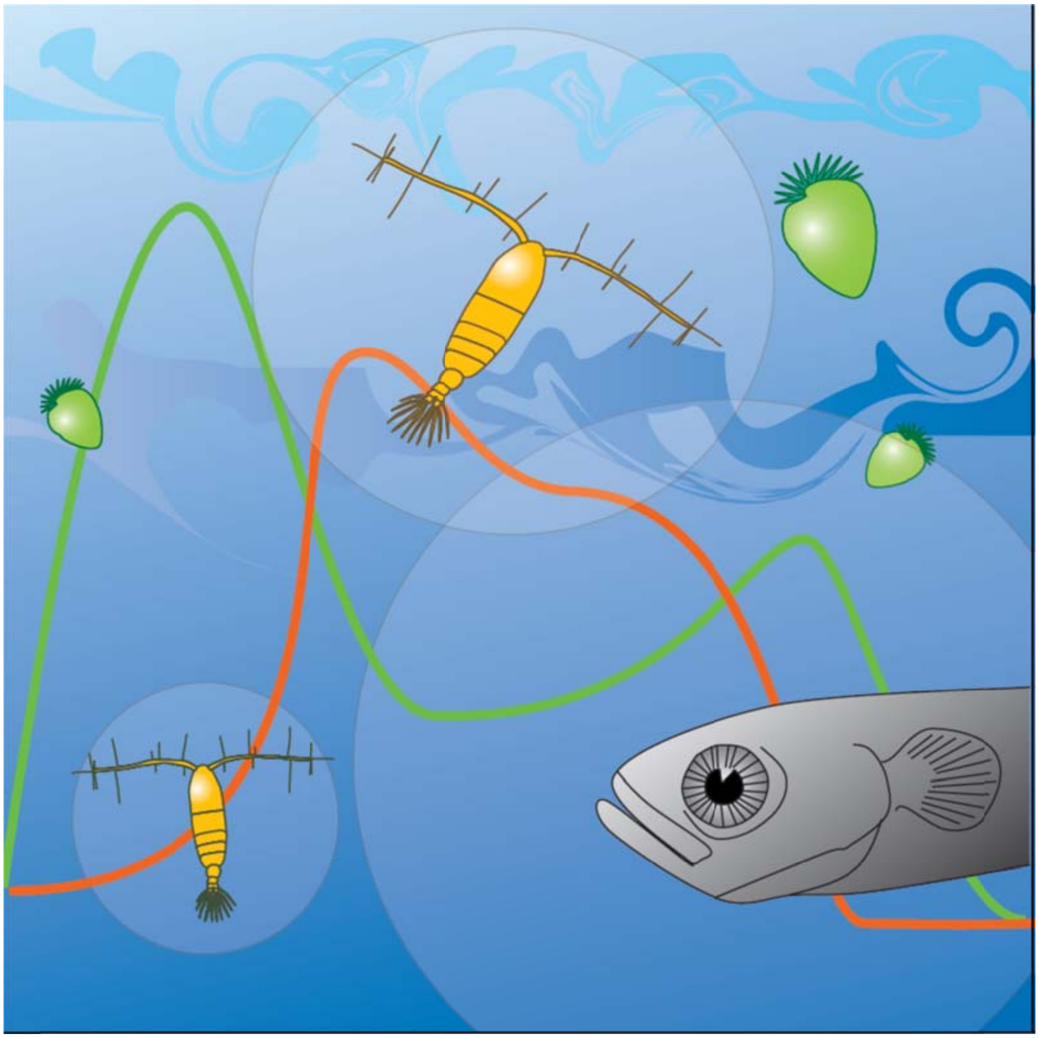
CENTRE FOR OCEAN LIFE

A VKR centre of excellence for the study of life in a changing ocean



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SUMMARY

How will life in the oceans respond to environmental change? With our increasing awareness and concern for human impact on the marine environment and its role in regulating global climate, the need for predicting the future of life in the ocean becomes pressing. Our goal is to develop a fundamental understanding and predictive capability of marine ecosystems.

We will develop a novel trait-based approach that will allow us to tackle the complexity of marine ecosystems where traditional approaches have failed: rather than considering species *per se*, we characterize individual organisms by a few essential traits that describe the ensemble properties of the many species. Further simplifying principles can be derived because an individual's behaviour and life strategy reflect trade-offs: in accordance with the laws of natural selection, individuals optimize their reproductive potential in the face of continually changing competition, predation and environmental pressures. Optimization of life strategies at the individual level is the fundamental mechanism through which evolution is manifest and by which properties of ecosystems emerge. The specification of trade-offs is the core of the mechanistic description of individual level interactions. The trait-based approach can only be realized through a concerted effort by biologists, mathematicians and physicists. It is therefore an inherently interdisciplinary endeavour.

Our aim is ambitious in covering organisms from bacteria to whales. The goal is to use trait-based methods to understand ecosystem function and dynamics and to examine the responses to natural variation and anthropogenic alterations. Steering towards such a goal fundamentally changes the way we perceive life in the oceans and enables concrete prediction about how life will change in response to natural and anthropogenic impacts, e.g., climate change and fishing.

The Centre is organized around 3 main research activities: (i) *The individual*: identification and mechanistic description of the traits and trade-offs required to characterize the main Darwinian missions (feed, survive, reproduce) of the various life forms in the ocean through experimental and theoretical work as well as analysis of literature data; (ii) *Models*: scaling of individual behaviour to population and ecosystem dynamics through the development of trait-based models; and (iii) *Nature*: testing model prediction by comparing to observed trait patterns in the ocean.

The Centre has a very strong training component through the supervision of master students and about 20 PhD and postdoctoral fellows as well as by offering PhD summer schools and organizing international workshops.

The Centre consists of biologists, oceanographers, chemists, physicists, and mathematicians from 3 institutes at the Technical University of Denmark, and institutes at University of Aarhus, University of Copenhagen, and Roskilde University, and prominent foreign research groups specialized in trait-based marine ecology have been identified as formal collaborators. The Centre in addition hosts visiting professors and thus offers a vibrant and interdisciplinary atmosphere promoting the best research and training opportunities.

IDEAS, VISIONS, APPROACH, AND HYPOTHESES

What will the ocean look like in the future? How will micro-organisms cope with changing temperatures, pH, and growing seasons? How will fish respond, will there be more or fewer, and of what species? How will the uptake of CO_2 change? These and many other questions may be addressed by understanding the mechanisms behind the organization of life in the oceans.

Background and vision

Marine life is hidden beneath the surface of the ocean. It unfolds in a world to which we have limited access, a three-dimensional, high-density, heterogeneous environment, which is radically different from the essentially two-dimensional macroscopic terrestrial world in which we have developed our intuitions. The very heterogeneous distribution of solutes, the sticky nature of water, and the absence of inertia at small scales, for example, are not part of our sensed experience. Compared to our understanding of terrestrial life, our perception of marine life is rudimentary. Therefore, important properties of life in the oceans, the varied forms, how they function and interact in their enigmatic realm, remain among the mysteries of the natural world. We need to construct tools to see the organisms and perceive their world. With such perception we can describe how they function and how they interact with one another. Such insight is a prerequisite for understanding the working of the larger ecosystem of which they are a part. Observations, experiments, physics and mathematics provide the instruments we use to dissect the workings of aquatic systems and construct descriptions of this world. The resulting quantitative insights allow us to use models to assemble its components and describe its properties. As we worry ever more about human impact on the marine environment and of the role of the ocean in regulating global climate, the models developed from this work are crucial for predicting the future of the marine environment and the life they support.

This proposal seeks to establish a cross-disciplinary research Centre whose mission is to promote a fundamental understanding of the dynamics of marine ecosystems. In addition to being a curiosity-driven topic of considerable intellectual challenge benefiting from interdisciplinary cooperation, the research has practical applications, ranging from the harvesting of resources to understanding the role that marine life plays in global climate.

Our vision is to replace current statistical and heuristic approaches for describing marine ecosystems with a mechanistic understanding of the underlying biological and physical processes. This will make it possible to understand the function, interactions, and dynamics of life in the oceans and to predict the response to anthropogenic impacts and natural variation (Buckley et al. 2010). Our approach is reductionist, founded on first principles, and harnesses many different disciplines. As a tool, we will develop a novel paradigm for describing and modelling life in the oceans: the *trait-based approach*.

Basic hypotheses

Our work will evolve around developing and testing two overarching hypotheses:

- interactions between individual marine organisms can be derived from organism characteristics and from the fundamentals of physics, chemistry, and evolutionary biology.

- dynamics of populations and ecosystems emerge from mechanistic descriptions of the functioning of the individuals and the properties of the environment.

For example, we hypothesize that individual organisms have been tailored through natural selection to optimize encounters with food and mates and to avoid encounters with predators. The predictable optimal solution to the trade-offs between gains and risks with respect to behaviour and other traits of an organism depends on its characteristics as well as the chemical, physical, and biological environment within which it operates. The optimal solution dictates the rate of interactions with other individuals. Emergent properties at population or ecosystem level are temporal dynamics, biodiversity, and productivity as well as regime shifts and relation to global climate. Mechanistic descriptions will not account for all individual species, as this would render the description meaninglessly complex, but will focus on describing the few *key traits* that best describes the fitness of individual organisms.

Approach

Trait-based descriptions (Norberg et al. 2001, Wirtz & Eckhardt 1996) were pioneered in plant ecology (Green et al. 2008, McGill et al. 2006, Westoby & Wright 2006) and trait-based theories are now developing rapidly (Webb et al. 2010, Polly et al 2011). They have recently been used to describe fish communities (Andersen & Beyer 2006), phytoplankton systems (Bruggeman & Kooijman. 2007, Dutkiewicz et al. 2009, Follows et al. 2007, Litchman & Klausmeier 2008, Litchman et al. 2007), pelagic systems (Pahlow et al. 2008), and trait-based models are promising candidates to replace traditional food-web box models that are fraught with problems (Anderson 2005, Flynn 2005). The traditional models typically operate with a few species or functional groups. Attempts to approach the complexity of real systems by adding more species makes the models infinitely complicated and results in a never ending demand for parameters. Rather than considering species or functional groups, the trait-based approach considers individuals with mechanistically based traits that can be described by few parameters. Ecosystem structure and functioning, distributional and seasonal patterns, and biodiversity are emergent properties of trait-based models, not their input. The traits that survive in a particular environment and in interaction (predation, competition) with other individuals predict system properties and the principal for survival is Darwinian fitness. This approach respects the fact that interactions in the ocean are at the level of the individual – it is individuals that eat one another and mate with one another, it is not species or functional groups that interact. By disposing of the species concept the trait-based approach arrives at a succinct description with few basic parameters, and sidesteps the complexity trap of species-centric modelling approaches.

The trait-based approach is radical because it disposes of the concept of the species while at the same time emphasizing the links to the Darwinian concepts of fitness and selection. It will alter the way we analyze and model life in the oceans fundamentally by moving the focus from species to traits, it will generate novel insights in marine organisms and ecosystem function, and it will allow predictions of how natural and anthropogenic perturbations will change the organization of life in the oceans in the future.

Central to a trait-based description of pelagic ecosystems is a mechanistic understanding of the main functions of the individuals and of the associated trade-offs. The three main missions of any organism – to feed, survive and reproduce – all depend on encounters with food and mates and avoiding encounters with predators, and the execution of one function has implications for the others. For example, non-motile ambush feeders may have a very low chance of encountering a mate, while a cruise-feeder will run a high risk of encountering a predator. Thus, there are no ‘super-organisms’ that perform optimally in all respects. Behaviours and life-histories are shaped by natural selection and/or adaptation by balancing these trade-offs, and by environmental conditions that impact the trade-off functions. The key traits and associated trade-offs are rather well understood for phytoplankton (Litchman et al. 2007, Thingstad et al. 2005) but much less so for bacteria, zooplankton, and fish. Hence, our focus will be on these groups.

The novelty in our trait-based approach is two-fold: (i) we will develop *mechanistic descriptions* of traits and trade-offs instead of relying on statistical relationships as has been done previously; this will allow deeper insights and better predictive power (Buckley et al. 2010); and (ii) we apply the trait-based approach to a *trophic system* (i.e., a system with both animals and plants) in contrast to the purely competitive systems that - with only few exceptions (e.g. Pahlow et al. 2008) - have been considered so far (i.e. plants); this will allow us to describe more complete ecosystems and interactions between its components. We have recently successfully developed proof-of-concept for the plankton-zooplankton system (Mariani et al. 2011) and the fish community (Andersen & Beyer 2006, Andersen & Pedersen 2010); hence the time is ripe to engage in the formidable task of describing trophic systems.

Marine trophic systems are particularly well suited for trait-based descriptions because size is such a strong organizing principle. Primary production in the ocean is limited primarily by inorganic nutrients and small size is a strong advantage in the competition for nutrients. Therefore, nearly all plants in the ocean are microscopic, while terrestrial plants – limited mainly by water – are almost any size. Due to the principle of ‘large eats small’, this uniformity in the size of marine plants cascades and structures marine food webs. This size-structuring of life in the oceans infuses hope that the ambition of a general mechanistic trait-based approach can be fulfilled.

The crux in the trait-based approach is to select the few traits that are the most important determinants of the individual’s fitness and to quantify their associated trade-offs. ‘Size’ is a particularly good example of a key trait, both because marine food webs are size structured, but also because it (i) applies almost universally, (ii) so many properties of an organism relates to its size (growth, metabolism, feeding rate, etc), and (iii) it is heritable and is associated with clear trade-offs (nutrient uptake vs. survival for plants; reproductive output vs. survival for animals). Other examples of traits are feeding mode (Mariani et al. 2011), motility, overwintering strategy, sensory modality, heterotrophy vs. autotrophy. Each of these traits and their dependency of the environment can be described mechanistically for the various life forms in the ocean and their trade-offs quantified. Detailed description of the functional ecology of selected life forms combined with fitness optimization studies will allow us to subsequently dispose of details and identify the few key traits and associated trade-offs that account for most of the fitness of an individual. Together with a description of the environment, e.g., derived from existing local or global circulation models, the traits and trade-offs provide the input to trait-based models.

Expected results

A trait-based description predicts the distribution of trait values in a particular environment. The end product is models of the distribution of life forms with particular traits in time and space. Examples are: water-column models to describe the seasonal and latitudinal patterns of the dominant traits of phytoplankton, zooplankton, fish larvae and jelly-fish; models of the abundance of fish species characterized by their size and other traits as determined by secondary production, climate, and fishing effort; models describing regional and global distributions of the various life forms in the oceans. These models generate testable hypotheses that are validated by comparing with observed distributions in the ocean. The models allow us to explore the functioning of marine systems and address both generic and applied questions: What governs seasonal, regional, and global variation in diversity, productivity and resilience of marine systems? How are global patterns of biodiversity influenced by latitudinal changes in seasonality and temperature? What governs observed regime shifts from fish to jelly-dominated ecosystems? How does fishing change fish communities? How are the goods and services that the sea offers affected by climate change?

While trait based models are the main end goal of the Centre and the organising principle of our work, an equally important result of the project is the new discoveries that we expect to make as we steer towards this goal. We expect that the project group, by its combination of analytical and experimental power and the gathering of interdisciplinary expertise (micro- and macroscopic biology, mathematics, physics, chemistry, statistics) will lead to unexpected, exciting discoveries by addressing fundamental processes in the ocean at a multitude of scales. We are entering yet unchartered scientific areas where the radical new insights we expect are likely to become the most valuable and lasting contributions generated by the Centre and the primary criterion for its success.

An additional important outcome of the Centre is candidates trained in a cross-disciplinary environment filling the need for high level expertise in quantitative biology.

CAN WE MAKE A DIFFERENCE?

Worldwide, several groups are now trying to address fundamental questions of marine ecosystem functioning and resilience using trait based approaches, but the final breakthrough awaits the successful application to more complete, trophic ecosystems. Our group is in the perfect position to take a world-wide lead in this truly interdisciplinary endeavour. During the past decade we have pioneered the mechanistic approach to plankton ecology (Kiørboe 2008b), pioneered the size-based analysis of fish communities (Daan et al. 2005) and pioneered the trait-based approach to modeling fish communities (Andersen & Beyer 2006). We have an internationally unique tradition of integrating experimental and theoretical biology, physics, and mathematical and statistical modeling. Finally, we have assembled a strong, interdisciplinary group with the ideal complimentary combination of skills, experiences, and energy, and we have linked with outstanding international scientists that work with related problems and share our excitement for the challenge ahead.

The work we are proposing is related to other ongoing initiatives at the involved institutions. However, most of these have a short-sighted strategic or applied perspective, and none of them, apart from a small network grant on trait-based plankton ecology from the Danish Council for Independent Research, approaches life in the ocean from the trait-based perspective. The other activities provides backup to the Centre in terms of supplying field data, laboratory access, mathematical and statistical expertise, and experience with the whole range of life in the ocean, from virus to fish. We therefore see the Centre as a means of focusing the disparate scientific groups on the national level and provide the basis for a paradigm shift in our understanding of life in the oceans.

METHODS

The trait-based approach is based on three component activities or themes: (i) *The individual* – defining key traits and trade-offs; (ii) *Models* – up-scaling from individuals to populations and ecosystems; and (iii) *Nature* – analysing patterns of organisms in nature in terms of their trait distributions. All three themes will be addressed in parallel and young researchers will be encouraged to integrate across themes in their work.

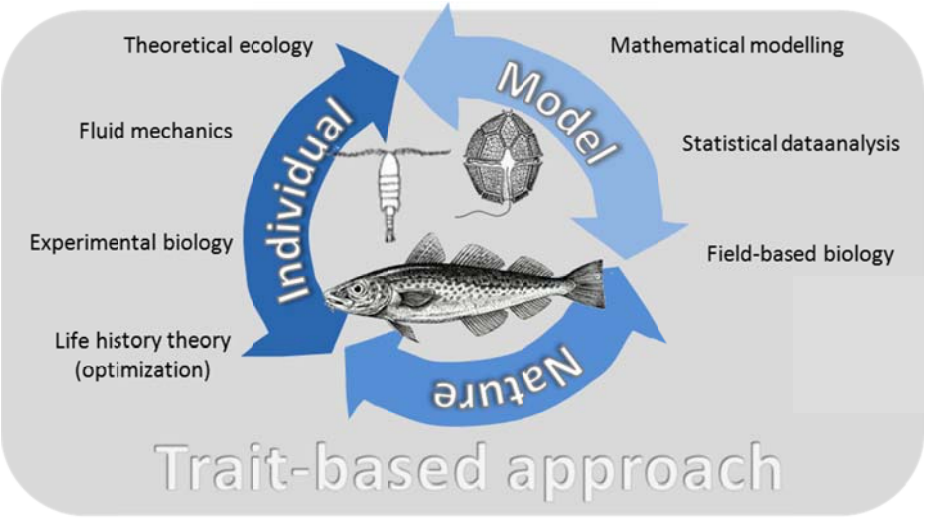


Illustration of the three themes of the trait-based approach and the involved scientific disciplines

Theme 1: The individual - defining key traits and trade-offs

Our approach is inherently individual-based and is built on a mechanistic description of essential traits and their trade-offs for the main life forms in the ocean (unicells, autotrophs, heterotrophs, zooplankton, gelatinous organisms, fish, and whales) with a focus on bacteria, zooplankton, and fish.

Our aim is to identify the few *key traits* that across species best capture fitness and its component fundamental activities of feeding, surviving, and reproducing and to describe mechanistically how these activities depend on trait values. The mechanistic description of the fundamental activities will allow us to quantify the conflicts between the optimal execution of these activities – the trade-offs – to search for the best compromise (maximum fitness) and its dependency on the environment, and to make the trait-based models truly predictive. We will identify key traits, quantify fundamental activities and reveal trade-offs through (i) data analysis, (ii) experimentation and observations and (iii) fitness optimization. These three approaches are used simultaneously, cycling information and concepts between tasks.

Identifying key traits through data analysis: There is no general systematic method to identify the key traits. A key trait for a particular group of organisms is one which varies significantly within the group, and for which a mechanistic description of the fundamental activities can be constructed. A wealth of information on marine organisms exists in the literature and in extant databases, in particular for fish where we have exclusive access to databases from regular fisheries surveys and assessments. The task here is to organize such information along the lines of potentially relevant traits. The art of identifying *key* traits is to examine their prevalence and the magnitude of their variance between marine organisms, and deduce the mechanisms by which they influence the fundamental activities. An additional aspect of identifying key traits is to examine correlations between traits to reduce the number of potential important traits. As mentioned earlier, many traits are correlated with organism size, and size may hence be used as a proxy for many fundamental traits. Other morphological features may similarly be quantitative measures of functional traits (Polly et al. 2011), e.g., fish shape is indicative of feeding habit (bottom feeder, pelagic feeder, predatory), and the occurrence of spines, toxin production, or large relative muscle mass may represent investment in defense. Negative correlations are particularly interesting as they may reveal trade-offs and inspire search for a mechanistic basis. An example is the negative relation between nutrient affinity and cell size in phytoplankton that fall out of empirical analyses (e.g. Litchman et al. 2007); the mechanism can be rationalized from fundamental laws of diffusion (e.g. Thingsted et al. 2005).

Experimentation and observations (*what organisms do, how they do it and quantifying fundamental activities*): To observe small aquatic organisms and to understand their behaviour is a particular challenge because they live in a non-intuitive, viscous environment that we cannot readily access. Recent developments facilitate significant advances in observing and describing the behaviour of marine organisms at the individual level. Video recordings using new illumination techniques will be used to shed light across a range of scales; from bacteria colonizing detrital particles (Tang et al. 2006), to the courtship of copepods (Kiørboe et al. 2005), to larval fish first learning to feed. High speed video is becoming less expensive and allows us to resolve the rapid motion of small plankters and to understand the mechanics and energetics of feeding and swimming (Kiørboe et al. 2009, 2010). We will employ particle image velocimetry to observe flow fields around swimming micro-organisms to determine how embedded particles are transported, how chemicals are advected and diffuse, and how hydromechanical signals propagate. New in situ video and sample collection techniques (Tiselius 1998, Kiørboe 2007) allow us to observe delicate plankters and marine snow in their natural environment with all its 3-D small-scale heterogeneity preserved. Molecular methods allow us to disentangle the functional traits (rather than species) of bacteria (Simon & Daniel 2011), and their differential utilization of organic matter can be studied using fluorogenic substrates (Hoppe et al. 1988), mass spectrometry and organic matter fluorescence (Stedmon & Bro 2008). Incubation techniques will be utilized to examine growth and competition in protistan plankton. Intuition is often insufficient to interpret observations and we have to appeal to hydrodynamics to understand how organisms do what they do. To describe, for instance, how solutes are taken up by swimming micro-organisms involves the physics of fluids as well as biology (Purcell 1977); the efficiency of searching draws on both the biology and physics of locomotion (e.g. Lighthill 1976) and turbulence (Rothschild & Osborn 1988) as well as the mathematics of stochastic processes (Visser & Thygesen 2003). It is precisely these bio-physical interactions at the scale of individuals that largely determine encounters with prey, mates and predators and determine their fitness. We will pursue questions of fundamental significance including how microscopic organisms exchange dissolved chemicals with their environment (Koehl et al. 2002), how zooplankton intercept and capture particles, how copepods track chemical trails, how much information zooplankton can deduce from hydromechanical signals (Fields & Yen 2002), and how bacteria utilize natural substrates. These questions will be addressed by utilizing expertise in fluid physics and computational fluid dynamics.

Fitness optimization (identifying trade-offs): The distribution of traits in nature (e.g. size, behavior, life strategies) reflect some optimization of an individual's reproductive success (i.e. its fitness). While precise mathematical definitions of fitness are notoriously difficult to formulate (Mylius & Diekmann 1995), two relatively simple definitions will most often be used: the net population reproduction rate r, the solution of the Euler-Lotka equation;

$$1 = \int_0^\infty e^{-r(\phi)t} \alpha(\phi, t) p(\phi, t) \mathrm{d}t$$

(Sharpe & Lotka 1911) and the lifetime expected reproductive value R_0 defined by

$$R_0 = \int_0^\infty \alpha(\phi, t) p(\phi, t) \mathrm{d}t$$

(Fisher 1930). These two fitness definitions relate to so-called r and K strategists respectively, and collapse to the same functional form for populations in steady-state. Both of these fitness definitions depend on the trait value ϕ through the reproduction rate $\alpha(\phi,t)$, and survivorship $p(\phi,t)$ as they vary with age t. Both α and p are specified through the activities, in particular the encounter with food and predators, expressed at the level of an individual (e.g. size, behavior), its state (e.g. maturity, energy reserves), and the environment it experiences (e.g. light, abundance and type of predators and prey). The mechanistic approach espoused here is to deduce the functional dependence of α and p on traits to quantify the almost certainly opposing impact a trait value will have on reproduction rate and survivorship, and thereby fitness: a trade-off.

While traits are generally considered properties of individuals, we will also treat behavior (or more properly behavioural algorithms) as traits where the same principles of trade-off and optimization apply. Optimized life strategies can arise from a number of trade-offs, for instance between energy invested in growth or maturation (Charnov et al. 2001), survival or feeding opportunities through vertical migration behaviour (Fiksen 1997), mate finding or feeding (Kiørboe 2008a), or a choice of migration routes from feeding, mating and nursery grounds (Block et al. 2005). Optimization will be used as a guiding principle in all ecological modelling. In many cases, the question can be posed in terms of a risk-benefit-cost analysis of foraging behaviours (Houston & McNamara 1999, Visser 2007). In other situations, fitness maximising strategies, encounter kernels, and their sensitivities to environmental parameters, can be better determined in the framework of dynamic optimisation. We will apply these approaches to concrete problems, which will allow for experimental testing (Kiørboe 2008a).

Theme 2: Models - scaling from individuals to ecosystems

The aim of Theme 2 is to construct models by scaling from the individual level processes up to the levels of populations, communities, ecosystem, and the globe scale and, further, to subject the models to natural and anthropogenic perturbations. The work links Theme 1, which provides the specification of how the fundamental activities varies with the traits for the models, and Theme 3 providing the observed patterns that are used for inspiration and validation. The development of the models will be guided by our own previous efforts in size- and trait-based modelling of the fish community (Andersen & Beyer 2006, Andersen & Pedersen 2010) and by recent advances of other groups on trait-based models of phytoplankton communities (Bruggeman & Kooijman 2007, Follows et al. 2007), and terrestrial vegetation (Falster et al. 2010).

The outcome of the scaling is a trait-distribution, i.e. the abundance of individuals with a given trait or combination of trait values. The emerging trait distributions can either be continuous, e.g., size distributions, or discrete, e.g., feeding traits (filter feeding vs. ambush feeding). Once a trait-based model is setup the response of the trait-distribution to perturbations can be explored. Two classes of perturbation will be applied: changes in the natural environment, e.g., changes in seasonality or temperature (Follows and Dutkiewitz 2011), and anthropogenic perturbations, in particular fishing (Andersen & Rice, 2010).

For the models to be useful, it is essential to examine their robustness or structural stability. Some of the models will inevitably be quite complicated and involve parameters, for which the values are not very well known. It is crucial for the usefulness of our models that they remain as economic as possible and that unnecessary terms are avoided. Similarly, it is crucial that our increasing knowledge of the small-scale processes allows the best choices of these terms and parameters. Even so, testing the robustness of our model predictions with respect to variations in parameters or even the structure of the models is absolutely essential, and will thus be a major task. The evidence of structural stability of the models with respect to certain possible model extensions will demonstrate that the model represent important process and are able to reproduce the right qualitative behavior while extensions only lead to quantitative changes.

Our methodology to scale from individuals to ecosystems can be illustrated with an analogy to kinetic gas theory in classical theoretical physics. In kinetic gas theory a microscopic description of the collision of individual molecules (the “encounter kernel”) is scaled up to macroscopic equations of the motion of the molecules as a fluid in the form of the Navier-Stokes equations. Many details of the molecules are not important for the macroscopic equations and all of the details are represented in the parameter describing the viscosity of the fluid. The trait-based model we have previously developed (and intend to develop further) for the fish community has the same robustness properties: it is based on the description of the encounter between larger predators and smaller prey. The details of the encounter process matters for setting the time-scale of dynamics in the system and for the quantitative behaviour of the model, but the details do not matter for the qualitative macroscopic behaviour.

The word “universal” is often used more or less synonymously with “robust” in the sense of structural stability mentioned above. Universal properties were introduced into physics in the 60’ies, where it turned out that certain properties, like the critical exponents of various correlation functions, are equal within large classes of models for continuous phase transitions, whereas others, like the critical temperature, are model-dependent. Whether our modelling can be universal in the sense of static critical phenomena is, however, not clear. First of all, nothing is yet known about the existence and structure of universality classes in such models and second, the predictions of our models are by nature non-universal in the sense that they involve regions (e.g. the North Sea) and taxa (e.g. copepods), which are non-generic and have specific non-universal properties that have to be taken into account. Nevertheless it is of utmost importance that our modelling is kept as simple and transparent as possible, since this means that our results are not only predictions of specific phenomena or abundances, but actually lead to an understanding of the basic mechanisms involved.

How to scale. Scaling from the mechanistic individual-level descriptions to trait distributions requires mathematical models in the form of 1) systems of ordinary differential equations (Wirtz and Eckhardt 1996, Norberg et al. 2001, Bruggeman & Kooijman 2007), 2) partial integro-differential equations (Benoit & Rochet 2004,Andersen & Pedersen 2010), or 3) agent-based simulations (Grimm & Railsback 2005). We will here give examples of the first two kinds of models:

1. Unstructured trait-based models. The rate of change of the number of individuals $N(\phi)$ with a trait ϕ can be written as a system of ODEs:

$$\frac{\partial N(\phi)}{\partial t} = f(\phi, N(\phi), E(\boldsymbol{x}))$$

where $E(\boldsymbol{x})$ is the external environment as a function of space $\boldsymbol{x}$. The function f describes the reproductive rate of individuals with trait ϕ, which is largely determined by the encounter with food $\beta_f(\phi, E)$ and the encounter with predators $\beta_p(\phi, E)$. These encounter kernels represents the main trade-offs associated with the trait value ϕ. If, for example, the trait is "foraging intensity", then a higher trait value will lead to a larger encounter with prey, but also to a larger encounter with predators. Other trade-offs enter via the physical environment $E(\boldsymbol{x})$, e.g., how the encounter rates are modulated by turbulence and light. The mathematical analysis of such a dynamical system is straightforward, namely to identify equilibria and their stability, and to characterize the dynamical behaviour of unstable states. Most often such an analysis will be performed through numerical integration with standard methods. Examples of models of this kind are given in (Wirtz and Eckhardt 1996, Norberg et al. 2001, Bruggeman and Kooijman 2007, Mariani et al. submitted). Further mathematical analysis of this type of models is to develop moment closures of the distribution $N(\phi)$ (Savage et al. 2007, Merico et al. 2009).

2. Structured trait-based models. If the ratio between the size of offspring and size at maturation is large, it is often necessary to resolve the population structure, i.e., how individuals grow from offspring to adults. This is the case for larger zooplankton (copepods), and in particular for fish which have an egg size of 1 mg but may have adult sizes ranging from 1 g to 100 kg. To do so, the growth rate of an individual $g(w,\phi)$ and the mortality rate $\mu(w,\phi)$ as functions of individual size w have to be accounted for, and the model structure is in the form of a conservation equation:

$$\frac{\partial N(w,\phi)}{\partial t}+\frac{\partial g(w,\phi)N(w,\phi)}{\partial w}=-\mu(w,\phi)N(w,\phi)$$

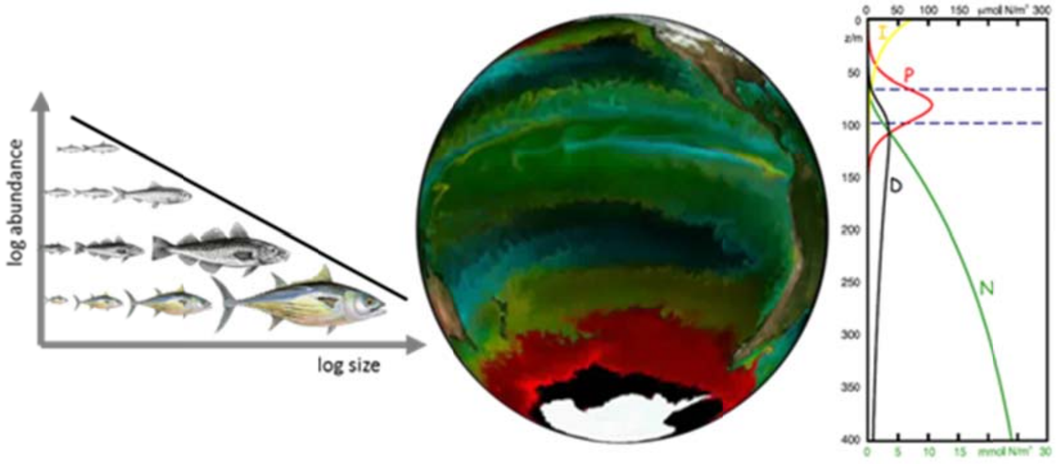
In this case the food encounter kernel $\beta_f(w,\phi,E)$ enters into the specification of growth, which will be an integral over all the smaller individuals:

$$\beta_f(w,\phi,E)\sim\int\psi(w,w_p)N(w,\phi)\,\mathrm{d}w_p$$

with a size preference of prey of size w_p: $\psi(w,w_p)$ and likewise for the encounter with predators, $\beta_p(w,\phi,E)$. The total system to be solved is therefore a partial integro-differential equation in two variables, w and ϕ. The equilibrium solution may be found analytically under various simplifying assumptions (Andersen & Beyer 2006), but in general the equation has to be solved numerically, which can be done with standard finite-difference or finite-volume techniques borrowed from computational fluid mechanics (see Hartvig et al, 2011). Stability properties can be found semi-analytically (Datta et al. 2010).

Response to perturbations. The ultimate aim is to expose the models to perturbations and examine the response in terms of changes in the emerging trait distributions. Two types of perturbations will receive particular attention: perturbations from the seasonal forcing in light and perturbations from fishery. The largest global gradient in natural forcing of ecosystems is the changes in seasonality, from near absence around the equator to strongly seasonally forced system around the poles. On a local scale climate change is expected to lead to changes in seasonality, e.g., earlier spring and longer growing seasons, which will affect the existing communities. On a global scale differences in seasonality is correlated with availability of nutrients for the plankton community and affects the importance of overwintering or reproduction strategies. The largest anthropogenic perturbation of marine ecosystems is from fishing and whaling. The impact of fishing has been demonstrated to have ecosystem-wide effects (Daan et al. 2005) and to extend far beyond the exploited populations and affect zooplankton, phytoplankton, and even nutrient concentrations (Frank et al. 2005). Our focus on fishing will be on examining the impact on the trait distribution within the fish and plankton community, and on operationalizing our existing trait-based fish community models to be applicable in a practical ecosystem oriented context.

Environmental forcing, $E(\boldsymbol{x})$. The trait distributions will be influenced by the environment $E(\boldsymbol{x})$ which describes both the physical environment (light, turbulence, temperature, etc.) and the biotic environment (availability of food and presence of predators and competitors). The work in Theme 2 will rely on three model systems to describe the environment: size-spectra/food-web type of models (Andersen and Pedersen 2010, Hartvig et al 2011), which only describe the biotic environment; a global circulation model (GCM) based on the MIT Integrated Global Systems Model (IGSM2.3; an earth system model of intermediate complexity; Dutkiewicz et al. 2005b); and a water column model based on the General Ocean Turbulence Model (GOTM; Burchard et al. 2006) (See illustration below). The two latter systems describe both the physical environment and the food environment either as nutrients or as primary production. The three model systems are chosen to represent the full spectrum of temporal and spatial resolution, from time scales of hours to centuries and spatial scales of meters to the global ocean. Setups of size-spectrum models already exist in the group, while the water column and GCM type of model setups are new, but the expertise to setup and run these types of models is currently being developed (One PI, M. Payne, is currently being trained in GCM in Switzerland).



System	Scope	Spatial resolution	Temporal resolution
Size-spectra/food web	Ecosystem	None	Hours to centuries
Global Circulation Model (GCM)	The Earth	Horizontal; coarse	Within seasons
Water column model	Local	Vertical; meters	Diurnal and seasonal

Illustration of the three model systems: a size-spectrum model, a global circulation model where colours represent different phytoplankton trait combinations (Follows et al. 2007), and a water column model of light (I), nutrients (N), phytoplankton (P) and detritus (D) (Beckmann and Hense 2007).

Theme 3: Nature - analysis of patterns of traits
Fitness optimization (Theme 1, T1) and trait-based up-scaling (T2) give rise to predictions of trait distributions in the ocean. The goal of Theme 3 is to determine the trait distributions that have actually emerged, and perhaps changed, in nature. Examples are latitudinal variations of traits related to overwintering strategies, trait distributions on the ecosystem level, or vertical distributions of: feeding traits in zooplankton, mixotrophy in plankton, and asymptotic size in fish. In some cases the trait distributions may be used directly for validation or calibration of the trait-based models, in other cases they will be used as inspiration for determining the relevant governing traits.

Direct analysis. The analyses will be based on the vast existing information on fish and plankton databases as well as information from the scientific literature. Large repositories of data for fish originate from standard trawl surveys, where DTU-Aqua has access through its historical links to fisheries science. Further, databases like FishBase and literature sources will be used. Plankton data are available from the Continuous Plankton Recorder surveys and the literature. Though well-known and easily accessible, these sources of data have mainly been analysed from a species-centric perspective, and the trait-based perspective on these data is bound to generate novel insights as to what determines the patterns of traits at a given time and place. One trait which has been subject to considerable empirical analysis is body size: plankton to whales (Sheldon et al. 1972), phytoplankton, zooplankton, and fish (Boudreau and Dickey 1992), zooplankton (Rodriguez and Mullin 1986), and fish (Daan et al. 2005, Gislason et al. 2008). However, a significant part of the literature on body size is concerned with species abundance as a function of body size (e.g. Damuth 1987), which is not a trait distribution but a convolution of a trait distribution and species diversity. Our aim is to analyze distributions of body size of individuals more specific (e.g. vertical and latitudinal variations) and in particular analyse trait distribution other than body size. This will include analyses of body morphology, as this may be indicative of functional traits and allow (near) taxon-free analyses (Polly et al. 2011). Organisms differ in morphology depending on their habitat. Many families of demersal fish, for example, are cryptic, spiny or flat, while pelagic species often have silvery sides and body shapes adapted to minimize drag while swimming. Similarly, gape size in fish is indicative of feeding habits.

Most analyses of trait compositions in fish assemblages have focused on particular life history processes such as reproduction (e.g. Winemiller and Rose 1992), growth (e.g. Cury and Pauly 2000) or mortality (e.g. Gislason et al. 2010) and few have combined the processes to close the life cycle of the organisms (but see Andersen and Beyer 2006, Gislason et al. 2008). The models constructed in Theme 2 will allow us to close the life cycles of the different organisms and consider the fundamental life history processes simultaneously. This will reveal additional relationships between functional traits that can be tested by statistical analysis of trait abundance patterns in nature. Having selected a suite of relevant functional traits, analyses of correlations, cluster analysis and PCA will be used to distinguish between traits that covary and can be collapsed and those where negative correlations suggest that trade-offs are present (cf. T1).

Statistical modelling. Trait-based data may also be employed directly for formal statistical parameter estimation in trait-based models. Usual statistical modelling is based on pure descriptive formulations, typically in the form of correlation models in various degrees of sophistication. We will go beyond standard correlative statistical models, and use the trait-based models augmented with a statistical model of the error-structure in the data to construct “grey-box statistical models” as a basis for parameter estimation (Madsen 2007). This procedure will be particularly useful for making the fish community models operational by calibrating them with the notoriously noisy trawl-survey data. This type of statistical analysis serves two purposes: 1) to calibrate the model to a particular system, and 2) to validate the model.

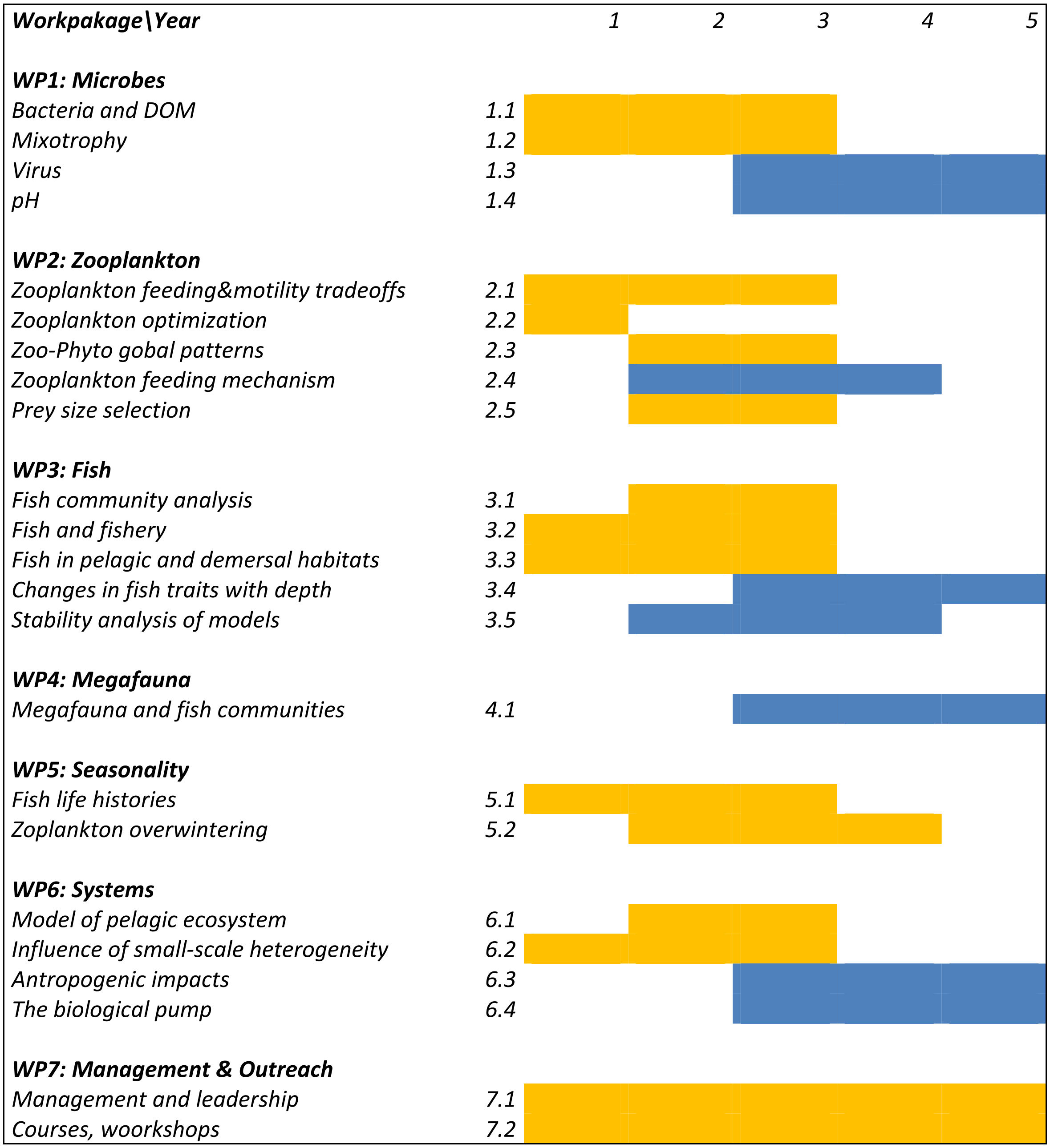
Work related to this Theme occurs in many of the proposed projects because an analysis of existing data forms a natural starting point for any scientific endeavour.

WORKPLAN

The work will be divided among 6 work packages. Work package and outline project descriptions are given in Appendix 1 and the timing and initiation of the individual projects is described in the table below. Projects that are initiated from the start of the Centre are described in most detail and are indicated by ‘yellow’ in the Table, while late projects are indicated ‘blue’.

The six work packages (WP) all transcend the three themes (T1-T3) of the trait based approach, as described above. WP1-4 are focused on identifying traits and associated tradeoffs for specific life forms and trophic groups (microbes, zooplankton, fish, megafauna) and on modelling and describing trait distributions for these life forms along environmental gradients and in response to perturbations. WP5 examines effects on biota of two major natural physical perturbations, namely those associated with latitude and seasonality. These are both perfect test cases for trait-based models because there are many field data available for model validation, but they are also particularly relevant for examining the effects of climate change perturbations. Length of growing season, temperature, mixing conditions, water column structure, etc. all vary with season and latitude and are at the same time the primary physical parameters subject to climate change. WP6 finally integrates across trophic levels to develop more complete trait-based system models that will be used to examine system properties (such as vertical material transport), regime shifts, and effects of anthropogenic impacts. The work packages are planned such that there is a balance throughout the life time of the Centre between work on specific life forms (WP 1-4) and analytical work that emphasize the global aspects of marine ecosystems (WP 4-6).

The work will be conducted by PI’s, collaborators, post docs, PhD students, and visiting scientists in collaboration, but will evolve around and be focused on concrete PhD and Post doctoral projects. Each project will have at least one student or post doc associated but the actual distribution of tasks between fellows will be fine tuned to the availability and interest of candidates.



Workpakage\Year		*1*	*2*	*3*	*4*	*5*
WP1: Microbes						
Bacteria and DOM	*1.1*	🟨	🟨	🟨		
Mixotrophy	*1.2*	🟨	🟨	🟨		
Virus	*1.3*			🟦	🟦	🟦
pH	*1.4*			🟦	🟦	🟦
WP2: Zooplankton						
Zooplankton feeding&motility tradeoffs	*2.1*	🟨	🟨	🟨		
Zooplankton optimization	*2.2*	🟨				
Zoo-Phyto gobal patterns	*2.3*		🟨	🟨		
Zooplankton feeding mechanism	*2.4*		🟦	🟦	🟦	
Prey size selection	*2.5*		🟨	🟨		
WP3: Fish						
Fish community analysis	*3.1*		🟨	🟨		
Fish and fishery	*3.2*	🟨	🟨	🟨		
Fish in pelagic and demersal habitats	*3.3*	🟨	🟨	🟨		
Changes in fish traits with depth	*3.4*			🟦	🟦	🟦
Stability analysis of models	*3.5*		🟦	🟦	🟦	
WP4: Megafauna						
Megafauna and fish communities	*4.1*			🟦	🟦	🟦
WP5: Seasonality						
Fish life histories	*5.1*	🟨	🟨	🟨		
Zoplankton overwintering	*5.2*		🟨	🟨	🟨	
WP6: Systems						
Model of pelagic ecosystem	*6.1*		🟨	🟨		
Influence of small-scale heterogeneity	*6.2*	🟨	🟨	🟨		
Antropogenic impacts	*6.3*			🟦	🟦	🟦
The biological pump	*6.4*			🟦	🟦	🟦
WP7: Management & Outreach						
Management and leadership	*7.1*	🟨	🟨	🟨	🟨	🟨
Courses, woorkshops	*7.2*	🟨	🟨	🟨	🟨	🟨

Plan for the division of time and effort on the 6 workpackages over the time period of the Centre. Early projects with the most detailed descriptions are marked yellow, while late project are in blue. WP and project descriptions in Appendix 1.

DISSEMINATION OF RESULTS AND EDUCATIONAL ACTIVITIES

The main medium for dissemination of our primary research will be papers in peer reviewed scientific journals and presentations at international workshops and conferences. In addition to this, we will engage in dissemination, teaching, and outreach activities as follows:

1. *Supervision of students and young scientists*. In addition to the ca. 20 PhD and Postdoctoral fellows that will be financed by the Centre (and co-financed by our universities), we expect to attract many additional post doctoral scientists that will be financed by other programmes, notably the European Union Marie Curie programme, or their own national funding. We have had much success in attracting these types of candidates and funding in the past.
2. *Supervision of undergraduate students*. We will offer thesis projects to bachelor and masters students and the multidisciplinary environment offered by the Centre will be very attractive to students. One major source of recruitment of undergraduate students will be the new Master programme in *Aquatic Sciences and Technology* that is offered jointly by DTU-Aqua and Biological Institute at Univ. Copenhagen (and taught by several of the Centre participants). This program aims at educating biologists with quantitative skills and engineers with biological insights, aligning with this Centres aims.
3. *International and inter-disciplinary summer schools and workshops.* The Centre will provide seed funding for these activities but we will apply to other agencies to cover bulk expenses. Plans so far is an application for an international PhD summer school in *Arctic Marine Ecology*, to be held in the summer of 2012 in Godhavn, Greenland, and an application to the Lorentz Center (*International Center for workshops in sciences*) for an international workshop in *Trait-based Ecology* to be held about 1½ year after the start of the VKR Centre. Instructors and speakers at these activities will be drawn from the international science community, including members of our International Advisory Board (see below), and we expect to engage in one such activity a year.
4. *Web page.* We will establish a web page to attract national and international awareness as well as candidates for the Centre.
5. *Public outreach*. The Centre will have lots to offer a lay audience, and we aim to produce popular articles and lectures, be guests in radio and TV programmes, and make news releases of exciting discoveries. We have a good record for such activities in the past, and DTU-Aqua has an efficient public relations office that will facilitate outreach.

THE CONSORTIUM: RESEARCH GROUP AND INTERNATIONAL COLLABORATORS

The research group

The proposed centre is interdisciplinary by nature and the group consequently comprises expertise in biology, mathematics, chemistry, and physics. The DTU-Aqua core group has a long, fruitful tradition for cross disciplinary research and is unique in that it already has three of the four disciplines represented in one group. It can thus function as a seed for the crystallization of the different disciplines into a truly unified effort. The DTU-Aqua group supplies expertise in applied mathematics and statistical modelling, ecosystem modelling and theoretical ecology, physical oceanography, zooplankton ecology (experimental and applied), and fisheries ecology. Other DTU institutes (Physics and Mathematics) bring in expertise in complex systems, dynamical systems, and fluid mechanics. Partners from Univ. Copenhagen have expertise in protist ecology, microbiology, and molecular biology, while chemical oceanography expertise is supplied by Aarhus University and meroplankton ecology by Roskilde University. International collaborators have partly overlapping and partly complementary expertise. Several of us have collaborated before in various combinations, and the Principal Investigator (PI) group has a good blend of matured experience and young energy. For practical reasons, we have limited the PI-group to 10 and listed the rest of us as collaborators. Together we have the necessary expertise and experience to reach the goals of the Centre.

International collaboration

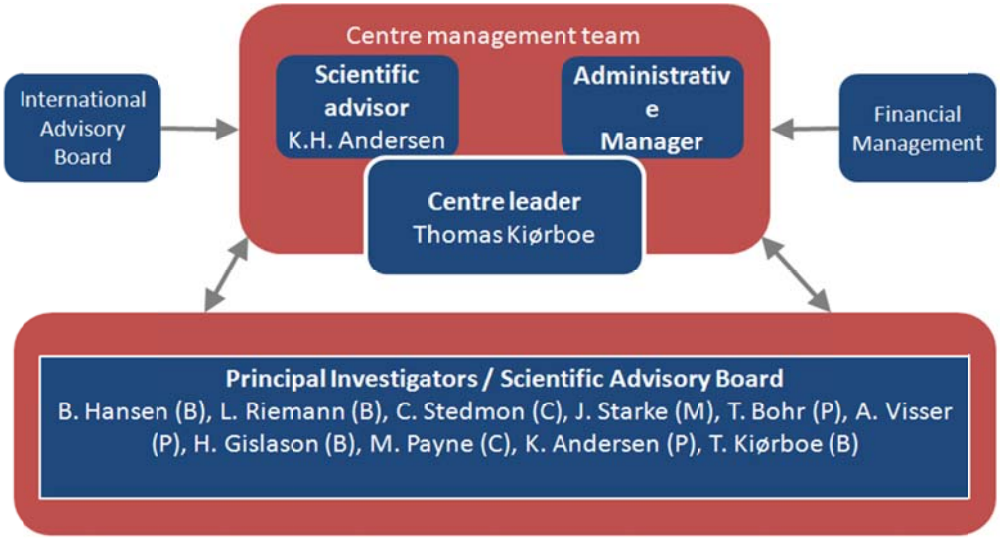
It is vital to the success of the Centre that it engages in strong and active international collaboration. All group members have well developed international networks, and we will draw on these. We expand the research group by formal arrangements with other international groups or individuals that specialise in trait-based marine ecology, and we will engage in less formal one-by-one ad hoc international collaboration when relevant.

Researcher Visitors Centre

As part of the VKR Centre, we will set up a researcher visitor's centre. This will provide a truly international, academic environment for students, staff, and visitors and will make the VKR Centre particularly attractive to foreign scientists. The secretariat of the VKR centre will together with DTUs International office help visitors with all practical arrangements (housing, residence and work permits, etc) and thus facilitate their smooth integration. In addition to hosting international students and post docs, we plan a visiting professors program that will host international scientists for periods of at least 1 month duration. We will provide seeding funds for professors on sabbatical from home universities, and help apply for funds for visiting scientists, e.g., through the Marie Curie programme. We already have funding for a number of named professors that will join our work.

IMPLEMENTATION AND MANAGEMENT

The inter-disciplinary nature of the group is its strength but also a potential weakness. We are aware of the challenge of cross-disciplinary communication and collaboration, but we have been able to tackle that problem before, albeit in smaller groups. A key to success is that all participants are motivated in consistency with a common goal and that a common language is developed to facilitate mutual inspiration. The PI group and leadership will strive to achieve this by (i) ensuring that all main activities help move the forefront of its respective disciplines, (ii) by having student and post doc projects co-advised by representatives from at least two disciplines, (iii) by having regular gatherings where scientists and students explain their research to the larger multidisciplinary community of the Centre, and (iv) by fund allocation strategies (see below).



Outline of management structure. The main disciplines of PIs have been indicated by a letter: B: biology. M. Mathematics, P: Physics, C: Chemistry

Management structure

The Centre leader (CL) is responsible for research leadership. To represent the interdisciplinary character of the Centre in the leadership, the CL is assisted by a deputy Centre Leader from a complementary discipline. Together with the head of DTU-Aqua’s research secretariat (‘Administrative manager’) they form a small management team that will be responsible for the day-to-day management of the Centre. The group of PIs will form a *Scientific advisory board* that advises the CL on general decisions and scientific directions, and upon whether to hire new young researchers. The board will meet twice a year; ad hoc meetings may be called by the CL or PIs as required.

We have established a small *International advisory board* consisting of our key international partners. The board advises on research directions and board members whelp teach summer schools and invited to participate in our conferences and annual retreats.

The administrative support function at DTU-Aqua provides management and coordination, assist with technical reporting, internal communication, and set-up the Researcher Visitors Centre. Public outreach is facilitated by DTU Aqua’s communication group. Financial management, auditing and reporting is implemented via the participating universities central administrations.

Hiring strategy

Young researchers (Ph.D. students and post docs) are hired in three phases. Shortly after the establishment of the Centre, an intensive phase of hiring will be undertaken to establish a scientific environment of sufficient critical mass. Subsequent longer and less intensive phase will then be initiated, partly depending on availability of suitable candidates and partly to offset loss of young researchers when the first wave of Ph.D. students reaches their final year of study.

All young scientists will be associated to a main supervisor and a secondary supervisor, preferably from another discipline. The young researchers will be technically hired by the primary supervisor’s university. Recruitment will be through broad international advertisement and competition, and prioritize talent over very specific skills.

Fund allocation strategy

Most of the funds in the Centre are devoted to hiring Ph.D. students and post docs. For the first phase of hiring we have defined specific projects. However, to ensure that the most talented candidates are acquired we will administer a degree of flexibility in the topics. Our strategy is to:

1) Attempt to achieve a ratio between post docs and Ph.D. students of 1 to 2.
2) Ensure that the breadth of the Centre is covered.
3) Attempt to distribute projects evenly among the PIs and collaborators.

For the second and third phases of hiring the performance of the activities in light of the goals of the Centre will be evaluated and the CL decides which activities to intensify/downscale, and whether new activities are required.

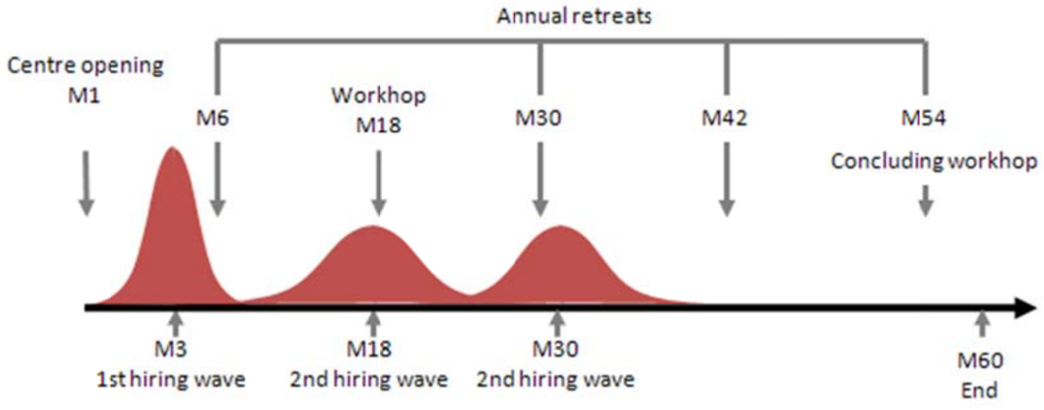
Science meetings

Meetings will take place on three levels: weekly meetings, annual retreats, and an international workshop on trait-based approaches.

Weekly meetings of ~1 h duration will be held during the spring and fall semesters. The meetings will take place at DTU-Aqua, with mandatory attendance of all PhD.s and Post docs in the Centre. To be able to attend the meeting without additional travel time, a workplace will be available at DTU-Aqua for each participant; alternatively, attendance via video conference facilities may be considered. The weekly meeting is a forum for scientific discussions and development of the core ideas in the Centre across disciplines. The meeting will also provide a convenient forum for discussion of relevant practical matters related to the Centre. Organisation of the meeting is the responsibility of alternating PIs.

In addition to the weekly meetings there will be annual "retreats" over several days with attendance of all young researchers, PIs, and collaborators, plus relevant invited researchers. The annual retreats are a forum for presentation of research and discussion of the future research direction of the centre, and a venue for one of the bi-annual meetings of the scientific advisory board.

Finally, at least one international workshop is planned; see the section on dissemination and educational activities.



Outline of major events in the life time of the VKR Centre

REFERENCES

Andersen, K.H., and Beyer, J.E. 2006. Asymptotic size determines species abundance in the marine size spectrum. American Naturalist, 168: 54-61.

Andersen, K.H., Beyer, J.E., Pedersen, M., et al. 2008. Life-history constraints on the success of the many small eggs reproductive strategy. Theor. Pop. Biol. 73: 490-497.

Andersen, K.H., Nielsen, A., Thygesen, U.H., Hinrichsen, H-H., and Neuenfeldt, S. 2007. Determining uncertainty in geolocation using the particle filter. Canadian Journal of Fisheries and Aquatic Science, 64 (4): 618-627.

Andersen, K.H., and Pedersen, M. 2010. Damped trophic cascades driven by fishing in marine ecosystems. Proc. Roy. Soc. London B 277: 795–802.

Andersen, K. H., and Rice, J. E. 2010. Direct and indirect community effects of rebuilding plans. *ICES J. Mar. Science* doi:10.1093/icesjms/fsq035 (2010).

Anderson, T.R., 2005. Plankton functional type modelling: running before we can walk. J. Plankton Res. 27: 1073-1081.

Anderson et al., 2010. Influence of grazing formulations on the emergent properties of a complex ecosystem model in a global ocean general circulation model. Progress in Oceanography, 87 (1-4): 201-213.

Aumount, O., and Bopp, L., 2006. Globalizing results from ocean in situ iron fertilization studies. Global Biogeochemical Cycles, 20 (2).

Beckmann and Hense 2007. Beneath the surface: Characteristics of oceanic ecosystems under weak mixing conditions – A theoretical investigation. Prog. in Oceanography, 75: 771–796.

Benoît, E., and Rochet, J. 2004. A continuous model of biomass size spectra governed by predation and the effects of fishing on them. Journal of Theoretical Biology, 226: 9–21.

Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., Weng, K.C., Dewar, H., and Williams, T.D. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. Nature, 434: 1121-1127.

Bonfil et al. 2005. Transoceanic Migration, Spatial Dynamics, and Population Linkages of White Sharks. Science 310 (5745): 100-103.

Bopp et al., 2005. Response of diatoms distributions to global warming and potential implications: A global study. Geophysical Research Letters, 32 (19).

Boudreau, P. R., and Dickie, L. M. 1992. Biomass spectra of aquatic ecosystems in relation to fisheries yield. Can. J. Fish. Aquat. Sci. 19: 1528-1538

Boyd, P.W. and Doney, S.C., 2002. Modelling regional responses by marine pelagic ecosystems to global climate change. Geophysical Research Letters, 29 (16).

Boyd, P.W., and Trull, T.W. 2007. Understanding the export of biogenic particles in oceanic waters: Is there consensus? Prog Oceanog, 72: 276-312.

Brodie, P.F. 1975. Cetacean energetics, and overview of intraspecific size variation. Ecology 56:152.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. 2004. Toward a metabolic theory of ecology. Ecology 85(7): 1771—1789.Bruggeman, J., and Kooijman, S.A.L.M. 2007. A biodiversity-inspired approach to aquatic ecosystem modeling. Limnol. Oceanogr. 52: 1533-1544.

Buckley, L.B., Mark C. Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J., and Sears, M.W. 2010. Can mechanism inform species' distribution models? Ecol. Lett. 12: 1041-1054.

Burchard, H., Bolding, K., Kuhn, W., Meister, A., Neumann, T., and Umlauf, L. 2006. Description of a flexible and extendable physical-biogeochemical model system for the water column. Journal of Marine Systems 61: 180-211.

Bårdsen, B.-J., Henden, J.-A., Fauchald, P., Tveraa, T., and Stien, A., 2011. Plastic reproductive allocation as a buffer against environmental stochasticity – linking life history and population dynamics to climate. Oikos 120: 245-257.

Capitan, J.A. and Delius G.W. 2010. A scale-invariant model of marine population dynamics. *Phys. Rev. E* 81, 061901

(2010).

Ceballos, S. and Kiørboe, T. 2010. First evidence of sexual selection by mate choice in marine zooplankton. Oecologia 164: 627–635. DOI 10.1007/s00442-010-1755-5

Charnov, E.L., Turner, T.F., and Winemiller, K.O. 2001. Reproductive constraints and the evolution of life histories with indeterminate growth. Proc. Nat. Acad. Sci. 98 (16): 9460-9464.

Cohen, D., 1968. A general model of optimal reproduction in a randomly varying environment. J. Ecol. 56: 219-228.

Corkeron PJ, Connor RC. Why Do Baleen Whales Migrate? Marine Mammal Science. 1999;15(4):1228-1245

Cury, P. and Pauly, D. 2000. Patterns and propensities in reproduction and growth of marine fishes. Ecol. Res. 15(1) 101-106.

Cushing, D.H. 1989. A difference in structure between ecosystems in strongly stratified waters and those that are only weakly stratified. J. Plankton Res., 11: 1-13.

Daan, N., Gislason, H., Pope, J., and J. Rice, 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing. ICES. J. Mar. Sci., 62: 177-188.

Damuth, J. 1987. Interspecific allometry of population density in mammals and other animals: The independence of body mass and population energy-use. Biological Journal of the Linnean Society 31(3) 193—246.

Datta, S, Delius, G.W., Law, R. and Plank, M.J. 2011. A stability analysis of the power-law steady state of marine size spectra. arXiv:1001.3826v3.

Dutkiewicz, S., Follows, M.J., and Bragg, J.G. 2009. Modeling the coupling of ocean ecology and biogeochemistry, Global Biogeochem. Cycles, 23, GB4017, doi:10.1029/2008GB003405.

Dutkiewicz, S., Follows, M.J., and Parekh, P. 2005. Interactions of the iron and phosphorus cycles: A three-dimensional model study. Global Biogeochem. Cycles 19: GB1021

Falk-Petersen, S., Timofeev, S., Pavlov, V., Sargent, J.R., 2007. Climate variability and possible effects on arctic food chains: The role of *Calanus*. In: Ørbæk, J.B., Tombre, T., Kallenborn, R., Hegseth, E., Falk-Petersen, S., Hoel, A.H. (eds) Arctic Alpine Ecosystems and People in a Changing Environment. Springer Verlag, Berlin, pp. 147-166.

Falster D.A., Brännström, Å., Dieckmann, U. and Westoby, M., 2010. Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: a theoretical investigation. Journal of Ecology (in press).

Fenchel, T. 2005. Cosmopolitan microbes and their 'cryptic' species. Aquat. Microb. Ecol. 41: 49-54.

Fields, D.M. and Yen, J., 2002. Fluid mechanosensory stimulation of behaviour from a planktonic marine copepod, *Euchaeta rimana* Bradford. J. Plankton Res., 24: 747-755.

Fiksen O., 1997. Allocation patterns and diel vertical migration: Modeling the optimal Daphnia Ecology 78(5): 1446-1456.

Fisher, J.A.D., Frank, K.T., and Leggett, W.C., 2010. Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. Marine Ecology Progress Series 405: 1-13.

Fisher, R.A. 1930. The Genetical Theory of Natural Selection. Oxford University Press, Oxford, UK.

Flynn, K.J., 2005. Castles built on sand: dysfunctionality in plankton models and the inadequacy of dialogue between biologists and modellers. J. Plankton Res. 27: 1205-1210.

Follows, M.J., Dutkiewicz, S., Grant, S., and Chisholm, S.W. 2007. Emergent biogeography of microbial communities in a model ocean. Science 315: 1843-1846.

Follows, M. J. and Dutkiewitz, S. 2011. Modeling Diverse Communities of Marine Microbes. Annu. Rev. Marine. Sci. 3: 427-451.

Frank, K.T., Petrie, B., Choi, J.S., and Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308: 1621-1623

Gislason, H., Daan, N., Rice, J.C., et al. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries, 11: 149-158.

Gislason, H., Pope, J.G., Rice, J.C., Daan, N., 2008. Coexistence in North Sea fish communities: implications for growth and natural mortality. ICES Journal of Marine Science 65: 514-530.

Goodwin, N. B., Dulvy, N. K. and Reynolds, J. D. 2005. Macroecology of live-bearing in fishes: latitudinal and depth range comparisons with egg-laying relatives. Oikos 110: 209-218.

Green, J.L., Bohannan, B.J.M., and Whitaker, R.J., 2008. Microbial biogeography: From taxon to trait. Science 320: 1039-1043.

Grimm, V. and Railsback, S.F., 2005. Individual-based modeling and ecology. Princeton University Press, Princeton.

Grünbaum, D., 2000. Predicting availability to consumers of spatially and temporally variable resources. Hydrobiologia 480: 175-191.

Hairston, N.G., and Bohonak, A.J., 1998. Copepod reproductive strategies: life-history theory, phylogenetic pattern and invasion of inland waters. J. Mar. Systems 15: 23-34.

Hansen, B., P. K. Bjørnsen & P. J. Hansen (1994): The size ratio between planktonic predators and their prey. Limnol. Oceanogr. 39:395-403.

Hansen, P.J., 2011. The role of photosynthesis and food uptake for the growth of marine mixotrophic dinoflagellates. Journal of Eukaryotic Microbiology. In press.

Hartvig, M., Andersen, K.H., and Beyer, J.E., 2011. Food web framework for size-structured populations. To appear in J. Theo. Biology.

Heymans, J.J., Howell, K.L., Ayers, M., Burrows, M.T., Gordon, J.D.M. , Jones, E.G., Neat, F., 2011. Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries? An example from the West of Scotland. ICES Journal of Marine Science 68 (2): 265-280.

Hoppe, H-G., Kim, S-J., and Gocke K., 1988. Microbial decomposition in aquatic environments: combined process of extracellular enzyme activity and substrate uptake. Appl Environ Microbiol 54: 784-790.

Houston, A.I., and McNamara, J.M., 1999. Models of Adaptive Behaviour: an approach based on state. Cambridge University Press, Cambridge.

Høpner-Pedersen, K. and Curtis, M.A., 1980. Differences in energy flow through major components of subarctic temperate and tropical marine shelf ecosystems. Dana 1: 53-64.

Jennings, S., Mulin, F., Blanchard, J.L, Forster, R.M., Dulvy, N.K., and Wilson, R.W. 2008. Global-scale predictions of community and ecosystem properties from simple ecological theory. Proc. Roc. Soc. London B 275: 1375-1383.

Jiang, H., and Kiørboe, T. (2011a). Propulsion efficiency and imposed flow fields of a copepod. J. Exp. Biol. 214: 476-486. doi:10.1242/jeb.049288

Jiang, H., and Kiørboe, T. (2011b). The fluid dynamics of swimming by jumps in copepods. J. Roy. Soc. interface, in press, doi:10.1098/rsif.2010.0481

Jones, R.I., 1994. Mixotrophy in planktonic protists as a spectrum of nutritional strategies. Marine Microbial Food Webs, 8: 87-96.

Kiørboe, T. 1992. Havmiljø og fiskeri. In Drivhuseffekt og klimaændringer: hvad kan det betyde for Danmark.Edited by J.Fenger and U.Torp. Department of the Environment, Copenhagen, Denmark.

Kiørboe, T. 2007. The Sea Core Sampler: a simple water sampler that allows direct observations of undisturbed plankton. J. Plankton Res. 29: 545-552.

Kiørboe, T. 2008a. Optimal swimming strategies in mate-searching pelagic copepods. Oecologia 155: 179-192.

Kiørboe, T. 2008b. A Mechanistic Approach to Plankton Ecology. Princeton: Princeton University Press, 209 pp.

Kiørboe, T. 2011. How zooplankton feed: Mechanisms, traits, and trade-offs. Biol. Rev. *In press*. Doi:10.1111/j.1469-185X.2010.00148.x

Kiørboe, T., Bagøien, E., and Thygesen, U.H. 2005. Blind dating – mate finding in planktonic copepods. II. The pheromone cloud of *Pseudocalanus elongatus*. Mar. Ecol. Prog. ser. 300: 117-128

Kiørboe, T., Andersen, A., Langlois, V., Jakobsen, H.H., and Bohr, T., 2009. Mechanisms and feasibility of prey capture in ambush feeding zooplankton. Proc. Natl. Acad. Sci., 106: 12394-12399.

Kiørboe, T., Jiang, H., and Colin, S.P., 2010. Danger of zooplankton feeding: The fluid signal generated by ambush feeding copepods. Proc. Roy. Soc. B., 277:3229-3237, doi:10.1098/rspb.2010.0629

Klausmeier, C.A., and Litchman, E., 2001: Algal games: The vertical distribution of phytoplankton in poorly mixed water columns. Limnol. Oceanogr., 46(8): 1998–2007.

Koehl, M.A.R., Jumars, P.A., and Karp-Boss, L. 2002. Algal biophysics. British Journal of Phycology

Lighthill, M.J. 1976. Flagellar hydrodynamics. SIAM Rev, 18: 161-230.

Litchman, E., Klausmeier, C.A., Schofield, O.M., and Falkowski, P.G., 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. Ecol. Lett. 10: 1170-1181.

Litchman, E. and Klausmeier, C.A., 2008. Trait-Based Community Ecology of Phytoplankton. Annual Review of Ecology, Evolution, and Systematics. 39: 615-639.

Lotze, H.K., and Worm, B., 2009. Historical baseline for large marine animals. Trends in Ecology & Evolution, 24: 254-262.

Madsen, H., 2007. Time series analysis. 400 pp, Chapman & Hall/CRC.

Manizza et al., 2010. Sensitivity of global ocean biogeochemical dynamics to ecosystem structure in a future climate. Geophysical Research Letters, 37.

Mariani, P., and Visser, A.W., 2010. Optimization and emergence in marine ecosystem models. Progress in Oceanography, 84: 89-92.

Mariani, P., Andersen, K.H., Visser, A.W., Kiørboe, T. (submitted) Adaptive grazing behavior and the seasonal succession of temperate plankton communities.

Merico, A, Bruggeman, J. and Wirtz, K. 2009. A trait-based approach for downscaling complexity in plankton ecosystem models. Ecol. Model. 220: 3001-3010.

McGill, B.J., Enquist, B.J., Weiher, E., and Westoby. M., 2006. Rebuilding ecology from functional traits. Trends in Ecology and Evolution, 21 (4): 178-185.

Melzner, F. et al. (2009) Physiological basis for high CO2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? Biogeosciences, 6, 2313-2331

Mitra, A., and Flynn, K.J., 2010. Modelling mixotrophy in harmful algal blooms: more or less the sum of parts? Journal of Marine Systems 83: 158-169.

Moore et al., 2004. Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. Global Biogeochemical Cycles, 18.

Mylius, S.D. and Diekmann, O.1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. Oikos 74:218-224

Norberg, J., Swaney, P.D., Dushoff, J., Lin, J., Casagrandi, R., and Levin, S.A., 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. Proceedings of the National Academy of Science U.S.A., 98: 11376-11381.

O’Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P., Weiss, J.M., 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proceedings of the National Academy of Science, 104:1266-1271.

Pahlow, M., Alain F., Vézina, A.F., Casault, B., Maass, H., Malloch, L. Wright, D.G., and Lu, Y., 2008. Adaptive model of plankton dynamics for the North Atlantic. Prog. Oceanogr. 76: 151–191.

Pahlow & Prowe, 2010. Model of zooplankton optimal current feeding. Marine Ecology Progress Series, 403: 129-144.

Pershing, A.J., Christensen, L.B., Record, N.R., Sherwood, G.D., Stetson, P.B., 2010. The Impact of Whaling on the Ocean Carbon Cycle: Why Bigger Was Better. PLoS ONE 5(8): e12444. doi:10.1371/journal.pone.0012444

Persson, L., Amundsen, P.-A., De Roos, A.M., Klementsen, A., Knudsen, R., and Primicerio, R., 2007. Culling prey promotes predator recovery – alternative states in a whole-lake experiment. Science, 316: 1743-1746.

Polly, D.P., Eronen, J.T., Fred, M., Dietl, G. P., Mosbrugger, V., Scheidegger, C.,. Frank, D.C., Damuth, J., Stenseth, N.C., and Fortelius, M., 2011. History matters: ecometrics and integrative climate change biology. Proc. R. Soc. B, in press, doi:10.1098/rspb.2010.2233

Pope, J.G, Shepherd, J.G., and Webb, J., 1994. Successful surf-riding on size spectra: the secret to survival in the sea. Phil. Trans. R. Soc. Lond. B 343: 41-49.

Pope, J.G., Rice, J., Daan, N., Jennings, S., and Gislason, H., 2006. Modelling an exploited marine fish community with 15 parameters – results from a simple size-based model. ICES Journal of Marine Science, 63 (6): 1029-1044.

Purcell, E.M., 1977. Life at low Reynolds number. Am J Phys, 45: 3-11.

Raghib, M., Levin, S.A., and Kevrekidis, I.G., 2010. Multiscale analysis of collective motion and decision-making in swarms: An advection–diffusion equation with memory approach. Journal of Theoretical Biology 264: 893–913.

Raghib, M., Hill, N.A., and Dieckmann, U., 2010. A multiscale maximum entropy moment closure for locally regulated space–time point process models of population dynamics. J. Math. Biol.

Rodriguez, J., and Mullin, M.M. 1986. Relation between biomass and body weight of plankton in a steady state oceanic system. Limnol. Oceanogr. 31: 361 ff

Rothschild, B.J. and Osborn, T.R., 1988. Small-scale turbulence and plankton contact rates. J. Plankton Res., 10: 465-474.

Savage, V.M., Webb, C.T. and Norberg, J. 2007. A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. J. Theo. Biol. 247: 213-229.

Sharpe, F.R. and Lotka, A.J. 1911. A problem in age distribution. Philos. Mag., 21:435-438.

Sheldon, R.W., Sutcliff, W. H., and Prakash, A. 1972. Size distribution of particles in the ocean. Limnol. Oceanogr. 17: 327 ff.

Sheldon, R.W., Sutcliffe Jr., W.H., and Paranjape, M.A., 1977. Structure of pelagic food chain and relationship between plankton and fish production. J. Fish. Res. Board. Canada 34: 2344-2353.

Sichlau M.H., J.L.S. Hansen, T.J. Andersen & B.W. Hansen (2011) Distribution andmortality of diapause eggs from calanoid copepods in sediment profiles around Funen, Denmark (55°N 10°E). Mar. Biol. 158:665-676.

Simon, C., and Daniel, R., 2011. Metagenomic Analyses: Past and Future Trends. Appl. Environ. Microbiol. 77: 1153-1161.

Stedmon, C.A., and Bro, R., 2008. Characterizing dissolved organic matter fluorescence with parallel factor analysis: a tutorial. Limnol. Oceanogr. Methods 6: 572-579.

Steinberg, D.K., Van Mooy, B.A.S., Buesseler, K.O., Boyd, P.W., Kobari, T., and Karl, D.M., 2008. Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. Limnol. Oceanogr., 53: 1327-1338.

Stoecker, D.K., 1998. Conceptual models of mixotrophy in planktonic protists and some ecological and evolutionary implications. Europ. J. Protistol. 34: 281-290.

Swalethorp, R., Kjellerup, S., Dünweber, M., Nielsen, T.G., Møller, E.F., Rysgaard, S., and Hansen, B.W., in press. Production of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland, with emphasis on life strategy. Mar. Ecol. Prog. Ser.

Tang, K.W., Grossart, H.P., Yam, E.M., Jackson, G.A., Ducklow, H.W., and Kiørboe, T., 2006. Mesocosm study of particle dynamics and control of particle-associated bacteria by flagellate grazing. Mar. Ecol. Prog. Ser. 325: 15–27.

Thingstad, T. F., Havskum, H., Garde, K., et al. 1996. On the strategy of "eating your competitor": A mathematical analysis of algal mixotrophy. Ecology 77: 2108-2118

Thingstad, T.F., Øvreås, L., Egge, J.K., Løvdal, T., and Heldal, M., 2005. Use of non-limiting substrates to increase size: a generic strategy to simultaneously optimize uptake and minimize predation in osmotrophs. Ecol. Lett. 8: 675-82.

Tiselius, P., 1998. An in situ video camera for plankton studies: design and preliminary observations. Mar. Ecol. Prog. ser., 164: 293-299.

Titelman, J., Varpe, Ø., Eliassen, S., and Fiksen, Ø., 2007. Copepod mating: chance or choice? J. Plankton Res. 29: 1023-1030.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Vanden Berghe, E., and Worm, B., 2010. Global patterns and predictors of marine biodiversity across taxa. Science 466: 1098-1101.

Turing, A.M. 1952. The chemical basis of morphogenesis. Phil. Trans. Royal Soc. London (B), 237 (641): 37-72.

Visser, A.W., 2007. Motility of zooplankton: fitness, foraging and predation. J. Plankton Res., 29: 447-461.

Visser, A.W., and Thygesen, U.H., 2003. Random motility of plankton: Diffusive and aggregative contributions. J. Plankton Res., 25: 1157-1168.

Visser, A.W., Mariani, P., and Pigolotti, S., 2009. Swimming in turbulence: zooplankton fitness in terms of foraging efficiency and predation risk. J. Plankton Res. 31: 121-133.

Ward, B.A., Barton, A.D., Dutkiewicz, S., and Follows, M.J., In press. Biophysical aspects of mixotrophic acquisition and competition. Am. Nat.

Ware, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. J. Fish. Res. Bd. Can. 32: 33-41

Ware, D. M. 1978. Bioenergetics of pelagic fish – Theoretical changes in swimming speed and ration with body size. J. Fish. Res. Bd. Can. 35: 220-228

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., and LeRoy, N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecol. Lett. 13: 267–283.

Westoby, M., and Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. Trends Ecol. Evol. 21(5): 261-268.

Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. J. Fish. Res. Board. Canada 194 1-253.

Winemiller, K.O. and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci 49: 2196-2218.

Wirtz, K.W. and Eckhardt, B., 1996. Effective variables in ecosystem models with an application to phytoplankton succession. Ecol. Model. 92: 33-53.