind Fiksen has offered to chair the next meeting and it will very likely be based in Bergen, Norway with the possibility of support from the Hjort Centre (http://www.hjortcentre.no/en/projects/hjort-centre). Please contact Øyvind to participate.
- For future workshops, there is a general consensus to not exceed ~90-100 people, and to have a good balance between talks and discussion. The small group discussions and informal chalk talks in particular were popular, and should perhaps occupy more space in the next workshop. The footprint of plenary discussions/talks could perhaps be reduced to accommodate these smaller group functions.
- Participants found value in the exchange with other fields (e.g., terrestrial ecology) and would like to see this continued or expanded. Other fields with relevance to the workshop, some of which may have been underrepresented in the 2015 meeting, include freshwater plankton ecology, fisheries ecology, soil ecology, terrestrial ecology, astrobiology, and paleoceanography.

Small Group Discussions

When applying for the workshop, participants were given the opportunity to propose small group discussion topics, all of which were included in the program. The small group discussions were approximately one hour long and led by the attendee who proposed the idea, sometimes in collaboration with another person. During the workshop, participants chose which discussion groups to attend. Initial feedback from the workshop attendees suggested that this flexible format was quite popular. Below, we provide a brief overview of these discussions.

1. Phytoplankton Size: Challenges in Observation and Interpretation

Overview: This group discussed advantages and disadvantages of existing methods and approaches for characterizing cell size in the context of driving research questions. Participants were asked to consider how results from different methods could best be combined to meet the full range of needs and to highlight outstanding methodological challenges and promising areas for future development. This discussion was led by Heidi Sosik and Kristen Hunter-Cevera.

Discussion Summary: The research community needs both: a) highly detailed observations of cell shape and size, such as might be possible with emerging holographic imaging techniques or confocal microscopy, and b) "cheap, easy, and robust" tools that could provide capability for *in situ* observations of cell size distributions, ideally with an approach that separates phytoplankton from other particles that and can span the full range of phytoplankton sizes. These will require different investments and provide complementary information. The former will be important for

construction of taxon-specific libraries of shape metrics and the latter will enable widespread and consistent data at relevant space and time scales that can be useful for informing resource managers and scientists about episodic events (e.g., harmful algal blooms) or major shifts in community composition in various marine ecosystems.

Yet no single size metric can meet all research needs identified. Equivalent spherical diameter may be adequate in some cases, while surface area (or surface area-to-volume ratio) may be better for other problems. There is a need to explore new metrics that might be better at reflected processes directly influenced by flow fields and concentration gradients (e.g., nutrient uptake). This could be accomplished by adopting approaches established in other disciplines to compute "process-faithful" representative length scales by appropriate transformation (i.e., Laplacian for case of flow-related processes). There is a need to consider size metrics, at the level of both individual cells (e.g., for resource acquisition) and whole chains or colonies (e.g., for predator avoidance, buoyancy, and settling). A focused effort to compare and evaluate various size metrics across taxa and to consider their relevance for processes of interest might be very valuable. This could be accomplished by a small group of interested experts collaborating to produce coordinated analyses and a synthesis report or publication.

2. Key Traits and Trade-Offs Defining a Mixotrophic Lifestyle

Overview: Mixotrophic protists combine the ability to photosynthesize and to ingest food particles, and hence can be described by traits traditionally ascribed to phytoplankton and zooplankton separately. The goal of this discussion group was to define a key set of traits required to describe a mixotrophic lifestyle, identify potential trade-offs among them, and outline ideas to empirically test for such trade-offs. This discussion was led by Susanne Wilken.

Discussion Summary: Mixotrophs combine key traits usually ascribed separately to phytoplankton and zooplankton. Trade-offs exist between different routes of resource acquisition (light harvesting, carbon fixation, nutrient uptake, feeding). Given the ubiquity of mixotrophy the topic could be faced from the opposite direction, asking what benefits come along with specialization. There is a potential trade-off between the ability to ingest prey and using armor as a defense against grazers. Toxicity, on the other hand, can serve both as grazer deterrent and help during prey capture. For experimental characterization of nutritional trade-offs, species pairs comparable in size and prey spectrum need to be used.

3. Does the Ocean Behave Like Your Beaker? Linking Experimental and Natural Evolution

Overview: Evolutionary experiments are uncovering fascinating insights into how marine organisms may respond to global change stressors. But how well do these (typically lab-based) experiments reflect evolution as it occurs in nature, and how can they inform modeling and prediction efforts? This discussion brought together empiricists and theoreticians/modelers to address these issues and was led by Colin Kremer and Mridul Thomas.

Discussion Summary: We discussed disconnects between laboratory evolution experiments, evolution as it occurs in natural environments, and how evolution is incorporated in models. Experiments use small populations, and species responses arise from multiple overlapping mechanisms. This makes it difficult to estimate useful rates/modes of evolution from experimental results. We discussed ways of designing better experiments, using models and sensitivity analyses

to figure out which things are most important, tightening empirical-theoretical links, and coordinating and funding future experimental efforts.

Modelers need to know: a) how do traits change in response to evolution, and what tradeoffs constrain evolutionary responses? And b) how quickly can these changes occur? Evolutionary experiments are better at informing a) than b). We discussed the tension between population and quantitative genetics approaches to understanding evolution.

There are many problems with the current generation of experiments. Population sizes in beakers are vastly smaller than natural populations, which may realistically be able to access the majority of possible mutation space quite easily. It's difficult or impossible to estimate useful rates of adaptation for multi-dimensional or function valued traits. Responses to experimental treatments will occur through physiological acclimation, clonal selection, and new mutations (modifying regulatory networks, or adding new functions), all of which may occur on overlapping time scales, making it hard to disentangle separate forces. The largest increases in fitness happen early in experiments; maybe we should be measuring these rates of increase, and how quickly they saturate (using shorter experiments), rather than running experiments for 100's of generations.

With these limitations in mind, the group suggested ideas for new kinds of experiments. Closer collaborations between modelers and experimentalists are vital: models can be used to conduct sensitivity analyses, feeling out which responses or unknowns have the largest effects, then experiments can drill down into these areas, obtaining more useful, targeted results. Experiments could be used to at least place constraints on how *unlikely* a taxon is to adapt to a change. Having even a loose bound could be useful to modelers. The group discussed applying for a Research Coordination Network grant to bring together modelers and experimentalists interested in evolution and climate change.

4. A Community Repository for Trait-Based Model Code

Overview: To facilitate the sharing and development of model code, it could be beneficial to have an organized open code repository for trait-based models. This group discussed whether such a resource would be valuable to the research community, and if so, how it should be structured, maintained, and distributed. The leader of this discussion was Nick Record.

Discussion Summary: A model code repository would have a number of possible benefits: avoid many people recoding the same model many times; possible NSF funding (for cyber infrastructure); transparency; reproducibility; citability; coordination with global models; understanding the "taxonomy" of models; and journals are now starting to require code. The obvious drawbacks are that considerable work would be required on the part of the modeler, and the user community may not materialize or exist. The repository could include: walk-through tutorial examples; pseudocode; code; metadata (keyword searching, authors, contact - links to DOI); and standardized format. There are a number of questions that warrant additional consideration, namely: do we include all models (for example, simple 0D "toy" models as well as global ecosystem models)? Do we limit to oceans? Do we build something new or join something existing? In the coming months, participants will evaluate similar code repositories (e.g., GEOSOFT) and discuss links with NSF Earth Cube, NASA, and other organizations.

5. Trait Coverage For All Marine Taxa: Are There No Shortcuts?

Overview: Trait data availability for marine taxa is vanishingly thin over most species. Can we help fill in trait data gaps using edgy and scalable methods like text mining, crowdsourcing, and taxonomic extrapolation? This discussion was led by Jen Hammock.

Discussion Summary: There is a need to gather more trait data on marine organisms, but where should it come from? There is already a lot of untapped data in the published literature. These data take many forms. For example, the data might be a measurement with context metadata. More often, the data appear as a function, table or plot of trait values against one or more other variables (environmental parameters and/or other traits). Given the range of formats, how would it be possible to aggregate? One answer is to use crowdsourcing methods. We go out looking for this data for our own analyses anyway, and we generally copy from tables and/or pluck points from graphs. Instead, a wiki style interface could be developed to enter trait values, metadata, and DOI of the source, which would provide a citation to the data originator, where applicable, and would allow us to save the extracted data for future searchers. It is possible that such an interface could be set up on the Encyclopedia Of Life (ww.eol.org) and there was general support for this effort, subject to the ease of use and generation of citations for data originators.

6. Traits and Phylogeny

Overview: Recent studies reveal that microbial traits are differentially conserved across the tree-of-life and appear to be distributed in a hierarchical fashion, possibly linked to trait biochemical complexity. Developments in such a framework may offer predictions not only for how microbial composition responds to changing environmental conditions, but also for how these changes alter nutrient and energy cycling in marine systems. Participants of this group discussed a) if such a framework is useful to describe the distribution of key traits (e.g., light optimum, temperature optimum, nutrient uptake) across marine organisms and b) under what circumstances a phylogenetic framework would be useful - or not. This session was led by Adam Martiny and Jorn Bruggeman.

Discussion Summary: The session started out with a brief summary of the main points from Adam Martiny's workshop presentation linking phylogeny and traits. We clarified a few concepts including the distinction between discrete (i.e., presence vs. absence) and continuous (i.e., quantitative values) traits. Following the introductory comments, we provided a list of key traits currently used in ocean biogeochemical models and asked the participants to rank the traits in terms of expected phylogenetic conservatism. The traits included light, pH, and temperature optimum, cell size, nutrient uptake affinity, ability to fix nitrogen, and cell quota. The ranking led to a very interesting discussion about how to rank continuous traits. The conclusion was that small changes in trait values could probably be achieved by minor differences in genes and the biochemistry underlying the functioning. In contrast, a large change in trait values would require a substantial rearrangement of the underlying biochemistry and thus would likely be associated with deep clades. Thus, one of our major points in the session was you need to understand the link between traits and the underlying genetics and biochemistry in order to predict phylogenetic conservatism of a trait. Also, the link between phylogenetic conservatism of a trait and the trait value is not continuous but there are certain break points when major biochemical rearrangements are required.

In the second part of the discussion, Jorn Bruggeman illustrated the use of phylogenetic models and techniques to understand variations in trait values and predict values for uncharacterized lineages. In response to questions, it was emphasized that despite the simplicity of the assumptions that underlie most evolutionary models (e.g., Brownian motion), such methods can be considered the simplest possible approach that captures both relationships between traits (e.g., trade-offs and allometric scaling) and random jumps between clades ("evolutionary innovations"). In essence, it is a form of phylogeny-aware regression. When used for trait value inferences, the evolutionary models are recombined with all observed trait values to produce optimal estimates for missing values. As suggested by a participant, this is similar to data assimilation methods used for state estimation and, as such, has been shown to improve inferences, even if some assumptions of the evolutionary model are not met.

7. What are the Large-Scale Ecological Ramifications of Physiological and Behavioral Diversity at the Scale of Individual Organisms?

Overview: There is considerable species-specific variability in physiology, behavior, resource acquisition strategies and modes of cell interactions, all of which can be modulated by abiotic conditions. How can this variability at the small scale be adequately summarized to understand and predict emergent larger scale processes? This discussion was led by Susanne Menden-Deuer.

Discussion Summary: This discussion posed a number of key and open questions. Does it matter to global biogeochemistry that *Prochlorococcus* has many coexisting strains? Is food web structure and nutrient cycling in the oligotrophic ocean affected by the fact that there are dozens of strains of *Prochlorococcus*? How does the relative consistency of the North Atlantic spring bloom persist in spite of different (mostly diatom) species dominating the bloom? How are grazers with seemingly specific prey preferences maintained in an ocean that is generally dilute and dominated by varying algal types? Do we need to measure fine-scale processes? If so, how do we connect those measurements to our ultimate goal of understanding and predicting biogeochemical cycles? Where are gaps in our knowledge and analytical ability? How do we overcome those gaps?

While the answers to these questions will require sustained research, we know that individual-level trait variability has ramifications for large-scale processes (e.g., variation in species-specific nutrient uptake, foraging behaviors). In models, it is easy to show these large-scale ramifications, but it is unclear whether that kind of extrapolation is appropriate and has not been empirically documented, as far as we know. To connect these individual-level processes with larger-scale ecosystem dynamics, we need to understand the mechanistic underpinnings of the process. Many more data are needed to get a quantitative understanding of trait variation at all levels of biological organization, but there was concern about our collective ability to find support for this type of data collection.

8. What are the Most Important Traits and Do We Measure Them?

Overview: In this session, participants listed the key traits that are: a) important for ecological processes (species selection), b) important for biogeochemical cycles, and c) are easy to measure. Participants discussed the implications of the lists being different for a), b) and c), and how the lists are different for different size organisms (e.g., microbes vs. fish). This discussion was led by Anna Hickman.

Discussion Summary: Many important traits are hard to measure, especially in the field. Field measurements generally give a whole-community view. Trade-offs in traits are particularly hard to diagnose in the field or without large numbers of individual observations, and we should use models to inform observations. The discussion highlighted the ongoing need to invest in making essential trait and field measurements to help inform models.

9. Taken for a Ride: How Do Ocean Currents Affect Traits in Marine Organisms?

Overview: We all know that physics and biology interact closely in the ocean, but there is less agreement about the relative importance of different temporal and spatial scales. This question is critical in a traits perspective since large-scale processes can transport organisms between vastly different environmental conditions. Participants discussed if and how dispersal and other physical processes affect marine ecosystems, eco-regions, connectivity, Lagrangian versus Eulerian perspectives, land-ocean continuum, and resilience. This discussion was led by Bror Jonsson.

Discussion Summary: This group started with a general discussion about how temporal and spatial scales affect how physics and biology interact in the ocean. The discussion focused on the interplay between Lagrangian and Eulerian processes, and how the different approaches can affect traits and biodiversity. Regions near the coast probably have a longer residence time than the typical biological turnover times, and can host stationary populations of plankton. Intermediate regions such as the Gulf of Maine might have recirculation patterns that allow for organisms to stay in the area, even if they are exposed to varying conditions. Finally, the pelagic ocean may be assumed to be dominated by large-scale ocean currents and should be viewed entirely in a Lagrangian frame. This categorization could be useful to better understand eco-regions, biogeography, and resilience.

Chalk Talks

During the same time period as the small group discussions, participants could also attend "chalk talks." These half-hour presentations were designed for informal discussions of new and evolving research. Speakers were requested to not use pre-prepared material such as PowerPoint slides, but instead to sketch out ideas on a white board. The following are the abstracts (and speakers) from these chalk talks:

1. Adding traits to size-structured global fish model (Colleen Petrik): Life history has recently been added to a size-structured global fish model. We would like to use this model to examine questions about recruitment variability. One question is, "Can this model reproduce observed recruitment variability?" What types of biological traits (e.g., size at maturity, spawning season, duration of spawning period) are necessary to reproduce different observed patterns of recruitment variability?

2. Can genetic traits inform biogeochemical models? (Jeff Bowman): A possible functional prediction approach: We've recently developed a method for predicting metabolic pathways from bacterial 16S rRNA gene data. Our ultimate goal is to use these predictions to model the flow of carbon and nutrients in and out of the bacterial community. We are eager for chalk talk discussion on possible approaches, and on improving our current methods.

3. Modeling zooplankton community structure and particle flux attenuation in the ocean (Adrian Burd): The flux of sinking particulate material in the water column is usually modeled as either a simple power law, or as a function of the sinking particles. However, the decrease of flux with depth results from biological the activity of microbes and zooplankton. This chalk talk will outline some ideas we are currently developing to model the attenuation of flux using a trait-based approach within an agent-based model of zooplankton and particles and their interactions.

4. From fat to fit (Alexandra Marki): We plan to modify the optimality-based plankton ecosystem model (OPEM) to simulate the regulatory physiological responses of zooplankton to food quality and environmental stressor by balancing zooplankton lipid acquisition and metabolism, in particular, by implementing phosphorus and carbon allocation into structural, storage and active pools.

5. Size- and trait-based modeling of plankton trophic strategies (Ken H. Andersen): I will outline a simple idea for a size- and trait-based model of plankton. I will use the outline as a basis for a discussion of the applicability of such models and about how they are implemented in circulation models.

Posters

An important component of the workshop was the interactive poster sessions held on each of the three evenings. Nominally 1.5 hours each, these sessions provided a chance for participants to see almost all posters and chat with presenters. The posters were loosely assigned to each of the 9 science sessions. This list of posters is provided in Appendix 2, and pdfs of most posters are available at www.whoi.edu/workshop/traitworkshop2015/posters.

New Activities

A number of new scientific activities are emerging from the workshop, including review papers, a traits database, a traits model code clearinghouse, and new collaborations. We describe here new meeting-related activities that have progressed beyond early discussion phase and have the potential for publication, significant progress, and/or community buy-in.

1. The role of ocean physics in setting trait distributions

Ocean currents and mixing facilitate the dispersal of microbes and transport of heat and resources in the ocean, and therefore play a central role in setting the microbial community structure. In this synthesis paper, the relative impacts of ocean currents and mixing on apparent microbial community structure will be investigated through integration of a coupled global physical, biogeochemical, and plankton community model. In particular, the role of temperature traits in sustaining diversity will be examined. Collaborators: Andrew Barton (Princeton University), Stephanie Dutkiewicz (MIT), Sophie Clayton (University of Washington), and Tatiana Rynearson (University of Rhode Island).

2. Virus traits, microbial communities, and biogeochemistry

Trait-based approaches have helped to simplify complexity in many ecological systems, as traits describe organism properties in terms of taxon-transcending units. This review will summarize what we know about viral traits and trade-offs in the marine pelagic ecosystem and discuss their close links to host traits. Building on previous reviews of phytoplankton and zooplankton traits and trade-offs, this review will synthesize the trait-based perspective on virus ecology and its importance to the structure and function of marine ecosystems and identify the knowledge gaps that experimental work can fill. Collaborators: Nick Record (Bigelow Laboratory), David Talmy (Massachusetts Institute of Technology), and Selina Våge (University of Bergen).

3. Trait-Based Model Clearinghouse, Review, and Synthesis

Trait-based models of marine ecosystems are increasingly being used as important tools for testing and generating hypotheses and formalizing understanding of how marine ecosystems work. They are also increasing in number and complexity, and a broad range of alternative modeling strategies and platforms now exist. Though trait-based models have many similarities, there are important cross-model differences. In this synthesis effort, we hope to create a trait-based model community clearinghouse, where model code can be stored, documented, shared, and discussed. In addition, a review and synthesis of modeling approaches, successes, and limitations will be undertaken and published. Leader: Nick Record (Bigelow Laboratory).

4. Plankton Trait Database

The trait-based approach to ocean life depends upon appropriate and accessible trait data. While much has been done for terrestrial plants (TRY database), a new community effort in collaboration with the Encyclopedia of Life (EOL) and the World Register of Marine Species (WoRMS), is being started to develop a publicly available global plankton trait database, including data on any functional trait (e.g., growth and nitrogen fixation rates) for all plankton taxa in any habitat. This long-term initiative has the potential to stimulate new research in plankton physiology, ecology, and evolution, in addition to providing an important constraint and guide for biogeochemical and ecosystem models. An appropriate oceanographic analogy is the World Ocean Atlas: one depth profile of ocean temperature and salinity is interesting, but thousands together provide a powerful three-dimensional view of the ocean. Collaborators: Andrew Barton (Princeton University), Nick Record (Bigelow Laboratory), Thomas Kiørboe (Danish Technical University), Jennifer Hammock (Smithsonian Institution, EOL), and a growing consortium of scientists.

5. Workshop Website

Most of the talks, posters, and reports stemming from the workshop will be archived on the workshop website: www.whoi.edu/workshop/traitworkshop2015

Synthesis and Recommendations

The workshop brought together a broad range of scientists working on diverse aspects of trait-based marine ecology. Here, we synthesize the makeup of the research community represented at

the workshop, their interactions, and the flow of information between subgroups linked by methodological perspectives. We highlight notable successes of the research community, core areas of strength, and identify areas for further, targeted improvement.

Landscape of the Trait-Based Research Community

The expertise of meeting participants spanned taxonomic and trophic designations, from viruses to fish, and blended methodological perspectives, which we categorize as: *empirical*, *meta-analytical*, and *numerical modeling* (Fig. 2).

Examples of *empirical* trait-based work include, but are not limited to:

- Laboratory measurements of functional traits (e.g., maximum specific growth rates, temperature-growth curves, nutrient uptake rates for phytoplankton)
- Field measurements, inferences, or estimates of functional traits
- Satellite-derived estimates of community size-structure or functional traits (e.g., growth rates)
- Molecular ecology

Measurements of traits can be difficult and expensive, particularly in the field, yet empirical work provides an essential and fundamental basis for all trait-based approaches to ocean life.

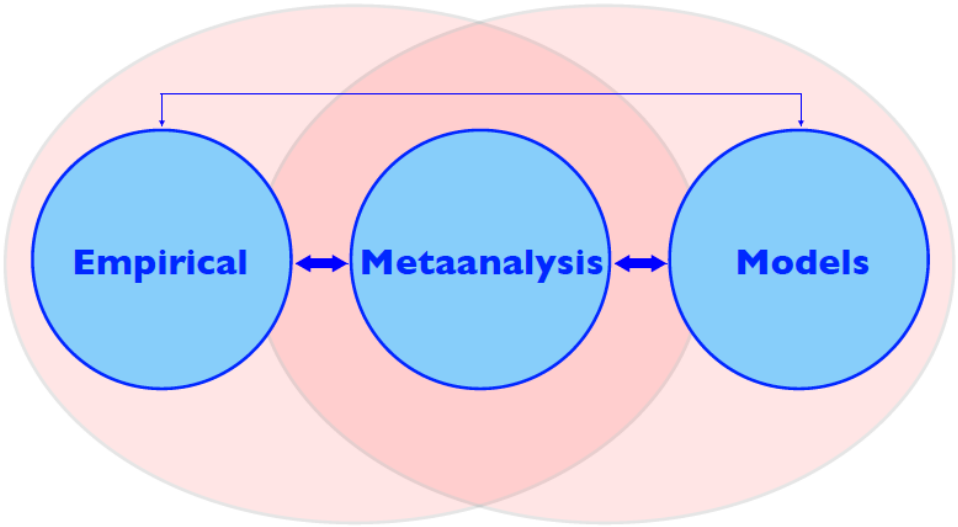

Figure 2. *Robust and two-way exchanges (blue arrows) of ideas and information currently exist between empirical and meta-analytical perspectives, and between modeling and meta-analytical perspectives. There is increasing but relatively weak interaction between empirical and modeling perspectives. Most researchers working in trait-based approaches to ocean life have expertise covering multiple and sometimes all disciplines (red ovals).*

The *meta-analytical* perspective synthesizes extensive empirical work to understand general patterns and trait distributions across taxonomic groups, trophic levels, body sizes, and regions. Examples include:

- Size scaling of physiological traits and predator-prey interactions
- Trade-offs between key physiological traits
- Relationship between the environment and traits (e.g., temperature growth curves)
- Biogeography of traits in the ocean
- Statistical syntheses of traits and environmental factors (e.g., identifying biogeographical patterns)

Uncovering trait scaling, trade-offs, and distributions requires careful curation of empirical source data, and provides a critical link between empirical and more theoretical perspectives.

Trait-based *numerical models* simulate the temporal and spatial evolution of organisms or populations by representing growth, mortality, reproduction, and survival of organisms or populations. They develop, formalize, and test hypotheses. Types of trait-based models include:

- Community models of varying complexity and numbers of trophic levels
- One-, two-, or three-dimensional representations of ocean circulation and biogeochemical cycles that embed trait-based models of varying complexity
- Other trait-structured simulations of ecosystems, such as those focusing on metabolic function, meta-transcriptomes, or other levels of organization

Collective Successes and Targeted Improvements

Linking Experiments and Models

A frequent discussion during the workshop was the need for closer collaborations between numerical modelers and empiricists, as well as the importance of linking perspectives through meta-analyses. There needs to be tighter empirical-theoretical links through a dynamic iterative process. For instance, laboratory and field studies can provide essential details of traits that can inform models. In turn, models can be used to conduct sensitivity analyses, exploring which responses or unknown processes and variables have the largest effects. Experiments can focus on and "drill down" into these areas, obtaining more useful, targeted results. Another area in which such collaborations could be helpful is in identifying tradeoffs that correspond to traits. Tradeoffs are often assumed in models without robust empirical evidence to support them. Experiments designed specifically to test these trade-offs would be an important step in advancing the field. Finally, an increasingly important way to link observations with models will be through meta-analyses. These are difficult, time-consuming processes that may not fit into traditional funding opportunities.

Specific recommendations:

- Modelers, meta-analyzers, and experimentalists or empiricists need to share ideas, define mutual questions, and coordinate around funding opportunities
- Essential and difficult laboratory and field measurements to support targeted information gaps in modeling work should be funded, given the links as suggested above

- Meta-analyses and large trait data compilations are essential and must be robustly supported

Size as a Master Trait

Size remains an important trait that transcends several broader topics addressed at the workshop. However, there were several recommendations that came from discussions during the workshop to improve our use of size as a master trait. In particular, it must be noted that no single size metric can meet all identified research needs. Equivalent spherical diameter may be adequate in some cases, while surface area (or surface area-to-volume ratio) may be better for other problems. There is a need to explore new metrics that might better reflect processes directly influenced by flow fields and concentration gradients (e.g., nutrient uptake), and that might better extend to higher trophic levels, where the spherical assumption does not work as well. The research community needs both: a) highly detailed observations of cell and body shape and size, such as might be possible with emerging holographic imaging techniques or confocal microscopy, and b) cheap, easy, and robust tools that could provide capability for *in situ* observations of cell and body size distributions, ideally with an approach that separates phytoplankton from other particles and can span the full range of phytoplankton and zooplankton sizes.

Specific Recommendations: A small group of interested experts could collaborate to produce a synthesis to:

- Describe detailed analysis protocols for determining several different metrics of size
- Determine which size metrics are most important for each process (e.g., nutrient uptake, predator avoidance)

Scaling from Genes to Traits, and Traits to Ecosystems and Biogeochemistry

In several discussions throughout the workshop, participants emphasized the need to better understand the links between different physical and biological scales. This includes links between traits and underlying genetics and biochemistry, and links between traits and environmental setting (ecology, biogeochemistry, ocean circulation).

From genes to traits: To connect organism-level processes with larger-scale ecosystem dynamics, we need to understand the mechanistic underpinnings of the processes, which requires an improved understanding at the gene and trait levels. More data are needed to acquire a quantitative understanding of trait variation at all levels of biological organization. One potential avenue that was discussed was to understand the phylogenetic conservatism of a trait, with the knowledge that trait value is not continuous but there are certain break points at which major biochemical rearrangements are required. Small changes in trait values could probably be achieved by minor differences in genes and the biochemistry underlying their functioning. In contrast, a large change in trait values would require a substantial rearrangement of the underlying biochemistry and thus likely associated with deep clades.

From traits to ecosystems and biogeochemistry: From the biogeochemical point of view, it is useful to separate traits into community-level traits (i.e., not single species), traits that encompass feedbacks (e.g., metabolism and connection to temperature), and "after life" or effect traits (see e.g., Hans Cornelissen invited talk). In some cases, singular traits may not be as informative as the ensemble of traits that describe entire biological communities. Furthermore, the coincidence and covariance

of particular traits within a community would likely reveal more about the functioning of a food web and its impact on geochemical cycles.

Specific recommendations:

- Closer links between those working at the 'omics level and those identifying key traits for models
- A community-level effort at linking traits to underlying ecological and biogeochemical processes

Big Trait Data

Nearly all of the research activities highlighted at the workshop require fundamental measurements of traits. In many cases, important inferences and the essential building blocks for trait-based models are made only by aggregating, curating, and quality-controlling many measurements of traits. Other ecological research communities and systems (particularly for terrestrial plants) have been very successful in coming together to collect, consolidate, and curate their trait data, though to date, this has not been the case for marine systems. Such an endeavor is not without significant challenges, including intellectual property concerns and funding. However, there is growing consensus that such an effort would be transformative for marine ecology, and pilot projects should be undertaken.

Specific recommendations:

- Marine trait-based ecologists should begin discussions with terrestrial trait-based ecologists to learn about the challenges and successes of aggregating and sharing large volumes of trait data
- To the extent possible, marine trait-based ecologists should submit their trait data to existing meta-analyses of traits
- Existing meta-analyses of traits should be synthesized, thereby improving inferences from the data and geographic and taxonomic coverage
- Subject to concerns over citations and intellectual property, trait data should be shared as freely as possible in standard and widely usable formats
- Utilize crowdsourcing methods to collect, curate, and document a trait database
- Create a trait-based numerical model community clearinghouse, where model code can be stored, documented, shared, and discussed (see "New Activities" above)
- Trait meta-analyses and database work, as well as model documentation and sharing endeavors should be supported through traditional and perhaps new funding streams

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Appendix 1. Workshop Agenda

MONDAY 5th OCT GETTING A HANDLE ON TRAITS

11:30-12:00	ARRIVE AT CONFERENCE CENTER, DROP OFF LUGGAGE	
12:00-13:00	LUNCH	
13:00-13:10	Andrew Barton	Opening comments
13:10-13:50	**Hans Cornelissen**	**Invited:** *Plant traits and biochemical cycling on land: parallels with marine ecosystems?*

SESSION 1: Measuring and Detecting Traits

13:50-14:00	Tatiana Rynearson	Introduction
14:00-14:20	Heidi Sosik	*Plankton traits from flow cytometry and imaging-in-flow cytometry*
14:20-14:40	Adam Martiny	*Microbiomes in light of traits: a phylogenetic perspective*
14:40-15:00	Harriet Alexander	*Functional group specific traits drive ecosystem state shift in the oligotrophic ocean*
15:00-15:50	COFFEE + CHECK-IN	

SESSION 2: Biogeography of Traits

15:50-16:00	Andrew Barton	Introduction
16:00-16:20	David Talmy	*The influence of viral reproduction strategies on marine microbial community dynamics*
16:20-16:50	Tim Moore /Colleen Mouw	*Approaches for detecting phytoplankton composition from space-based sensors*
16:50-17:10	Fi Prowe	*Effects of trade-off based zooplankton feeding in a global ocean ecosystem model*

SESSION 3: Linking Observations and Models

17:10-17:40	MODERATED DISCUSSION	Moderators: Anna Hickman/Tatiana Rynearson panelists: Philip Brun, Bethany Jenkins, Colin Kremer
17:40-19:00	POSTERS (Sessions 1,2,3)	
19:00-20:30	DINNER	
20:00-20:30	Steering Committee	Introductions
20:30	SOCIAL	

TUESDAY 6th OCT FRONTIERS OF TRAIT-BASED ECOLOGY IN THE OCEAN

7:30-9:00	BREAKFAST	
9:00-9:40	**Elena Litchman**	**Invited:** *Trait-based approaches to microbial ecology and evolution*

SESSION 4: Size as a master trait

9:40-9:50	Ken Andersen	Introduction

9:50-10:10	Andrew Hirst	*New insights from body surface: a major trait in determining life sustaining rates in metazoans*
10:10-10:30	Karen Stamieszkin	*Changes in North Atlantic copepod community size structure and fecal pellet carbon flux over 55 years*
10:30-10:50	COFFEE	
10:50-11:10	Subhendu Chakraborty	*Correlation between organism size and trophic strategies*
11:10-11:30	Kathy Mills	*Using size structure and metabolic theory to forecast fish community characteristics in a changing climate*
11:30-12:00	MODERATED DISCUSSION	Moderators: Heidi Sosik/Ken Andersen
12:00-12:15	Steering Committee	Introduction to afternoon plans
12:15-13:15	LUNCH	
13:15-15:15	CHALK TALKS/SMALL GROUP DISCUSSIONS	
15:15-15:30	COFFEE	

SESSION 5: Role of physics on setting and linking traits

15:30-15:40	Stephanie Dutkiewicz	Introduction
15:40-16:00	Lan Smith	*Trait-based modeling of phytoplankton under realistic sub-scale variability*
16:20-16:40	Marina Levy	*The dynamical landscape of marine phytoplankton diversity*
16:40-17:00	Bror Jonsson	*The effect of advection on temperature adaptation by phytoplankton communities in the global ocean*
17:00-17:30	MODERATED DISCUSSION	Moderators: Andrew Barton/Stephanie Dutkiewicz panelists: Thomas Kiørboe, Tatiana Rynearson, Sophie Clayton
17:30-19:00	POSTERS (Sessions 4,5,6) and continued small group discussions (if needed)	
19:00-20:30	DINNER	
20:30-21:10	**Thomas Kiørboe**	**Invited:** *How traits are interrelated through tradeoffs in zooplankton*
21:10	SOCIAL	

WEDNESDAY 7th OCT BROADER CONTRIBUTIONS OF TRAIT-BASED APPROACH

7:30-9:00	BREAKFAST	

SESSION 6: Contributions to cross-cutting principles in marine ecosystems

9:00-9:10	Øyvind Fiksen	Introduction
9:10-9:50	**Simon Jennings**	**Invited:** *Size- and trait-based structures and processes in marine ecosystems*
9:50-10:10	Jorn Bruggeman	*Traits of benthic fauna: from observations to community models*
10:10-10:30	Stephanie Dutkiewicz	*Combining phytoplankton size and functional traits in a global ocean ecosystem model*
10:30-10:50	COFFEE	
10:50-11:10	Susanne Menden-Deuer	*The role of intra-specific trait variability in plankton biodiversity: a gametheoretic and model examination*

11:10-11:30	Selina Våge	*Combining internal and external pelagic prokaryote community control links biodiversity to ecosystem function*
11:30-12:00	MODERATED DISCUSSION	Moderators: Øyvind Fiksen/Mick Follows panelists: Simon Jennings, Selina Våge, Susanne Menden-Deuer
12:00-12:15	Steering Committee	Introduction to afternoon plans
12:15-13:15	LUNCH	
13:15-17:00	OUTDOOR ACTIVITIES/FREE TIME	

SESSION 7: Contributions to climate science and biogeochemical cycles

17:00-17:30	MODERATED DISCUSSION	Moderator: Stephanie Dutkiewicz panelists: Mick Follows, Colleen Mouw, Adrian Burd
17:30-19:00	POSTERS (Sessions 7,8,9)	
19:00-20:30	DINNER	

SESSION 8: Contributions to policy

20:30-21:00	MODERATED DISCUSSION	Moderators: Nick Record / Andrew Pershing panelists: Lars Ravn-Jonsen, Janaína Bumbeer
21:00	SOCIAL	

THURSDAY 8th OCT NEW DIRECTIONS FOR TRAIT-BASED OCEAN SCIENCE

7:00-8:30	BREAKFAST	

SESSION 9: From the gene to the ecosystem

8:30-8:40	Nick Record	Introduction
8:40-9:20	**Sonya Dyhrman**	**Invited:** *Linking 'omic approaches to a trait-based view of ocean life: using transcripts to define microbial traits*
9:20-9:40	Frederic Maps	*Blurred lines between species in trait-based numerical approaches. A case study of Calanus hybrid*
9:40-10:00	Elizabeth Harvey	*Linking individual movement to population-level dynamics: strain-specific behaviors of Heterosigma akashiwo*
10:00-10:20	COFFEE	
10:200-10:40	Victoria Coles	*Emergent patterns of genes, transcripts and community structure in the GENOME model*
10:40-11:10	MODERATED DISCUSSION	Moderators: Nick Record/Bethany Jenkins panelists: Sonya Dyhrman, Jeff Bowman, Hans Cornelissen, Victoria Coles

SESSION 10: Summary and wrap-up

11:10-11:40	DISCUSSION	Moderators: Steering Committee
11:40-11:50	Andrew Barton	Final summary
11:50-13:00	LUNCH	

Appendix II. Posters

Most posters are available at http://www.whoi.edu/workshop/traitworkshop2015/posters

(* Indicates the poster is in multiple sessions)

SESSION 1: Measuring and Detecting Traits

3	*James Allen	*Retrieval of phytoplankton size distribution from satellite imagery*
8	*Jeff Bowman	*Inferring microbial ecosystem function from community structure*
19	Jen Hammock	*Making trait data flow*
25	*Bethany Jenkins	*Gene expression as a biological reporter of trace metal biogeochemistry*
38	*Amanda Montalbano	*Intra-specific variability in growth rates and behavior of a harmful dinoflagellate species: trait variation broadens ecological niche*

SESSION 2: Biogeography of Traits

9	*Philip Brun	*Understanding observed copepod distributions with a trait data base*
13	*Sophie Clayton	*Phytoplankton biogeography of the North Pacific from continuous flow cytometry*
16	*Øyvind Fiksen	*Trait-changes in fish populations as evolutionary response to fisheries*
17	Glaucia Fragoso	*Using phytoplankton functional traits to describe species distribution in the sub-Arctic North Atlantic*
22	Anna Hickman	*The role of bio-optical traits for phytoplankton biogeography*
28	Tiho Kostadinov	*Intercomparison of phytoplankton phenology from phytoplankton functional types satellite algorithms and Earth System Models*
42	Deepa Rao	*The paradox of the Prochlorococcus: A trait-based approach to modeling ecotype niche differentiation via light and nutrient resource competition*
44	Nick Record	*Mapping the jelly and fat of the world's oceans*
45	Sara Rivero-Calle	*Trichodesmium is not limited to tropical and subtropical latitudes*
47	*Tatiana Rynearson	*Global-scale gene flow in a marine plankton: implications for tracking and interpreting key traits in key organisms*
51	Mridul Thomas	*Tropical convergence, temperate divergence: evolutionary inferences from the biogeography of phytoplankton temperature traits*
53	Pieter van der Linden	*The performance of trait-based indices in an estuarine environment*
55	*Benjamin Weigel	*Maintained functional complexity despite long-term contrasting community developments within a low diverse coastal system*

SESSION 3: Linking Observations and Models

5	Cael Barry	*Ocean color inversion and information content for phytoplankton functional type classification*
7	*Kelsey Bisson	*Linking shifts in remotely sensed planktonic community structure to changes in carbon export flux from the surface ocean to the mesopelagic*
9	*Philip Brun	*Understanding observed copepod distributions with a trait data base*

15	Kyle Edwards	*How temperature changes light-use traits of phytoplankton, and how this scales up to ecosystem temperature sensitivity*
29	*Colin Kremer	*Temperature and phytoplankton growth rates: disentangling empirical patterns and competing paradigms*
30	Shubham Krishna	*Explaining variability observed in calcification during the PeECE-I experiment*
36	*Holly Moeller	*Acquired phototrophs as mediators of planktonic community dynamics*
49	Eva Smeti	*Important traits for phytoplankton species coexistence along a disturbance gradient*

SESSION 4: Size as a master trait

1	Esteban Acevedo-Trejos	*A comparative modelling analysis of phytoplankton size diversity*
3	*James Allen	*Retrieval of phytoplankton size distribution from satellite imagery*
4	Ken Andersen	*Characteristic sizes of life in the oceans, from bacteria to whales*
7	*Kelsey Bisson	*Linking shifts in remotely sensed planktonic community structure to changes in carbon export flux from the surface ocean to the mesopelagic*
24	*Kristen Hunter-Cevera	*Seasonal shifts in division rate determine Synechococcus population dynamics*
32	Arnault Le Bris	*Temperature induced variation in life-history trade-offs*
33	*Clint Leach	*Exploring the lack of recovery of Scotian Shelf cod through the development of a statistical framework for size-structured predator-prey models*
50	Darcy Taniguchi	*How top-down effects influence preadator:prey ratios and planktonic community diversity in a size-structured model of phyto- and microzooplankton*

SESSION 5: Role of physics on setting and linking traits

12	*Wilton Burns	*Primary productivity in future oceans: an analysis of how increased water mixing caused by global change will affect nutrient uptake by marine phytoplankton*
13	*Sophie Clayton	*Phytoplankton biogeography of the North Pacific from continuous flow cytometry*
21	*Chrissy Hernandez	*The influence of ontogenetic vertical distribution of coral reef fish larvae on dispersal and connectivity*
31	Tom Langbehn	*Visual search as a trait: consequences of sea ice change in high latitude ocean*
46	*Daniel Roelke	*Phytoplankton assemblage characteristics in recurrently fluctuating environments*
47	*Tatiana Rynearson	*Global-scale gene flow in a marine plankton: implications for tracking and interpreting key traits in key organisms*

SESSION 6: Contributions to cross-cutting principles in marine ecosystems

14	*Kim Davies	*Simulating planktonic ecosystem dynamics in the Bay of Biscay, France, using a trait-based, auto-emergent zooplankton model coupled to a 3-D biogeochemical model (MARS3D)*
18	*George Hagstrom	*Non-Redfield stoichiometry and the carbon cycle*
26	Kasia Kenitz	*Optimal zooplankton feeding mode in a seasonally-stratified shelf sea*
27	Onur Kerimoglu	*Role of phytoplankton adaptation in functioning of a coastal ecosystem*
34	*Patrizio Mariani	*Group formation and efficiency of migratory species*
35	Alexandra Marki	*Optimality-trait-based plankton ecosystem modelling of phosphorus uptake in microbes*

36	*Holly Moeller	*Acquired phototrophs as mediators of planktonic community dynamics*
37	*John Moisan	*Genetic programming for ocean microbial ecology and biodiversity*
48	Nicolas Schedler-Meyer	*A mechanistic model of jellyfish-fish competition*
52	Anna Törnroos	*Describing key traits and trade-offs of marine benthos: towards a mechanistic trait-based approach*
56	Susanne Wilken	*Bacterivorous phytoplankton - Primary producers or consumers?*
57	*Emily Zakem	*Exploring a microbial ecosystem approach to modeling deep ocean biogeochemical cycles*

SESSION 7: Contributions to climate science and biogeochemical cycles

2	Aurelie Albert	*Global physical/biogeochemical coupling for the 20th century*
6	Andrew Barton	*Tipping points in plankton community models*
7	*Kelsey Bisson	*Linking shifts in remotely sensed planktonic community structure to changes in carbon export flux from the surface ocean to the mesopelagic*
11	Adrian Burd	*Trait-based models, community structure, and biogeochemical function*
12	*Wilton Burns	*Primary productivity in future oceans: an analysis of how increased water mixing caused by global change will affect nutrient uptake by marine phytoplankton*
14	*Kim Davies	*Simulating planktonic ecosystem dynamics in the Bay of Biscay, France, using a trait-based, auto-emergent zooplankton model coupled to a 3-D biogeochemical model (MARS3D)*
18	*George Hagstrom	*Non-Redfield stoichiometry and the carbon cycle*
23	Dana Hunt	*Evidence for temperature-related trade-offs in bacterial community and population dynamics*
29	*Colin Kremer	*Temperature and phytoplankton growth rates: disentangling empirical patterns and competing paradigms*
40	Colleen Mouw	*Utilizing satellite estimates of phytoplankton size to understand global export flux variability*
54	Nicolas Van Oostende	*Phytoplankton succession explains size partitioning of new production during upwelling blooms*
55	*Benjamin Weigel	*Maintained functional complexity despite long-term contrasting community developments within a low diverse coastal system*
57	*Emily Zakem	*Exploring a microbial ecosystem approach to modeling deep ocean biogeochemical cycles*
58	Lai Zhang	*Food web dynamics of climate change*

SESSION 8: Contributions to policy

10	Janaina Bumbeer-Couto	*Invasion risk assessment of marine invertebrates: A unified approach linking species traits and social-environmental settings*
16	*Øyvind Fiksen	*Trait-changes in fish populations as evolutionary response to fisheries*
20	Megan Hepner	*Building demonstration Marine Biodiversity Observation Networks in the Florida Keys and Monterey Bay National Marine Sanctuaries*
21	*Chrissy Hernandez	*The influence of ontogenetic vertical distribution of coral reef fish larvae on dispersal and connectivity*

33	*Clint Leach	*Exploring the lack of recovery of Scotian Shelf cod through the development of a statistical framework for size-structured predator-prey models*
34	*Patrizio Mariani	*Group formation and efficiency of migratory species*
39	Enrique Montes	*National Marine Sanctuaries as sentinel sites for a demonstration Marine Biodiversity Observation Network (MBON)*
41	Andrew Pershing	*Trait-based strategies for estimating population abundance*
43	Lars Ravn-Jonsen	*How to share fish resources?*
46	*Daniel Roelke	*Phytoplankton assemblage characteristics in recurrently fluctuating environments*

SESSION 9: From the gene to the ecosystem

8	*Jeff Bowman	*Inferring microbial ecosystem function from community structure*
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38	*Amanda Montalbano	*Intra-specific variability in growth rates and behavior of a harmful dinoflagellate species: trait variation broadens ecological niche*
47	*Tatiana Rynearson	*Global-scale gene flow in a marine plankton: implications for tracking and interpreting key traits in key organisms*

Appendix III. Workshop Attendees

Esteban Acevedo-Trejos (Leibniz Center for Tropical Marine Ecology)
Aurélie A. Albert (Mercator)
Harriet Alexander (MIT-WHOI Joint Program in Oceanography)
James G. Allen (UCSB)
Ken H. Andersen (DTU Aqua)
Brendan C. Barry (MIT-WHOI Joint Program)
Andrew Barton (GFDL Princeton University)
Heather Benway (OCB, Woods Hole Oceanographic Institution)
Kelsey M. Bisson (UCSB)
Myriam Bormans (University of Rennes, CNRS)
Jeff S. Bowman (Lamont-Doherty Earth Observatory)
Jorn Bruggeman (Plymouth Marine Laboratory)
Philipp G. Brun (Centre for Ocean Life, DTU Aqua)
Janaina Bumbeer-Couto (Federal University of Paraná)
Adrian Burd (University of Georgia)
Wilton G. Burns (University of New Hampshire)
Marian Carlson (Simons Foundation)
Subhendu Chakraborty (VKR Centre for Ocean Life DTU Aqua)
Sophie A. Clayton (University of Washington)
Victoria J. Coles (UMCES)
Hans J.H.C. Cornelissen (University Amsterdam)
Kimberley T. Davies (Dalhousie University)
Stephanie Dutkiewicz (MIT)
Sonya T. Dyhrman (Columbia University Lamont-Doherty Earth Observatory)
Kyle F. Edwards (University of Hawaii)
Øyvind Ø.F. Fiksen (University of Bergen)
Mick Follows (MIT)
Glaucia M. Fragoso (University of Southampton)
George I. Hagstrom (Princeton University)
Jen A. Hammock (Encyclopedia of Life National Museum of Natural History)
Elizabeth L. Harvey Skidaway (Institute of Oceanography)
Megan E. Hepner (University of South Florida)
Christina M. Hernandez (MIT/WHOI)
Anna E. Hickman (University of Southampton Ocean and National Oceanography Centre)
Andrew G. Hirst (Queen Mary University of London)
Dana Hunt (Duke University)
Kristen R. Hunter-Cevera (University of Rhode Island)
Bethany Jenkins (University of Rhode Island)
Simon Jennings (Centre for Environment Fisheries and Aquaculture Science, Cefas)
Adam Jones (Gordon and Betty Moore Foundation)
Bror F. Jonsson (Princeton University)
Katarzyna M. Kenitz (DTU Aqua)
Thomas Kiørboe (Centre for Ocean Life, DTU Aqua)
Tihomir S. Kostadinov (University of Richmond)
Colin T. Kremer (Yale University / Princeton University)
Shubham Krishna (GEOMAR, Helmholtz Center for Ocean Research Kiel)

Tom Jasper Langbehn (University of Bremen)
Arnault Le Bris (Gulf of Maine Research Institute)
Clinton B. Leach (Colorado State University)
Marina Levy (CNRS LOCEAN-IPSL)
Elena Litchman (Michigan State University)
Frederic Maps (Université Laval)
Patrizio Mariani (Technical University of Denmark)
Alexandra Marki (GEOMAR Helmholtz Centre for Ocean Research Kiel)
Adam C. Martiny (UC Irvine)
Susanne Menden-Deuer (University of Rhode Island)
Katherine E. Mills (Gulf of Maine Research Institute)
Holly V. Moeller (Woods Hole Oceanographic Institution)
John R. Moisan (NASA Goddard Space Flight Center)
Amanda L. Montalbano (University of Rhode Island)
Enrique Montes (University of South Florida)
Tim Moore (University of New Hampshire)
Colleen B. Mouw (Michigan Technological University)
Andrew J. Pershing (Gulf of Maine Research Institute)
Colleen Petrik (Princeton University)
Friederike Prowe (GEOMAR Helmholtz Centre for Ocean Research Kiel)
Deepa Rao (MIT/WHOI Joint Program)
Lars J. Ravn-Jonsen (University of Southern Denmark)
Nicholas R. Record (Bigelow Laboratory for Ocean Sciences)
Daniel L. Roelke (Texas A&M University)
Tatiana Rynearson (University of Rhode Island)
Nicolas A. Schedler-Meyer (Centre for Ocean Life DTU Aqua)
Michael Sieracki (National Science Foundation)
Evangelia Smeti (University of the Aegean)
S. Lan Smith (JAMSTEC)
Heidi M. Sosik (Woods Hole Oceanographic Institution)
Karen S. Stamieszkin (University of Maine, Darling Marine Center)
David Talmy (Massachusetts Institute of Technology)
Darcy Taniguchi (Massachusetts Institute of Technology)
Mridul K. Thomas (Eawag: Swiss Federal Institute of Aquatic Science and Technology)
Anna Törnroos (Åbo Akademi University)
Selina Våge (University of Bergen)
Pieter P. van der Linden (University of Coimbra)
Nicolas Van Oostende (Princeton University)
Benjamin Weigel (Åbo Akademi University)
Susanne Wilken (MBARI)
Emily Zakem (Massachusetts Institute of Technology)
Lai Zhang (Umeå University)