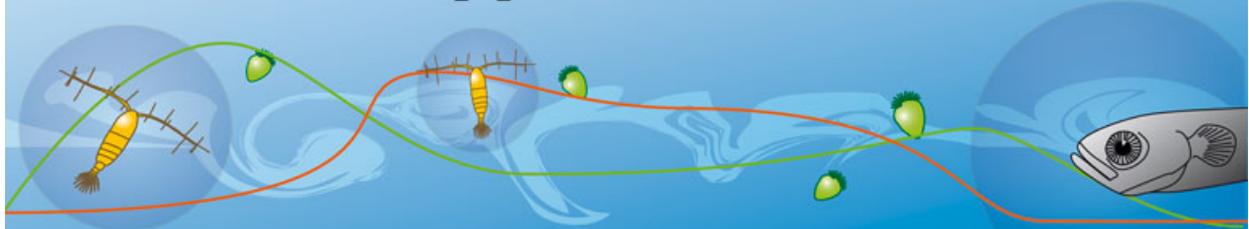


International Workshop on

Trait-based approaches to Ocean Life



Copenhagen • 26-28 August 2013

Book of Abstracts

André W Visser:

Behavioral traits and their trade-off in the plankton

The central concept of trait-based modeling is to focus on the key characteristics of individuals and mechanistically describe the trade-offs these characteristics (traits) impose on the ensuing fitness of the organisms that express them. Traits that survive within particular environment settings and against interactions (predation, competition) with other individuals thus predict system properties. That is, community and ecosystem structure and function are emergent properties of trait-based models, not their input as in more traditional ecosystem models. This trait-based approach provides extra information that constrains and lends a dynamic aspect to the interaction rates in ecosystem models, and focusses models on their biological, rather than physico-chemical aspects. While these concepts can be argued in a theoretical setting, I will illustrate their feasibility in a particular application to the optimal foraging of zooplankton grazers, the emergence of functional response curves and implications for simulations of biodiversity.

Andrew Barton:

Estimating the Response of North Atlantic Phytoplankton Communities to Climate Change

Anthropogenic climate change is expected to significantly alter the marine environment over the coming century, but the climate impacts on individual phytoplankton species and the resulting community structure are not well known. Here, using environmental and biological observations spanning the previous half-century in the North Atlantic, we quantify the realized ecological niches, in terms of sea surface temperature, sea surface salinity, mixed layer depth, photosynthetically active radiation, nitrate, phosphate, and silicate, for greater than 100 commonly-sampled phytoplankton species.

These estimates of realized niches for the observational record are then used to map the biogeographies of the studied species, both in the modern era and for mean conditions in the years 2050-2100, where the future environmental conditions have been simulated using an earth system model forced by increasing greenhouse gas emissions. By comparing the estimated species distributions through time, our analysis of the impacts of climate change on North Atlantic phytoplankton indicates that: a) the biogeographic range of most, but not all, species may shift northward, b) the relatively species-rich subtropical biome may expand northward, while the equator-to-pole decrease in species-richness persists, and c) mid-latitudes on the boundary between subpolar and subtropical gyres are likely to experience the greatest changes in phytoplankton community structure. We discuss how the climate response of each species or functional group is tied to their characteristic functional traits, including cell size, nutrient acquisition and growth rates, and trophic strategy. The North Atlantic phytoplankton community appears poised for marked change in the coming century.

Anna Törnroos:

Multiple traits and benthic functioning: from toolbox to application in a system rich in functions but poor in species

The use of multiple biological and ecological characteristics of species for understanding more applied questions have recently greatly increased in marine community ecology. We present the methodology behind Biological Trait Analysis (BTA), a method that is based on categorical usage of multiple traits. In addition we show results of its application using benthic macrofauna in a system, the Baltic Sea, which is species poor but shown to provide high functional diversity and is structured by steep environmental and anthropogenic stress gradients. In total we use 23 traits and 102 sub-categories or "modalities" in our analysis. We show results that highlight the advantages of using the trait analysis over traditional species-based assessments, in a pure methodological perspective in regard to sampling effort. Further, we present benthic functional diversity patterns and generalities covering long-term (10 years) and large spatial scale (1250 km of coastline, 782 stations), as well as recent results linking the BTA to the food web concept. Thus we highlight the applicability of the methodology for both theoretical understanding of functional diversity and the role for BTA in marine conservation and spatial planning.

Christian Jørgensen:

Optimization and evolution of traits in models of fish

Trait-based approaches are used to explain biodiversity among species and broad ecological patterns. In parallel, there has been an array of models that consider adaptations of traits within a species. These focus on the functional role of the trait as an adaptation, are closely linked to trade-offs. Understanding within-species approaches to traits and adaptations can help one think about between-species and community-level effects of trait distributions. In this talk I will present some approaches for studying traits and adaptations, mainly optimization and evolving individual-based models. I will present some models for fish, in particular for traits related to life history theory and behaviour. These often include rich ecological mechanisms derived from empirical observations, and point to advantages of considering several traits in combination rather than single-trait models.

Christopher Klausmeier:

Trait-based approaches to species abundance distributions

The species abundance distribution (SAD) is one of the most common descriptors of community structure. Typically communities are dominated by a few common species and many rare ones. Despite the ubiquity of these patterns, until recently there was little process-based theory to explain them. Traditional niche models usually do not permit coexistence of more than a few species, so are unable to generate realistic SADs. Neutral models, based on the interplay between ecological drift and speciation, can generate realistic SADs but the assumption of strict neutrality is questionable. Here I take a metacommunity perspective where local abundance is driven by the interplay between immigration and selection (competition), where species are defined by functional traits that affect fitness. This niche-based framework not only produces realistic SADs but also predicts the relationship between traits and abundance. These models can be analyzed numerically and further understood using analytical approximations. The strength of immigration relative to selection is a key parameter that shapes SADs, while the emergent shape of the fitness landscape and the traits of the metacommunity species pool determine patterns of trait diversity. Whether environmental factors affect birth rate or mortality is also important in determining the abundance of rare species. This theory provides a simple alternative framework to explain SADs in different communities and makes testable predictions about the traits of common versus rare species.

Colleen Webb:

Using Traits-based Approaches to Understand the Dynamics of Marine Biodiversity and Productivity

Predicting changes in community composition and ecosystem function in a rapidly changing world is a major research challenge in ecology and evolution. I will discuss a proposed theoretical framework for addressing this challenge comprised of three elements: an underlying trait distribution (e.g., frequency distribution of photosynthetic rate across individuals and species in a community), a performance filter defining the fitness of traits in different environments, and a dynamic projection of the performance filter along some environmental gradient. This framework allows changes in the trait distribution and associated modifications to community composition or ecosystem function to be predicted across time or space. I will also present a data-driven modeling application of this framework to predicting species composition changes in a Marine system, which helps to illustrate the difficulties in applying traits-based approaches to empirical data.

Daniel Falster:

Trait-based approaches in plant ecology: successes and future challenges

Plants are the foundation of terrestrial ecosystems, capturing the energy that sustains terrestrial food webs and human activity. Today there exist more than 250 000 plant species worldwide. In an effort to organise knowledge about this hyper-diverse and important group of organisms, researchers have employed a range of structural and allocation traits as indicators of a species' ecology. In this talk I review the successes and challenges of this trait-based approach to plant ecology, and outline how some of the lessons learned might generalise to other systems. The utility of a trait-based approach for plants arises from the fact that all species use the same basic resources, so the differences between them are in rates of resource uptake and allocation among different tissues. The most useful traits capture fundamental, economic differences in how plants capture and use a common set of resources. The major successes in trait-based research have arisen from the pragmatic decision to focus on traits that are easy to measure, and thus quantify across large numbers of species. This has enabled large scale -- often global -- quantification of trait variation, comparison among species, and mapping onto phylogenetic trees. Yet, the utility of the trait-based approach is far from proven. Some outstanding challenges are to i) identify the leading dimensions of variation; ii) establish how trait mixtures are maintained, and iii) show that knowledge about traits enables us to predict many features of ecosystem function. The ultimate goal of the trait-based approach is a theory that predicts both the structure and trait diversity of ecosystems, from first principles.

Esteban Acevedo-Trejos:

Emerging properties of phytoplankton community size structures in regions of contrasting environmental conditions of the Atlantic Ocean

Esteban Acevedo-Trejos*,1,2, Gunnar Brandt1, and Agostino Merico1,2

1.Systems Ecology, Leibniz Center for Tropical Marine Ecology, Bremen, Germany

2.School of Engineering and Science, Jacobs University, Bremen, Germany

We developed a trait-based model to study the mechanisms that produce shifts in phytoplankton community compositions under changing environmental conditions. The model is based on cell size and on a trade-off between nutrient acquisition capabilities and resistance to grazing, and is applied to the upper mixed-layer of two regions of the Atlantic Ocean with contrasting environmental conditions (i.e. temperate vs. tropics). The model set-ups for the two regions differ only by the local environmental forcing and by two parameters controlling the availability of nutrients (i.e. mixing between the deep layer and the upper mixed layer and sinking rate). By doing so, we were able to capture the different phytoplankton community structures of the two regions as observed by satellitederived size data (i.e. larger organisms in colder and nutrient-rich waters vs. smaller organisms in warmer and nutrient-depleted waters). Our approach provides further insights into the mechanisms controlling the size composition of phytoplankton communities and demonstrates the capability of the complex adaptive system approach to describe the temporal evolution of macroscopic properties (such as total biomass, mean trait, and trait variance) in large assemblages of species.

Hans G Dam:

Trait heritability: A Neglected Aspect of Adaptation Studies in Zooplankton

Natural selection works on heritable traits. Both the rate of evolution and the critical rate of environmental change that is sustainable by a population are directly proportional to heritability. To date, very few studies have measured trait heritability (the fraction of phenotypic variance attributable to genes) in zooplankton. In this presentation, I will briefly review approaches to measuring heritability and present a case study of fitness-related trait heritability in the copepods *Acartia tonsa* and *Acartia hudsonica* that may shed light on the potential for evolutionary adaptation of these species to global warming.

Inga Hense:

Modelling phytoplankton life cycles

Observations indicate that certain life cycle traits of phytoplankton regulate phenological patterns. For instance, cyanobacteria and dinoflagellates produce resting stages that require a certain dormancy period before germination can take place. Sudden outbreaks are often the consequence of synchronized germination of resting cells and subsequent growth. During the life cycle of diatoms, cells become smaller and changes in trait characteristics like nutrient uptake behaviour occur. Examples of life cycle modelling for three important phytoplankton groups (cyanobacteria, dinoflagellates and diatoms) are presented; the models distinguish between growing and resting stages or different size classes. Each stage and size class has specific nutrient requirements and motility behaviour. The results show that the overall bloom characteristics, i.e. timing and duration of these species in the Baltic Sea are very well reproduced.

Kai Wirtz:

Limits of predictability and mechanistic understanding exposed by trait-based models

Trait-based models recently started to prosper in aquatic ecology. These models come with the prospect to enhance our predictive capability, which is much needed given the very extent of ecosystem complexity and external pressures. In this talk I first aim to lower the expectation: the trait-based approach, indeed, may not much improve the short-term forecasting capability of aquatic ecosystem models. This will be explained using validation experiments of a size-based plankton model at daily to weekly scales and data for the German Bight as well as from mesocosm studies. Although a great correspondence is revealed between observations and model trajectories, the latter rely on quantitative knowledge of community trait values which in general is not available for natural systems. Fortunately, the picture changes when addressing long-term ecosystem dynamics. Examples from freshwater and marine systems show that – on annual to decadal scales- trait approaches can much enhance the validity of our scenarios. To do so, however, we require functional representations for how traits affect the physiology and ecology of organisms and communities. These functions, usually collected under the term “trade-offs”, call for a mechanistic consideration. Behind the way how a quantitative trait such as size determines an ecophysiological characteristic such as maximum photosynthesis rate, we should identify clear-cut biophysical laws. I will outline major related gaps in our mechanistic understanding of plankton ecophysiology and suggest a strategy to close those gaps. In summary, trait-based models will not always provide better answers than classical approaches (e.g., to forecasting requests), but face us anew with questions that may inspire and guide scientific curiosity.

Ken H Andersen:

Characteristic sizes of life in the oceans -- from bacteria to whales

K.H. Andersen, T. Berge, R. Goncalves, M. Hartvig, S. Hylander, N.S. Jacobsen, C. Lindemann, E.A. Martens, A. Neuheimer, K. Olsson, M. Payne, F. Prowe, J. Sainmont, S.J. Traving, A. Visser, N. Wadhwa, and T. Kiørboe

The size of an individual organism has been proposed as a “master trait” to characterize the physiology and the feeding ecology of the organism. Such descriptions are formulated as scaling laws with power functions, however, these scaling laws often have a limited size range of validity or they undergo a transition from one scaling law to another at some characteristic size. Here we move beyond the idea of characterizing all life in the ocean by a single scaling law and instead focus on identifying the characteristic sizes where there is a change or a break-down in scaling laws. Within the “Center for Ocean Life” we have made a common effort to review and collate data on size-based scaling laws for food encounter, mobility, sensory range and offspring size for all marine life, from bacteria to whales, and developed simple theoretical arguments for the scaling laws. We use the theoretical insights to describe life in the ocean divided into seven major realms based on their prey/nutrient capture, physiology, and life history strategy. Such a division represents a move away from taxonomically oriented descriptions towards a trait-based description of life in the ocean.

Kyle Edwards:

Opportunities and challenges for quantifying functional tradeoffs

Functional tradeoffs ensure that no species performs best under all conditions, and thus tradeoffs underlie the functional diversity we see within and across environments. In order to better predict the structure of communities from the environmental conditions they experience, it will be essential to quantify how these tradeoffs work. I will present examples from phytoplankton and other taxa of evidence for tradeoffs and how this promotes trait-based theory that is empirically grounded. I will also discuss several challenges in quantifying tradeoffs from interspecific trait correlations; these include statistical issues such as missing data and conceptual issues such as high-dimensional trait variation and the role of environmental correlation in selecting for trait correlation.

Marina Levy:

Phytoplankton diversity affected by oceanic dispersal and mesoscale currents

A marine ecosystem model seeded with many phytoplankton types, whose physiological traits are randomly assigned from ranges defined by field and laboratory data, is embedded into an eddy-resolving physical model of seasonally varying oceanic gyres. This flexible representation of community structure is used to explore the role of the physical environment on resource competition. More specifically, we examine how phytoplankton diversity is affected by the physical dispersion induced by ocean currents, over spatial scales ranging from $O(1000)$ km to $O(10)$ km. In this model, the community structure and diversity are not imposed, but emerge from a wider set of possibilities. In parallel to the changes in diversity, we examine how mesoscale transport modifies the community structure.

Mark D Ohman:

Risks and rewards in the zooplankton: nonlinear dependencies on body size

Zooplankton body size is a trait that co-varies with a spectrum of different fitness-related variables, including swimming velocity, feeding rate, metabolic rate, visual conspicuousness, and susceptibility to different guilds of predators. Here we illustrate a fundamental trade-off associated with body size, since both predation risk - due to visual predators - and predator avoidance behavior are a positive function of body size. There is not a single optimum balance between size-related risk and predator avoidance, expressed as diel vertical migration (DVM) behavior. Instead, this balance changes with body size in a nonlinear manner. Empirical support for a size-dependent trade-off comes from the California Current Ecosystem LTER site, which includes waters of widely disparate optical characteristics. Encounter rates with visually-hunting predators are dependent upon zooplankton body size and are therefore sensitive to variations in optical transparency. The ability to avoid predators, through diel vertical migration (DVM) behavior, is dependent upon body size-related swimming ability. Our results show that the amplitude of DVM behavior varies widely with copepod body size: smaller-bodied copepods in this region tend to show low amplitude DVM, remaining in near-surface waters day and night; intermediate body-sized copepods exhibit DVM behavior; and the very largest-bodied copepods also show little evidence of DVM, but remain in deeper waters. The trade-off is influenced by ambient environmental conditions, since the amplitude of copepod DVM is directly proportional to the optical transparency of the water column.

Nicholas R Record:

Emergent copepod communities in an adaptive traitstructured Model

We have a decent mechanistic understanding of population dynamics for many of the dominant taxa in the ocean. However, important ecosystem shifts involve whole communities. My work focuses on understanding community-level patterns in ocean ecosystems. Algorithms adopted from evolutionary computation provide one avenue for understanding community-level properties like biodiversity. I will discuss a copepod community model designed based on ecological tradeoffs in trait space. The model is generalized to represent a broad range of possible copepod taxa. I used this framework in an adaptive-computing context to examine the different communities that assemble under different temperature and food regimes across a latitudinal gradient. Emergent communities were characterized by analogues of species observed in nature. Biodiversity was dynamic across a wide range of temporal scales. This type of model has the potential to address how the structure of ocean communities will change with changing ocean conditions.

Stephanie Dutkiewicz:

Modeling phytoplankton traits, trade-offs and biogeography

Stephanie Dutkiewicz, Mick Follows, Anna Hickman, Ben Ward, Fanny Monteiro and Oliver Jahn

Phytoplankton biogeography is dictated by the relative fitness imparted by specific organism traits and trade-offs in different physical and chemical environments. We use an ecosystem model coupled to a three-dimensional physical-biogeochemical model to illustrate how the co-evolution of traits can lead to multiple, consistent interpretations of the controls on biogeography. We use numerical simulations to illustrate how traits including cell size, elemental requirements, temperature tolerance, and pigment composition can each independently shape which plankton are competitive in oligotrophic regimes. When size alone is considered, the analogs of the cyanobacterium *Prochlorococcus*, the smallest photo-autotrophs with highest nutrient affinities, are most competitive in strongly nutrient depleted regions. When the only difference between modeled phytoplankton types is pigment composition and spectral efficiency of light-harvesting, *Prochlorococcus*-analogs again dominate in the most oligotrophic (and clearest) waters. When temperature tolerances are taken into account, only *Prochlorococcus*-analogs with imposed warm temperature optima are viable. Though each of these traits can be used separately to describe the biogeography of *Prochlorococcus*, they appear to have co-evolved and reinforce one another for the specific habitat. We comment on analogous views of *Synechococcus* and diazotrophs traits and trade-offs in the subtropical oceans.

Ursula Gaedke:

Interplay between evolutionary and phenotypic trait changes and biomass dynamics in multi-trophic food webs.

Ursula Gaedke¹, Toni Klauschies¹, Renato Mendes Coutinho^{1,2}

¹Institute for Biochemistry and Biology, Potsdam University, Germany

²Instituto de Física Teórica, Universidade Estadual Paulista, Sao Paulo, Brazil

There is increasing evidence that trait variation between and within species, as well as trade-offs among traits, can profoundly influence species coexistence and population dynamics. For example, the classical quarter phase lagged predator-prey cycles may be silenced by fast trait changes, producing out-of-phase and/or so-called cryptic cycles. We consider predator-prey systems with functionally different predator and prey species. Prey species differ in their maximum growth rate and vulnerability to predation and predator species in their half saturation constant and selectivity for prey items and the trait values are subject to trade-offs (e.g. high growth rates implies high vulnerability to predation). We use either a multispecies (i.e. species sorting, evolutionary changes; cf. Tirok & Gaedke 2010) or a dynamic trait approach (i.e. phenotypic or evolutionary change; cf. Tirok et al. 2011) or a combination of both. The latter allows to combine trait variation arising from interspecific (genetic) and intraspecific (phenotypic plasticity) changes to identify their joint influence on the maintenance of biodiversity, i.e. species richness, evenness of community composition and functional diversity. The individual prey and predator species exhibited a variable amount of phenotypic plasticity which enabled them to change their trait values in response to altered predation pressure and resource levels. Biodiversity was strongly influenced by the degree and the speed of phenotypic plasticity as well as initial species richness. Intermediate phenotypic variation allowed species to make clear adjustments to their trait values in order to reduce predation pressure and/or enhance growth rates and therefore maintain higher average fitness over time. This greatly prolonged coexistence of numerous functional different predator and prey species at high biomass levels. Increased speed of phenotypic plasticity stabilized predator-prey dynamics and enhanced biodiversity whereas too slow phenotypic adjustment prevented species coexistence. Our results suggest that phenotypic plasticity may strongly promote the maintenance of biodiversity.

Furthermore, we present first results from a novel theoretical framework comprising a tri-trophic system where the intermediate consumer has two sets of independent traits which are influenced by the biomass and traits of the top predator and the basal prey. This approach allows great generality, since it does not restrict the possible trait values as the shape of the trait distribution(s) at each trophic level is not predefined but evolves continuously. We find that biomass changes are indeed strongly influenced by the trait distributions and shifts in top-predator or resource traits propagate through the entire food chain.

The existence of two interacting biomass cycles (consumer-resource and top predator-consumer) gives origin to a rich dynamics with complex solutions which is enhanced by the presence of trade-offs between traits. The latter also play a central role for maintaining trait variation at every trophic level as different traits may be favored at different times.

Allison Smith:

A role for bacterial quorum sensing in remineralization models

The presence of signal molecules within sinking organic particles in the ocean suggests that bacterial quorum sensing plays a role in the remineralization of organic nutrients. Quorum sensing is used to coordinate behavior including production of exoenzymes which are used by heterotrophic bacteria to efficiently strip edible hydrolysate from particles. However, loss of exoenzymes and hydrolysate from particles due to diffusion and advection can be energetically costly for bacteria. The microbial remineralization model was developed to explicitly describe the interactions between sinking particles and heterotrophic bacteria using 9 state variables, particulate organic carbon as well as bacteria, active exoenzyme, inactive exoenzyme, and hydrolysate associated with two physical environments, dissolved and particulate. The model has a vertical range from the upper mesopelagic zone to the ocean bottom. A functional form for exoenzyme production based on bacterial population density, which is consistent with quorum sensing, emerged as a result. In addition, high population densities were assumed to retain solutes which greatly increased bacterial production. Solute retention increased particle dissolution rates, and thus has ramifications for models of carbon flux remineralization.

Anders Andersen:

Hydrodynamics of Filter Feeding in Choanoflagellates

Choanoflagellate filter feeding is a poorly understood process. Studies indicate that the pressure differences created by the beating of the flagellum are insufficient to produce an adequate water flow through the collar – the mechanism believed to ultimately transport food particles to the protoplast. We are using high-speed video of live material to explore the flagellar motion and prey capture, and we have designed a hydrodynamically scaled mechanical model to investigate the role of the collar morphology on the flow patterns. We present early observations of particle retention in *Diaphanoeca grandis* and flow visualizations using the scale model.

Andrew Hirst:

Shape shifting resolves conflicts in major theories of metabolic scaling

Respiration is a measure of the overall 'pace of life' of an organism. Understanding what controls this rate, and how it scales to body mass, are central questions in physiology and ecology. Two contrasting hypotheses which attempt to mechanistically explain this scaling are the Metabolic Theory of Ecology (MTE), and Surface-Area (SA) models. Intraspecifically, the MTE predicts $3/4$ scaling regardless of how the surface area changes during ontogeny. By contrast, the SA-model predicts $2/3$ scaling with isometric enlargement, but when organisms diverge from geometric similarity and increase surface area more rapidly, the scaling power is predicted to increase. Pelagic invertebrates provide an excellent test of these competing theories, many species utilize a large portion of their surface for gaseous exchange, while there is a huge divergence from isometry across the wide range of aquatic phyla. Here we compare the predictions of both major metabolic models against empirical data on metabolic and surface area scaling of marine and freshwater zooplankton and nekton. The results demonstrate excellent prediction ability of the SA model, whereas a very poor fit for MTE. The wider implications of these findings are finally explored.

Andrew Irwin:

Testing the stability of the realized niches of phytoplankton in response to changing climate

Decadal-scale time series of phytoplankton species provide a way to test ideas about how individual phytoplankton species niches and community structure will respond to climate change. Conditions at the CARIACO ocean time series station have changed dramatically over the past 15 years, with an approximate 1°C increase in temperature, and 1-2 % yr⁻¹ decrease in macronutrient inventories, chlorophyll concentrations, and primary production. Using a MaxEnt analysis of the niches of 67 species of phytoplankton we identify individual responses to the environmental change for each species.

These responses allow us to characterize a realized niche for each species as a function of several environmental variables (temperature, salinity, irradiance, and macronutrient concentrations). We compare changes in the niches to the observed environmental change to differentiate between two hypotheses: species' realized niches track environmental changes versus species' realized niches are essentially fixed. Preliminary results indicate that many species are able to adapt to temperature changes but are less able to adapt to changes in resource availability.

Anna Hickman:

Shedding light on phytoplankton biogeography

Authors: Anna Hickman, Stephanie Dutkiewicz, Oliver Jahn, Mick Follows

Light is fundamental for photosynthesis and becomes a limiting resource in almost all global oceans. Consequently, the optical characteristics of autotrophs, such as their intracellular pigments, are key functional traits that can shape autotrophic communities through species selection or coexistence. However, where, how, and to what extent light availability impacts phytoplankton biogeography in the ocean remains unclear. We use a global numerical model to explore how the pigment compositions of different phytoplankton functional types contribute to setting their global horizontal and vertical distributions. The model resolves a three-stream radiative transfer of photosynthetically available radiation (PAR, 400-700nm), which is dependent on the spectral absorption and scattering properties of water, phytoplankton, detritus and coloured dissolved organic matter (CDOM). The optical properties of each of several different phytoplankton types are prescribed from a representative species in culture. A series of sensitivity experiments reveal that the specific light absorption spectra are very important in determining the competitiveness of the different phytoplankton, the ecosystem structure, and the feedback to biogeochemistry. The model provides new insight into the role of light as a resource, in the context of resource competition theory. In particular, we explore the importance of photoacclimation, as well as the complex feedbacks between the phytoplankton community structure, the concentration of optical constituents CDOM and detritus, and spectral light field.

Artur Palacz:

Distribution of plankton functional types in response to changes in their ecological niches

Combining information obtained from remote sensing and dynamic plankton models, we design a new diagnostic ecological indicator model of plankton functional types (PFTs). Our model is based on an artificial neural network which has the potential to interpret complex nonlinear interactions between PFTs and the environment – interactions characteristic of complex adaptive systems such as marine ecosystems. The results of our diagnostic model reveal apparent PFT-specific ecological niches that are not always consistent with those inferred from a dynamic plankton model. Our model is sensitive to large seasonal and inter-annual shifts in phytoplankton community composition observed in many regions. Moreover, we demonstrate that in our model silicifiers and calcifiers can be co-dominant in the sub-polar high-nitrate and low-chlorophyll regions, such as the North East Pacific and the Antarctic Atlantic Ocean. Though consistent with in situ and remote sensing observations, this result is in contrast to many if not all state-of-the-art dynamic plankton models which struggle to resolve the paradox of the plankton. We conclude that the ecological indicator approach can be used to potentially improve both past and future model estimates of PFT distributions, and thus also primary productivity, especially in the most remote and under-sampled parts of world's oceans.

Benjamin Weigel:

Does decreasing benthic biomass trigger shift in the functional trait composition over time?

Benjamin Weigel, Anna Törnroos, Erik Bonsdorff
Åbo Akademi University, Department of Biosciences, Environmental and Marine
Biology, Artillerigatan 6, FI-20520 Åbo, Finland

Ecological studies based on time series often investigate community changes based on species density or diversity but rarely focus on the resulting functional aspects of the changes. Here we analyse the effects of a decrease in zoobenthic biomass on the functional trait composition in a well-studied area of the Åland Islands, Northern Baltic Sea, over 12 years (1994-2006). By relating scores of 23 functional traits, including 89 trait modalities, to species biomass, we describe the common functional traits over time and further analyse the composition of those traits, which are increasing in their expression, i.e. their relative importance, over time. Modifications in trait compositions such as body design, environmental position or reproductive frequency of the benthic fauna may affect its quality as food resource for higher trophic levels. Thus, in addition, we filter out and analyse the trait importance based on benthivorous fish predation relevance. Our results indicate that despite the decrease in biomass, the modalities experiencing the highest scores remain similar in their composition throughout the investigated period, i.e. the type organism. However, changes in biomass appear to alter the relative importance of certain modalities over time, which could serve as indication for upcoming functional shifts in the system.

Chisato Yoshikawa:

An ecologically flexible type model applied to two contrasting time-series stations in the western North Pacific

Chisato Yoshikawa, S. Lan Smith, and Agostino Merico

We are currently developing the first prototype ecologically of a flexible type (EFT) model based on a physiological trade-off to constrain the adaptive response for nutrient uptake by phytoplankton. We apply this model to two timeseries stations in the western North Pacific: a subarctic station K2 (47N / 160E) and a subtropical station S1 (30N / 145E), using observed time-series as forcing for the seasonal variations in environmental conditions. We will present the adaptive response of phytoplankton communities to the environmental seasonal cycles and discuss the differences in the two contrasting regions.

Chris Lindemann:

Towards an adaptive evolutionary and ecological trait-based model

The ET (Evolutionary Trait) model is a spatially explicit Individual-Based-Model which uses trait and trade-off concepts to model complex trophic interactions in marine ecosystems on both evolutionary and ecological timescales. The model is designed to capture a wide range of size classes (viruses to whales) and trophic positions (parasites to top predator). The model community is characterized by three main traits (size, mobility, functional composition) and a number of associated trade-offs (e.g. generalist vs. specialist). Base traits, defining each individual in general terms (e.g. species, functional role) change on evolutionary timescale due to mutation and recombination, while the current condition of each individual is given by their ecological state. This is computed from their respective base traits via an adaptive internal model taking into account the feeding history and environmental conditions. Predator-prey dynamics mimic the interactions between adaptive agents similar to John Holland's Echo model. Here the outcome of an encounter is the result of comparing offense and defense tags of the interacting agents thereby assigning predator and prey roles and assessing trophic interaction in a non-predefined manner. The combination of traits, trophic interaction and the adaptive internal model drive the emergent dynamics of this model and result in complex nonlinear interactions commonly found in (marine) ecosystems.

Clinton Leach:

Application of size-structured population models to explain the decline in mean body size on the Scotian Shelf

Over the last several decades there has been a dramatic and persistent decline in the average body size of predator fish on the Scotian Shelf (Fisher et al. 2010). Proposed mechanisms for the maintenance of this shift include predator-prey role reversal, wherein numerically dominant forage fish prey upon the early life stages of large predator fish, and intensified competition between these forage fish and small-bodied predators. Both of these mechanisms involve size-structured interactions, and require that we account for intraspecific variability in body size and diet. Size-structured PDE models have been developed recently as a powerful tool to capture the structure and dynamics of marine fish communities, but there have been relatively few attempts to fit these models to data. We develop and fit a tri-trophic (predator fish, forage fish, plankton) model to 33 years of size-spectra data for the Scotian Shelf to evaluate the importance of size-structured mechanisms in generating the observed dynamics and preventing recovery. This model will provide the foundation for future work incorporating additional trait diversity (i.e. expanding the three trophic levels) and species-specific feeding preferences (i.e. food web structure), to explore the amount of detail required to effectively model the dynamics of real communities.

Daniel Grunbaum:

Effects of unresolved spatial and temporal heterogeneity on diversity and productivity in trait-based consumer-resource models in marine environments.

The resources of most marine organisms vary spatially and temporally across a wide range of scales. In contrast, the models used to understand and predict the these organisms' populations typically adopt a mean-field approach, in which most heterogeneity is intentionally excluded.

Consequences of the missing dynamics potentially include inaccurate estimates of trophic interaction rates, ineffective management policies, and compromised explanations of fundamental characteristics of marine ecosystems such as diversity, productivity and stability. Here, I present a scaling analysis of consumer-resource interactions in heterogeneous or "patchy" environments. The analysis yields nondimensional ecological indices that summarize the relative impacts of three primary mechanisms: consumers' foraging behaviors, consumers' resource-limited reproductive rates, and depletion of high-resource patches. Using published allometries as constraints for movement, reproduction and feeding traits, I use the patch dynamics scaling framework to consider conditions under which environmental heterogeneity at various time and space scales acts to enhance diversity and productivity in marine ecosystems. The framework predicts observable variations in "transduction" of resource heterogeneity into consumer heterogeneity as functions of time and space scales.

Elena Litchman:

Eco-evolutionary responses of phytoplankton to global Change

Phytoplankton are sensitive to various aspects of global change and their responses may be species and trait-specific. Understanding how communities would reorganize in the future requires the knowledge of mechanisms of responses. Phytoplankton may have plastic responses, they can evolve via mutation, there can be selection on intraspecific standing variation in relevant traits and also species sorting, with better-adapted species being selected for. These mechanisms may differ in their relative importance and need to be assessed to adequately predict future phytoplankton communities.

Elizabeth Miller:

Trait-wise investigation of phytoplankton communities reveals predictable responses to seasonal environmental variation

To understand the mechanistic basis of seasonal phytoplankton succession. We measured 4 physiological traits (maximum growth rate, phosphorus affinity, light affinity, and predation resistance) on 27 phytoplankton species during the course of succession in a Northern temperate lake, and looked at how the trait distribution of the community responded to changes in the physical and biotic environment over the course of 6 seasons. Our research asked whether the traits of the community were well predicted by the environmental time series and whether the species themselves or the community as a whole exhibited tradeoffs between success along major trait axes. Using species growth rates as a measure of fitness, we see strong tradeoffs in species performance under different environmental conditions. We also see the characteristic succession pattern of species replacement borne-out in the community trait distributions leading to a correlation between average community trait and environmental condition. The tradeoffs among the species traits themselves, however, do not begin to emerge until multiple axes are taken into consideration.

Erik A Martens:

Trait-based modeling of trophic chains and seasonal forcing

How do seasons affect predator-prey interactions in the marine ecosystem? This study aims at understanding how seasonality and its varying strength along different latitudes affects marine ecosystem structure. Specifically, we like to understand how many trophic layers can be supported given a certain latitude, and at what rate the amplitude of seasonal succession attenuates along the trophic chain. First results are presented by studying a simple null-model of the trophic chain in marine systems. We discard the concept of species or functional groups and use a trait-based approach, where we describe individuals with mechanistically based traits such as size. Future directions aims at extending this null model to resolve each trophic layer by including further traits, and by including life history to study traits such as reproductive and overwintering strategies.

Friederike Prowe:

Zooplankton feeding traits and community composition in a global ecosystem model

Global marine ecosystem models are being used to investigate plankton biogeography and its effects on ocean ecosystem dynamics.

In these models, typically a fairly refined representation of phytoplankton functional types contrasts with an oversimplified implementation of zooplankton characterized by rigid plankton interactions. Top-down control by zooplankton, however, may govern simulated plankton community composition and diversity, and thereby affect ecosystem dynamics and food web structure.

In order to assess potential effects of an improved representation of plankton communities, we present a new trait-based model of plankton interactions. Focusing on zooplankton feeding strategies and their trade-offs, this model explicitly resolves variable top-down control of the phytoplankton community. Coupled to a diverse phytoplankton assemblage in a global ocean ecosystem model, it aims at exploring effects of community composition on seasonal succession, plankton biogeography and trophic dynamics. This setup allows us to directly quantify differences compared to more traditional zooplankton formulations and compare communities under different environmental regimes.

Geir Huse:

Modelling emergent life histories of *Calanus finmarchicus*

The copepod *Calanus finmarchicus* is the dominant species of the meso-zooplankton in the Norwegian Sea ecosystem and is a key grazer of phytoplankton and prey for the abundant planktivorous fish stocks. Spatially explicit models are key tools for understanding spatial-temporal zooplankton dynamics as a function of currents, behaviour and selective growth, mortality and reproduction. Here, we present a 3D individual based model with emergent life-history and behavior for *C. finmarchicus*. The objectives are to investigate the importance of the simulated adaptive process on retention and fitness of *C. finmarchicus* and the importance of spatial and inter-annual variability and different predator densities on the evolved life history traits of *C. finmarchicus*. The results show that in most of the simulations the populations remain viable within the Norwegian Sea throughout the hundred years. In simulations with fixed spatial position there were small differences between the replicates. Inter-annual variability in forcing resulted in increased difference in fitness between years. Simulations with spatial-, but without inter-annual variability produced large differences in centre of mass, fitness and life history strategies between replicates. This was due to the repetition of a single year with a particular current pattern. In simulations with both spatial and inter-annual variability the replicates had small variability. Increased predator density resulted in increased day depth. The model can be used for a range of different applications such as individual and population responses to climate change. The adapted trait values from this model are useful in parameterizing *C. finmarchicus* components of ecosystem models.

Harvey Tyler-Walters:

Biological Traits Information Catalogue (BIOTIC)

We will outline the history of biological traits databases in the UK (at MarLIN/BIOTIC) and their development. We will look at their application in environmental management, in particular sensitivity assessment. And outline planned development of a common traits vocabulary through the EMODNET- Biology project.

Houshuo Jiang:

Why does the jumping ciliate *Mesodinium rubrum* possess an equatorially located propulsive ciliary belt?

It has long been thought that jumping by the ciliate *Mesodinium rubrum* can enhance its nutrient uptake. However, jumping can be energetically costly and also dangerous by inducing hydrodynamic disturbances detectable by rheotactic predators. Here, a computational fluid dynamics (CFD) model, driven by published empirical data, is developed to simulate the jump-induced unsteady flow as well as chemical field around a self-propelled jumping ciliate. The associated phosphorus uptake, hydrodynamic signal strength, mechanical energy cost and Froude propulsion efficiency are also calculated. An equatorial ciliary belt (ECB), i.e. the morphology used by *M. rubrum* for propulsion, is considered. For the purpose of comparison, three other strategies (pulled or pushed by cilia, or towed) are also considered. Comparison of the CFD results among the four strategies considered suggests: (i) jumping enhances phosphorus uptake with simulated values consistent with available field data; (ii) the *M. rubrum*-like propulsion generates the weakest and spatially most limited hydrodynamic disturbance and therefore may effectively minimize the jump-induced predation risk; and (iii) the *M. rubrum*-like propulsion achieves a high Froude propulsion efficiency (~ 0.78) and is least costly in mechanical energy expenditure among the three self-propelled strategies considered. Thus, using the ECB for propulsion can be essential in ensuring that *M. rubrum* is a successful 'fast-jumping' primary producer.

James Clark:

Environmental selection for small cell size in phytoplankton

Small cell size in phytoplankton confers a significant advantage in terms of resource acquisition and utilisation in resource-scarce environments, but must be traded-off against the necessary increased allocation of resources to non-scalable structural components (DNA, membranes).

Using a model for cellular resource allocation, we show that this leads to a tradeoff between cell size, nutrient and light affinity, and growth rate. Within the most extreme nutrient-limited, stratified environments, resource competition theory then predicts a trend towards larger cell size with increasing depth. We demonstrate that this explains observed trends using a marine ecosystem model that represents selection and adaptation in a diverse community defined by traits for cell size and subcellular resource allocation.

Jan Heuschele:

Female choice in eutrophied waters - an individual based model of sticklebacks

Ecological changes of the environment can alter selection pressures in mating systems. Human induced eutrophication is known to influence mate choice and competition in several fish species. In three-spined sticklebacks it can alter mate preferences and reduce female choosiness for nesting males, but several mechanisms may explain the observed patterns. Here we use an individual based model to explore how environmentally induced changes in the ability to locate and assess mates, mate density and quality will affect mate choice decisions of female sticklebacks.

Jennifer Hammock:

To Increase Utility, Add More Data; sharing and interoperability for marine trait datasets

Where do marine trait datasets live? Online, trait data can be found at marlin.ac.uk/biotic, genustraitshandbook.org.uk, fishbase.org, marinespecies.org, crustacea.net, decapoda.free.fr, spongemaps.com, researchdata.museum.vic.gov.au/squatlobster, and many other sites, in many formats. Sometimes it appears as structured data, sometimes as text, sometimes in proprietary key formats. There is a wealth of information, which is good, because rich information is needed in order to address large-scale questions and discover regional and global patterns. However, even among digital datasets, the variety of formats presents a barrier to aggregation of large, taxonomically or geographically broad datasets.

There are a number of repositories that could provide infrastructure for aggregating trait data. The Encyclopedia of Life, eol.org, is an aggregator of biodiversity information. Our mission is to facilitate dissemination and re-use of this information in research and education. Information posted to eol.org is freely available, to website visitors, and by API for large scale queries, text-mining, etc. We are embarking in 2013 on an expansion of our service to include structured data, and in particular, marine data. We are in need of input about data sharing formats and fields used or needed by the marine community for exchanging this information.

Which existing ontologies and other data structures are in common use? What filters, search tools and download formats would be needed for researchers to be able to extract useful datasets? Is quality control a concern? How should provenance and attribution be documented, and usage communicated back to data providers? What large scale questions can be made tractable if existing trait data sources are leveraged together? What would it take for you to be interested in depositing datasets in a global repository, and in using one as a tool for your research?

Jessica A Bryant:

Temporal Variation in Marine Microbial Trait Diversity

Metagenomic (community genome sequencing) approaches provide a genetic 'parts list' of the traits microbes utilize to persist in their environment. We are harnessing this genetic 'parts list' to study temporal variation in planktonic marine microbial communities. Microbial community samples were collected at 25m depth at approximately monthly intervals across a 2-year period alongside the long-term environmental monitoring program, Hawaii Ocean Time Series (HOT) at the North Pacific Subtropical Gyre station, ALOHA.

Microbial communities within the samples were characterized using shotgun metagenomic sequencing. We then used a database independent clustering technique to bin protein-coding sequences within the metagenomic data into clusters or putative traits based on sequence similarity.

We found that trait richness across our samples is correlated with species diversity measured using 16s marker genes (r^2 : 0.5, p value < 0.001). The two would not have been well correlated if traits were highly redundant across microbial taxa or horizontal gene transfer was highly prevalent. We also found that microbial trait richness can vary by up to 1.5 fold between time points. The variation appears to be largely driven by wind driven mixing events. It was unexpected that microbial dispersal rather than the chemistry of the water column or seasonal cycles would be the major determinant of microbial diversity in surface water at station ALOHA.

Johanna Yletyinen:

Traits and species interactions affect the response and dynamics of marine social-ecological systems to multiple drivers

The important role of marine areas in provision of ecosystem services is under an increasing pressure of anthropogenic stressors, such as climate change. The understanding of these effects on marine ecosystems requires complex system perspective and analysis on powerful reciprocal feedbacks between social and ecological systems. Many studies have looked at the species diversity connected to ecosystem properties, but less attention has been given to interactions that may amplify or modify the direct effects of climate change on ecosystems. Network analysis is increasingly recognizing the importance of traits in ecological communities. Methodologically traits are an important factor in networks as node attributes that can affect relationships between different species, responses to environmental drivers, and ecosystem services. Our research project applies network theory and ecological and social network analysis to analyze the structural patterns of interactions in Nordic marine social-ecological systems exposed to climate impact. The first part of this project consisted of ecological network analysis on 21 functional groups in the central Baltic Sea. The food web model was forced by climate variables and fishing to perform an ecological network analysis for the time period of 1974 - 2006. Our results emphasized the cumulative nature of anthropogenic stressors, and the ecological network indices succeeded in showing the food-web changes of the late-1980s' regime shift and the changed topology of the food web. This research will continue with investigating the effect of network properties on the response of traits and food web properties to changing multiple drivers, and further on with the analysis on linkages between food webs and institutional, economic and social dynamics of the marine resource management.

Julie Sainmont:

Relative success of Income and Capital breeder in a seasonal environment

Among life history traits, reproduction strategy is a strong component of the specie's fitness in a given environment. Capital and Income breeding terms have emerged in the literature to describe resource allocation to reproduction. Capital breeding is associated with the resource accumulation to be able to spawn detached from food availability, while income breeding refers to the direct allocation of ingested food to reproduction. Motivated by copepod studies, we use an analytical model to compare the fitness of income against capital spawning as a function of the feeding season duration, and size at maturity. Small capital breeder performs better in short feeding season, but are overcome by bigger individual when the length of the spring bloom increases. Income breeding favors smaller individuals in any circumstances and out-compete capital spawning in long feeding season.

Karen Stamieszkin:

A synthesis of copepod fecal pellet characteristics and implications for carbon cycling in the ocean

The sinking of particulate organic carbon (POC) from oceanic surface waters is a major component of the marine biological carbon pump. Large particles generally sink faster than small particles in the ocean. Mesozooplankton can increase carbon export efficiency by repackaging small food particles into larger fecal pellets that sink. We hypothesize that copepod body size is of first order importance to fecal pellet size, but that diet exerts a strong influence on carbon content. Based on the numerous copepod-POC experiments reported in the literature, we are building an allometric multivariate linear model that relates copepod fecal pellet size to copepod body size, prey type, and environmental conditions. Copepod community composition is shifting as oceanographic conditions respond to climate change. The range and seasonal duration of warmer conditions is expanding, implying a spatial and temporal range expansion of smaller-bodied copepods. Therefore, prediction of copepod fecal pellet characteristics based upon traits such as body size can clarify how oceanic carbon cycling may change with changing climate.

Karin Olsson:

Offspring size as a strategic life history trait

Offspring size is a central aspect to life history and a key feature to lifetime fitness due to its expected inverse relation to fecundity. Comparing offspring size to adult size in fish, we were able to confirm the existence of two apparently distinct offspring size strategies: the small-size strategy whereby species produce small offspring irrespective of adult size, and the proportional strategy by which species produce offspring of a size that is a relatively fixed fraction of the adult size. Broad classifications of fish, such as viviparous and oviparous, as well as teleost and elasmobranch, only partially correspond to these offspring strategies. Here we compare life history parameters for oviparous and viviparous species of both elasmobranchs and bony fish in search of a matching pattern. We collected data on size at birth, size at maturity, growth, natural mortality and reproductive output for elasmobranchs and bony fish. We discuss potential associations between offspring size and reproductive mode and phylogenetic belonging. We go on to propose a modified offspring-size model based on simultaneous effects of size-dependent mortality and predator size-preference to help account for the diverging strategies.

Katharina Maj Ottosen:

Spatial distribution of cod on the Faroe Plateau

The Faroe Plateau cod occupy the shelf area around the Faroe Islands at depths down to 500 m and is isolated from other Atlantic stocks. In the spring the Faroe Plateau cod migrates towards one of the two main spawning areas located west and north of the Islands. After spawning, the cod disperse all over the plateau. The preferred spawning temperature of cod varies among cod stocks and ranges from 0 to 6 °C. Exceeding 6 °C, the spawning success is probably negatively affected by the temperature. During the last two decades the Faroe Shelf water temperature has experienced an increase of about 1 °C, from 7.8-8.8 °C. Somehow, this increase in temperature might affect the spawning activities and success of the Faroe Plateau cod.

Preliminary studies of cod on the Faroe Plateau have shown a change in the spawning centre towards east in the spring while no change in the mass centre was shown in the autumn. On the basis of bottom trawl survey data collected on the Faroe Plateau in spring and summer during the years 1994-2013 and data on surface and bottom temperature collected in the same period, correlations between the spatial changes of cod and temperature on the Faroe Plateau will be carried out, both within and out of the spawning season. In addition, stomach data on cod, plankton data and data on other fish species will be analysed to elucidate changes in the spatial distribution and determine how those changes affect recruitment in the cod stock.

Lasse Tor Nielsen:

Traits and trade-offs in microzooplankton feeding modes: from filter feeding choanoflagellates to ambush feeding dinoflagellates

Various zooplankton feeding modes are easily recognized and each has advantages as well as disadvantages. We unravel the feeding mechanisms in various microzooplankton organisms, and quantify the associated trade-offs. Study organisms range from filter feeding choanoflagellates to ambush feeding dinoflagellates, and feeding mechanisms are resolved using high speed video and particle tracking. This allows for analyses of hydromechanical flow fields, and for the identification of potential constraints and limits governing the different feeding modes.

Maria Huete-Ortega:

Size-scaling of phytoplankton abundance and metabolism: a review of recent field and laboratory studies

Authors: Huete-Ortega, M., Rodríguez-Ramos, T., López-Sandoval, D. C., Cermeño, P., Blanco, J. M., Palomino, R. L., Rodríguez, J. and Marañón, E.

The size structure of phytoplankton plays a key role in pelagic ecosystems, affecting the trophic organization of plankton communities and, hence, their functioning in the biogeochemical cycling of many elements, including nitrogen or carbon. Phytoplankton cell size spans over more than nine orders of magnitude in cell volume, and its taxonomic affiliation varies along the size spectrum from the smallest cyanobacteria to the largest diatoms. Cell size influences many aspects of the metabolism and ecology of phytoplankton, such as growth, metabolic rate, access to and use of resources, sedimentation rates and grazing pressure. Therefore, cell size is considered to be a master trait for conducting trait-based studies in phytoplankton ecology and contributes significantly to the knowledge of pelagic ocean ecosystems dynamics. In this communication, conclusions from recent experimental studies on the size-scaling relationships of phytoplankton abundance and metabolism both in culture and natural communities of coastal and open-ocean ecosystems will be reviewed. The effect of environmental factors on these relationships will be discussed in order to explain patterns in the size structure and function of phytoplankton communities in marine ecosystems. This review aims to define the current state of phytoplankton size-scaling studies and to identify future lines of research.

Martin Hartvig:

Food webs in a changing climate; inter- and intraspecific temperature dependencies

How do food webs and communities vary across a temperature gradient? And how do these webs react to temperature changes?

Meike Vogt:

Observation-based plankton biogeography in the global ocean

Marine plankton play a central role in the biogeochemical cycling of important elements such as carbon, nitrogen, and sulphur, but our knowledge about their distribution and relative importance is still scarce and episodic. However, several recent observational studies confirm that marine ecosystems have been changing due to recent climate change, overfishing, and coastal eutrophication. In order to better understand marine ecosystem structure and dynamics, the MARine Ecosystem DATa (MAREDAT) initiative has recently collected abundance and biomass data for 5 autotrophic (diatoms, Phaeocystis, coccolithophores, nitrogen fixers, picophytoplankton), and 6 heterotrophic plankton functional types (PFTs; bacteria, micro-, meso- and macrozooplankton, foraminifera and pteropods). Here, we describe spatial patterns of different plankton functional groups, and quantify their relative importance as a function of latitude and depth. We use species distribution models (SDMs) to derive information about the habitats of different plankton species in space and time, and simulate global habitat suitability and extent for different plankton species in the modern ocean. Habitat suitability is derived from presence-only MAREDAT data and the observed annual and monthly mean levels of physiologically relevant variables such as SST, nutrient concentration or photosynthetic active radiation received in the mixed layer. The results give a first indication what present and future plankton habitats may look like, and what consequences we may have to expect for future marine ecosystem service provision in a warmer world.

Nathan Terseleer:

Trait-based representation of diatom diversity in a Plankton Functional Type model

Biogeochemical models often reduce biological complexity by assembling a large number of species sharing common ecological and biogeochemical functions into Plankton Functional Types (PFTs). In this approach, species diversity inside each PFT is generally not considered. Conversely, recent adaptive modelling approaches emphasize plankton diversity by letting communities self-assemble through competition amongst large numbers of species. Here, we combine adaptive and PFT approaches by introducing a trait-based description of diatoms in the existing MIRO model. The latter describes carbon and nutrient cycles in the Southern North Sea ecosystem with three autotrophic (diatoms, Phaeocystis, nanoflagellates) and three heterotrophic (bacteria, micro- and meso-zooplankton) PFTs. The new trait-based module relates fundamental properties of diatoms to their size: smaller diatoms have a higher maximum growth rate, photosynthetic efficiency and nutrient affinity, while larger diatoms benefit from reduced grazing pressure. This tradeoff makes optimal diatom size dependent on resource availability and predation pressure, favouring species succession in a variable environment. The diatom community is modelled as a continuum of sizes, which is represented by the total diatom biomass, their mean biovolume and its variance. The model is implemented in the Belgian coastal zone, where high quality observations allow a reconstruction of nutrients, PFT concentrations and diatom community structure for 1988-2000. The added value of the trait-based description of diatoms is evaluated by comparing outcomes from a model without diatom diversity and the trait-based approach. Applicability of the trait-based model across a gradient from open ocean-like waters to enriched coastal waters is investigated. Results are further analysed to identify the mechanisms driving diatom succession.

Navish Wadhwa:

Size dependent flow structure changes in swimming copepods

Swimming by jumping in adult copepods is suggested to be energetically favorable and hydrodynamically quieter than more continuous swimming, due to the formation of vortex rings (Jiang and Kjørboe, *J. Roy. Soc. Interface* 8, 1090 (2011)). Hydrodynamic considerations suggest that there must be a lower size limit to form vortex rings. To investigate this limit, we examine the fluid motion caused by jumping copepods, adults as well as nauplii, using particle image velocimetry (PIV). Our result show a remarkable difference between the flow structures around jumping nauplii and copepods.

Neil Banas:

Size-based seasonal phytoplankton dynamics at Helgoland Roads, German Bight

Rich observations of phytoplankton species composition and abundance at Helgoland Roads, along with observations of the abundance of their dominant grazers, are used in combination with the trait-based plankton model of Wirtz (2013) to explore the interaction of bottom-up and top-down controls in shaping phytoplankton productivity and diversity patterns over spring-autumn 2005. Trait-based and discrete-size-class versions of the model are compared, in order to assess the effect on model behavior of relaxing the assumption of a unimodal, symmetrical size distribution inherent to the trait-based formulation. Results will be added to this abstract after the answer is determined, which will occur sometime between the end of the course I'm teaching and August 26.

Nis Sand Jacobsen:

Comparing ecosystem models as fisheries management tools: a case study in the California current

Nis Sand Jacobsen, Laura Koehn, Emma Hodgson, Ken Haste Andersen and Tim Essington

As ecosystem modeling is becoming a more integral part of fisheries management, there is a need to quantify differences between various models currently being employed for scientific and management purposes. Using two models, Ecosim and a size- and –trait based model, we simulate the ecological consequences of fishing to identify commonalities and differences in model predictions for the California Current food web. We simulated extreme ecosystem fishing scenarios targeting specific parts of an ecosystem, as well as the ecological consequences of employing four separate fleets. We find that the most important differences between models are 1) competition in the trait-based model causes increased abundance of larger species when forage fish are removed whereas bottom up consequences are more unpredictable in Ecosim, 2) diet matrices in Ecosim change the responses of individual species compared to a size based food selection approach, 3) size- and trait based models predict a higher degree of top-down control than Ecosim. We also find that there is a multispecies maximum sustainable yield in the size structured model where no species crash. We conclude that the choice of ecosystem model critically influences the outcome of a given fishing scenario and conclusions from a single model should be drawn carefully.

Pieter Vandromme:

A New Trait-Based Auto-Emergent Model for Zooplankton and Confrontation with Size-Structured Observations from the Bay of Biscay

Zooplankton plays a significant role in marine ecosystems bridging the gap between primary producers and top consumers and interacting with the particle flux through complex dynamics. Scarcity of data and complexity of observing zooplankton make it difficult to integrate it in biogeochemical models where it is most often formulated in a simpler manner, i.e. classic box models with usually two compartments (micro and meso/macro zooplankton). Recent advances in automatic sizing, counting and identification allow better estimates of the dynamics and distribution of zooplankton, notably through the measurement of its size structure, and for zooplankton size matter. Most zooplankton physiological rates as well as predator:prey interactions can be significantly related to individuals size through allometric relations. Such sizedependency was used in recent models. Yet, these models were neither confronted to observations nor integrated in 3D biogeochemical models. Here we propose a newly developed model of zooplankton dynamics based on sizedependent allometric relations but which allows various diet types regardless of the size. A size and a degree of herbivory is randomly drawn for each zooplankton species generated within the model (up to 400 here, limited by actual computational costs). By generating random degree of herbivory zooplankton species of same size could have various diet (from herbivore to carnivore). Other parameters leading to various reproductive strategies or vertical migration could also be drawn randomly (not tested here). The zooplankton model is coupled to the 3D biogeochemical model MARS3D on a test case representing a simplified view of the Bay of Biscay (i.e., continental shelf, estuary, tides). The model shows auto-emergent properties with the selection of size/diet most adapted to local conditions (here offshore vs. coastal, estuary...). Then, patterns of the modeled size-structure of the zooplankton are confronted to the ones observed during Spring-time cruises in the Bay of Biscay. The usefulness of the proposed zooplankton model for large scale biogeochemical models is further discussed.

Rebecca Holt:

Climate-Induced Adaptations of Behaviour and Life History for Atlantic Cod

At the individual level, increasing temperature influences bioenergetics and numerous physiological and life history processes, and consequences are expected for populations, communities, and the functioning of marine ecosystems. We provide a mechanistic model that predicts temperature-induced adaptations for life histories and behaviour of Atlantic cod (*Gadhus morhua*). Temperature dependent physiological functions for respiration and ecological parameters of mortality, harvesting, migrations and temperature seasonality are input within the model. Dynamic programming is used to find the optimal strategies of foraging, energy allocation, survival, growth and reproduction, providing intra-specific stock comparisons. Emergent life history strategies result through evolutionary optimisation, and optimal individual strategies are simulated in populations to provide predictions of individual and stock responses to climate change. Climate warming changes the optimal maturation age, reproductive investment, and foraging strategy beyond what is expected by physiological considerations alone, and there are strong interactions with harvesting mortality. The model illustrates how climate change effects may influence the life history strategies of cod in diverse ways, and how stocks may differ in their response. We incorporate and challenge the concept of physiological performance thresholds by showing how the effect of temperature on adaptations depends on the ecological setting.

Rodrigo Gonçalves:

Prey/predator size ratio in feeding of *Temora Longicornis*

The copepod *Temora longicornis* creates a micro current to catch and ingest particles (eg algae cells) entrained in its flow. Some cells are detected, ingested, but some are also missed. It is not clear how this work and what is the relationship with the capture success and prey size (or prey/copepod size ratio). We use a combination of digital high speed videography, bottle incubations and particle image velocimetry to get more insight into the feeding behavior of this copepod.

These results will help us understand the mechanistic underpinning for the feeding process to provide input to trait-based models.

Selina Våge:

Trade-offs between defensive and competitive traits shape the marine microbial food web

The marine microbial food web is characterized by an enormous complexity and diversity. Can this complexity be understood from simple ecological principles? Answers from three models, ranging from a generic 3-population model to a more complex model of virus-host communities to a cell size and foraging-mode structured mixotrophic food web model, are presented. The idealized food web models show that much of the diversity can be explained by top-down control of competitors, which themselves experience a trade-off between competitive and defensive traits.

Sofia Ferreira:

Estimating phytoplankton phenology metrics from noisy, gappy data

A Sofia A Ferreira, Andre W Visser, Brian MacKenzie, and Mark R Payne

Phytoplankton phenology has been used to assess marine ecosystems response to climate change. However, there are several causes for uncertainty when estimating phenology metrics, such as observational noise, missing data, and amplitude, and the choice of temporal resolution, pre-processing technique, and phenology metric. Here, we review phenology estimations for continuous variables, which may apply beyond the marine environment. We first assess how error estimations behave with noise and gappiness degree in synthetically generated data. Both accuracy (mean, degree of veracity) and precision (standard deviation, degree of reproducibility) are scanned for each temporal resolution available from satellite-based ocean colour (daily, weekly, and monthly). Secondly, we apply true satellite masks of missing data within the North Atlantic to test the applicability of different phenology metrics: timing of maximum, of 5% increase above the median, of maximum growth rate, and of 15% of the annual cumulative distribution.

We show that weekly data are best suited for low amplitudes, whereas daily data perform better in high amplitude regions. However, variability of error estimations between phenology metrics appeared to be greater than between different temporal resolutions or pre-processing techniques.

We further show that the most robust approach to estimate phytoplankton phenology in the North-east Atlantic is to define bloom initiation as TCUD on pre-processed, weekly data. We believe that the current knowledge of phytoplankton phenology is prone to improvements based on our results.

Terje Berge:

Mixotrophy in pigmented flagellates

Terje Berge & Per Juel Hansen

Abstract: Observations suggest that mixotrophy, in the sense of the ability to use photoautotrophy and phagoheterotrophy as nutritional sources in the same organism is the ecologically most significant life strategy of marine phytoplankton. We use laboratory experiments to study effects of light intensity on photosynthesis, feeding and growth of mixotrophic flagellates previously assigned to as phytoplankton. Supported by our observations, several other findings indicate that most pigmented flagellates are obligatory dependent on light and their feeding rates are stimulated by higher light intensities. The interactive effects of ingestion and photosynthesis on growth observed in the laboratory suggest that a conceptual model should include at least two essential elements: carbon and nutrients.

Lise Marty:

Fisheries-induced neutral and adaptive evolution at the genotypic and phenotypic levels in exploited fish populations

Lise Marty, Ulf Diekmann, Bruno Ernande

Fishing may induce neutral and adaptive evolution affecting life-history traits such as growth, maturation, and reproductive investment, but molecular evidence for adaptive evolution is still lacking in wild populations. Genetic analyses have focused on neutral genetic diversity only and showed that it has declined in some exploited populations. Here we theoretically study the interplay between neutral and adaptive evolution caused by fishing and their consequences at the genetic and phenotypic levels. An individual-based eco-genetic model is devised that includes neutral genetic markers and functional loci coding for quantitative life-history traits in a realistic ecological setting. We report the following findings. First, fishing reduces neutral genetic diversity as measured by effective population size, which is co-varying linearly with important population demographic features. Second, fishing induces an erosion of functional genetic diversity, which can prevent life-history traits from recovering when fishing pressure stops. Third, the contribution of selection to functional genetic diversity erosion clearly dominates that of genetic drift for traits related to maturation, but not for others. Together, our results suggest that effective population size and neutral genetic diversity could be respectively used as indicators of population demography and functional genetic diversity for fish stock management, the latter being empirically controversial.

Yury Zablotski:

Sympatric speciation by optimal specialisation

Sympatric speciation is one of the most debated and intriguing concepts in evolutionary biology, because in contrast to allopatric speciation it happens without geographic isolation (Via,2001, Bolnick,2007, Bird,2012). Speciation can reduce resource competition (Bolnick:2007) via niche partitioning. It can result from disruptive selection and assortative mating, leading to reproductive isolation, e.g., by divergent mate timing or habitat choice (Bolnick,2007). However, a concrete mechanism which allows sympatric speciation has been difficult to pin down. Here we show that specialisation can lead to sympatric speciation, provided that sufficient ability is retained to eat the less-preferred prey. We define a specialisation trade-off between the improved ability to eat the preferred prey (gain) and reduced ability to eat the lesspreferred prey (cost). We find that the degree of specialisation strongly depends on specialisation cost and that high costs can prevent speciation. Low and intermediate specialisation costs show disruptive selection and, for two prey items, create two niches via resource partitioning. Our model associates specialisation costs with interaction strength and implies that weak interactions (Emmerson,2004) are a prerequisite for sympatric speciation. This study provides a new approach for tracing the mechanisms of speciation via trade-offs.

Yvan Lagadeuc:

Microscale nutrient fluctuations : what functional traits allowing to face?

At microscale environments, the availability of nutrients and chemical signals for microorganisms can be highly intermittent, due to the effect of turbulence or to the distribution of producers. The ability of the phytoplanktonic cells to respond to the patchy nutrient availability could be influenced by physiological processes allowing uptake which do not follow the classical Michaelis Menten function. We have used a new microfluidic technology design for studying the effects of temporal fluctuations in signals or nutrients on nutrient uptake. The device allows a small population of phytoplankton to be exposed to arbitrary signal < 10 second time constant. These physiological features have been tested as a new functional trait compared with other known functional traits.

Zair P Burris:

Copepod sex-ratios may be female-biased at birth

Calanoid copepods commonly have female-biased adult sex-ratios, possibly as a result of skewed ratios at birth, higher male mortality rate, or environmental sex-determination (ESD). There is little information on copepod sex-ratios at birth, making it difficult to draw conclusions about the importance of other factors influencing adult ratios. Sex-ratios for field caught *Acartia tonsa* females were determined by rearing individual families in the laboratory. Of 21 females, 9 produced significantly female dominated clutches (between 70-100% female), whereas 4 produced mostly males (69-79% male). The population sex-ratio was female biased (1 male to 1.5 females). Because egg hatching success was high and mortality was low for all copepod stages, we infer that adult sex ratios were determined mostly at birth. Compared to adult sexratios observed in the field (ranging from 1:1.5 to 1:2.9), female-biased sexratios at birth may account for some of the adult sex ratio for this species.

Øystein Varpe:

Optimal life-histories in seasonal environments: modeling copepod strategies

Animal behavior and life-history strategies have evolved in response to seasonal cycles in food availability, predation risk and abiotic conditions. A common and overarching adaptation for organisms in seasonal environments is the evolution of schedules of activities over the annual cycle, sometimes referred to as annual routines. Allocation to growth, energy storage and reproduction are central parts of life-history strategies and the timing of these processes within life and within the annual cycle has important fitness consequences. We wish to understand the optimal schedule of these components in a given environment, that is, to predict the strategy that maximizes fitness. Here I will illustrate how optimality models can guide us in this endeavor. I present examples from models on high latitude copepods and explain how these models can be used to study phenology, life-history strategies, and population dynamics, and importantly, to predict responses to environmental change. Specific research questions include: What are the consequences of earlier food availability (primary production) on the optimal timing of copepod reproduction? What is the optimal schedule of activities when the food source has bimodal seasonality, such as when Arctic copepods feed on both ice algae and pelagic phytoplankton? Our findings lead to discussions of central concepts in ecology and evolution such as the match-mismatch hypothesis, state-dependent strategies, parent offspring conflict, and the reproductive modes of capital and income breeding.

Sachia Jo Traving:

Extracellular enzymes: foraging strategy for free-living marine bacteria

Dissolved organic matter (DOM) in the oceans is one of the largest reservoirs of carbon in the biosphere (Hansell *et al.* 2009). The entire ecosystem contributes to the DOM pool, but the pool is almost exclusively exploited by the bacterioplankton through the microbial loop and this represents a major trophic pathway (Pomeroy 1974; Azam *et al.* 1983). Up to 50% of marine carbon fixation is processed by the microbial loop (Cole *et al.* 1988) and bacterioplankton therefore play an important role in biogeochemical fluxes, marine productivity and food web structure. DOM consists of a complex mixture of compounds ranging from simple monomeric substrates to large structures such as colloids which can be considered non-sinking particles. Bacteria possess extracellular enzymes for hydrolyzing high molecular weight organic matter into substrate of a size, sufficiently small for cellular uptake (600-800 Da) and play a central role in heterotrophic microbial cycling of carbon. There are two main extracellular enzyme strategies: surface-associated; and dissolved (freely released). Here we present the results of a model study on the efficiency of these two strategies for single free-living bacteria and find that under open ocean conditions, surface-associated enzymes yield the highest efficiency. Additionally, the enzyme strategy may help explain the presence of compounds at dilute concentrations (nM) in the open ocean.