CENTRE FOR OCEAN LIFE

A VKR Centre for studies of Life in a Changing Ocean

5-YEAR EVALUATION REPORT

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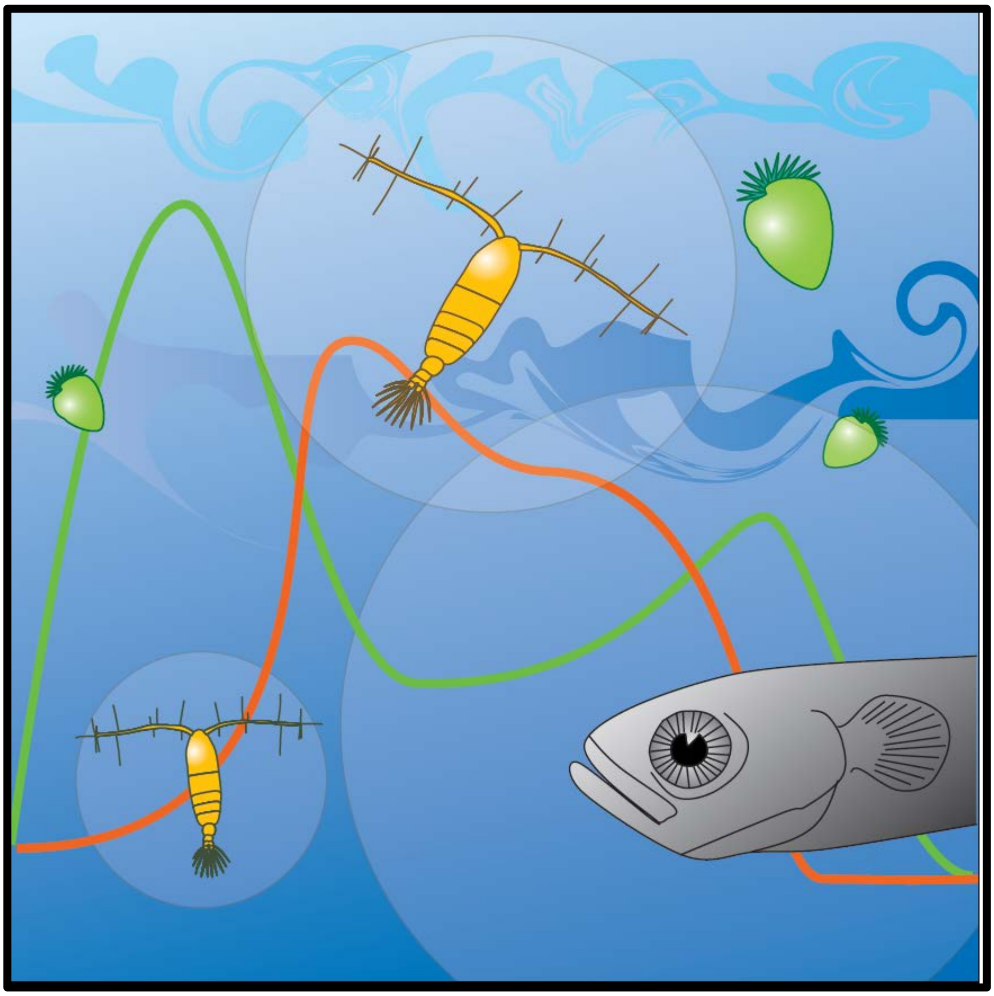

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Summary

The overarching goal of the Centre for Ocean Life is to develop a trait-based approach to promote a fundamental understanding and predictive capacity of marine ecosystems. An equally important goal is to train young scientists in interdisciplinary marine sciences. The Centre is cross-disciplinary (biology, physics, mathematics, chemistry) and represents a collaborative effort between five departments distributed at three universities.

The work at the Centre evolves along three closely related themes, each with particular and independent values: (i) *The individual*: identification and mechanistic description of the traits and trade-offs required to characterize the main Darwinian missions (i.e., to feed, survive and reproduce) of the main life forms in the ocean; (ii) *Models*: scaling of individual behavior to population and ecosystem dynamics through the development of trait-based models; and (iii) *Nature*: describing trait distributions in the ocean and their relation to the environment and to test model predictions by comparing to observed trait patterns.

In Theme I, a major taxa-transcending analysis of size as a ‘master trait’, derived to a large extent from first principles, has formed a solid platform for the identification of key traits and associated trade-offs for the major life forms in the ocean. Further work has focused on pelagic bacteria, phyto- and zooplankton, and fish. Main discoveries include a mechanisms to explain why most dissolved organic matter in the ocean is refractory to bacterial breakdown, quantification photo-mixo-heterotroph trade-offs in protists, a quantification of taxa-transcending feeding and swimming trade-offs in protozoa and zooplankton, and identification of fundamentally different reproductive strategies in fish (and other marine life) and simple models to explain these. The work crystalizes in the identification of 3 life-form transcending traits (size, resource acquisition, and defense) that materializes differently for different life forms but are necessary and sufficient for the development of trait-based models.

Theme II utilizes the mechanistic descriptions of trade-offs to develop trait based models of populations and ecosystems. Among other things, we have developed trait-based model that describe spatio-temporal distributions of plankton, we have a global model of the susceptibility of coastal ecosystems to jellyfish dominance, and we have matured our fish community models to a state where they are now used to address applied questions (e.g., on fisheries management strategies).

Work in Theme III has built extensive trait data-bases from information in the literature and produced the first ever global trait biogeographies of fish and zooplankton. The theme has adressed fundamental ecological questions relating to marine biogeography, e.g., the occurrence and drivers of trait variation along environmental gradients, and the abiotic and biotic processes shaping community composition.

There are about 10 PIs associated with the Centre and until now, 35 PhD and Post docs have been funded by or associated the Centre. We have produced more than 250 scientific papers relevant to the Centres research agenda, a similar number of presentation, as well as extensive popular outreach material. By hosting long-term research visitors (n = 148 man-months), organizing multiple international workshops and conference sessions, and through weekly group meetings,

seminars, and annual research retreats we have created a unique international, attractive, and vibrant environment that is conducive to research and training of candidates in cross-disciplinary marine science.

1. Introduction

The Centre for Ocean Life opened Jan 1st 2012 based on a grant from The Villum Foundation. The Centre represents a cross-disciplinary, collaborative effort between biologists, physicists, chemists, and mathematicians from three universities and five departments. A list of young researchers employed by the Centre is given in Appendix 1. Here, we report on the establishment of the Centre, its mission and activities, and the results achieved so far. The report is an update of the mid-term report produced 2 years ago.

2. Purpose of the Centre: mission and overarching goals

The overarching aims of the Centre are: (i) to develop a trait based approach to promote a fundamental understanding and predictive capacity of marine ecosystems, and (ii) to train PhD students and your researchers in interdisciplinary quantitative marine sciences. The rationale and main research ideas of the Centre are fully described in the original proposal and remain valid here 5 years into the life of the Centre, and are therefore only briefly summarized below.

2.1 The trait-based approach

The development of trait-based approaches to describe and model marine populations and ecosystems provides the organizing principle for the work of the Centre. Trait-based approaches allow us to tackle the complexity of marine ecosystems: 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 history strategies 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.

Central to a trait-based description of pelagic ecosystems is the identification of key traits and a specification 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.

While trait-based approaches have a long history in terrestrial ecology and have been developing during the past 10 years in marine ecology, they have been focused mainly on primary producers. The novelty in our trait-based approach is two-fold: (i) we have developed *mechanistic descriptions* of traits and trade-offs instead of relying on statistical relationships as has often been done previously; this will allow deeper insights and better predictive power. And (ii) we have applied the trait-based approach to *trophic systems* (i.e., systems with more than one trophic level).

2.2 Organization of the work

The work of the Centre is organized in three, interrelated themes, each of which has a particular value on its own. *Theme I* (The individual) identifies key traits of the main life forms in the ocean (i.e., those traits that contribute mostly to the fitness of the individuals) and quantifies the associated trade-offs. We aim at mechanistic approaches, i.e., quantification of trade-offs through an understanding of the underlying mechanisms. These can be revealed through a combination of experimental, statistical, and theoretical approaches. *Theme II* (Models) utilizes the mechanistic identification of key traits and quantification of trade-offs to develop models of populations, communities, food webs, and ecosystems. We have focused the work on three model types: size-spectra/food-web type of models that only describe the biotic environment; a global circulation model (GCM) and a water column model based on the General Ocean Turbulence Model to describe the physical environment within which the biotic trait-based models are embedded. Finally, *theme III* (Nature) aims at describing the distribution of traits in the ocean and of developing a trait biogeography. This work is based on mining existing data bases as well as on developing trait data bases. These observations are used both to test model predictions, and to develop various types of trait-distribution and trait-diversity descriptions and models of marine systems.

3. Research achievements

In the initial phase of the Centre's life we have, together with other research groups, spent quite some efforts defining and exploring the trait-based approach through the development of several 'position' papers. We have defined the conceptual and practical differences in the approach to terrestrial and marine systems and made initial steps to define a plankton trait biogeography (Barton et al. 2013), outlined principles of the application of trait-based modelling to marine systems (Plankton: Andersen, Aksnes, et al. 2015; Fish: Andersen, Jacobsen, & Farnsworth 2016), explored trait-based approaches to describe zooplankton communities (Litchman et al. 2013), and suggested a division of ocean life in several realms to facilitate trait-based approaches (Andersen et al. 2016a). These conceptual studies and explorations have formed an important basis for the direction of more specific studies that we report on below. In the following sections we present a summary of the work performed within each of the 3 interrelated themes defined above. Reference is made only to our own work (Appendix 2), not to other relevant literature. All young researchers associated the Centre have in addition produced progress reports on their work (Appendix 6), which forms the main basis for the synthesis below.

3.1 Theme I: The individual

The key traits of an individual relate to its ability to feed, survive, and reproduce, i.e., the main factors governing its fitness. While reproduction may be the ultimate Darwinian mission of an individual it is essentially the product of the organisms ability to feed and survive, and resource acquisition can probably be considered the most basic feature. To set the scene, we have opened research under this theme by a major theoretical and empirical analysis of the size-dependency of the different fundamental ways of nutrient acquisition in marine organisms, ranging from harvesting of light and diffusive uptake of molecules to the active encountering and capture of prey across all life forms in the ocean, from bacteria to whales (Andersen et al. 2016a). The project has been ambitious in its scope: to explain the differences in the strategies of all the major life forms in the ocean based only on the size of individuals. The analysis covered fundamental aspects of marine life (resource acquisition, motility, sensing mode, life history strategy, and body temperature) and how the physical environment constrains these aspects in a size-dependent manner (Fig. 1).

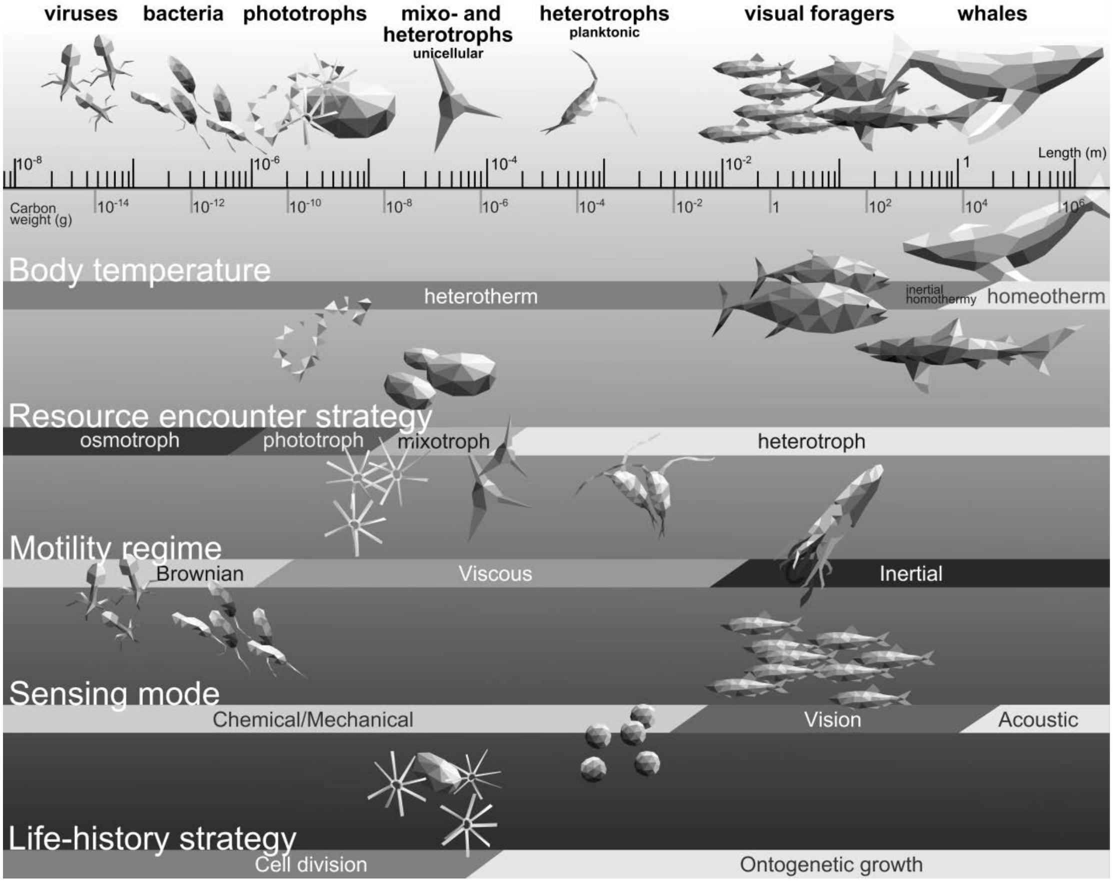

Figure 1. Cartoon describing the ‘Size in the Ocean’ project. The five aspects of pelagic marine life examined (body temperature, resource encounter strategy, motility regime, sensing mode and life-history strategy) are illustrated with horizontal bars with the characteristic transitions indicated by changes in gray-scale. The drawings in the top row illustrate the seven realms of life: viruses, osmo-heterotrophic bacteria, unicellular phototrophs, unicellular mixo- and heterotrophs, planktonic multi-cellular heterotrophs, visually foraging poikilotherms (bony fish, squid and sharks) and homeothermic animals (whales). (Andersen et al. 2016a)

We have reviewed data on size-based scaling laws for resource acquisition, mobility, sensory range and progeny size for all pelagic marine life and developed simple theoretical arguments for observed validity ranges of scaling laws. We use these theoretical insights to divide life in the ocean into seven major realms based on their trophic strategy, physiology and life history strategy. The results have a form that allows implementation in trait-based models and has been a cornerstone in our subsequent work. This analysis defines organism size as a ‘master trait’ and both describes how many vital rates and functions scale with size, and provide theoretical explanations hereof. This work has been very important for several reasons: 1) The very broad analysis involved all the disciplines covered by the Centre (chemistry, physics, mathematics, biology), 2) it involved almost all students and post docs as well as many of the PIs and thereby became instrumental in creating interdisciplinary interactions and collaboration, and 3) it represented the broad scope of the center by involving all aspects of marine life, from bacteria to whale. The work was backed up by an analysis of trait-data from data bases generated by the Centre (see also theme III). In addition to the main synthesis paper (Andersen et al. 2016a), this analysis has resulted in multiple papers providing more detailed empirical or theoretical analyses of various aspects, including size scaling of vital rates (metabolism, clearance rates, feeding rates, growth rates; Kiørboe & Hirst (2014)), reproduction strategies (Neuheimer et al. 2015, 2016; Olsson et al. 2016), sensory systems (Martens et al. 2015), and trophic strategies of unicellular organisms (Andersen et al. 2014).

3.1.1 Traits and trade-offs for important life forms

Following this taxa-transcending analysis, we have focused our work on selected life forms, viz., bacteria, phytoplankton (mainly mixotrophs), zooplankton, fish, and benthic invertebrates. These are arguably the most important life forms in the ocean, because small organisms dominate the biological processes in the ocean, and fish have direct societal relevance.

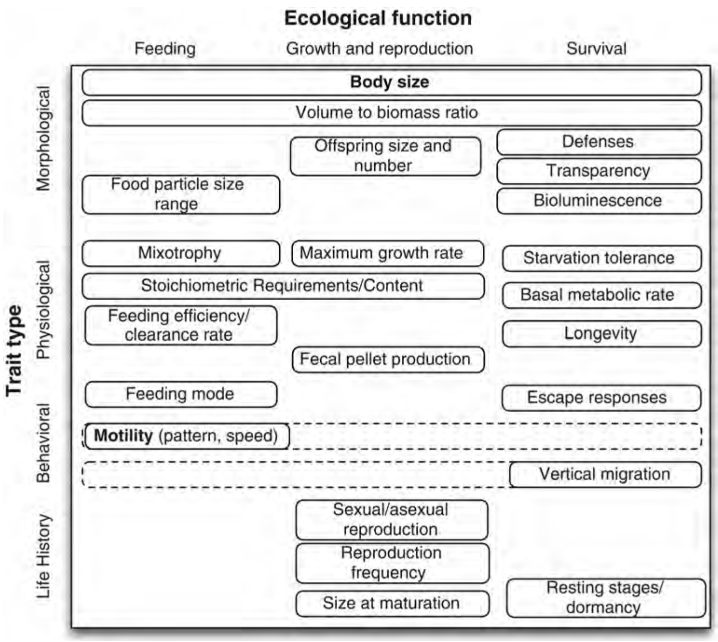

Fig. 2. Zooplankton trait classification according to function and type. With minor modification, this scheme may apply to the other marine heterotrophs. From (Litchman et al. 2013).

We have attempted a complete mapping of the traits characterizing zooplankton, and their ecological functions, but this mapping applies, with minor modifications, also to other heterotrophic life forms that our work is focused on (Fig. 2). Key traits and trade-offs relate to resource acquisition, as noted above, and we have used this as the 'guiding' trait to quantify trade-offs for the various life forms. In unicellular organisms nutrient acquisition and reproduction are closely related, since cell division is near proportional to resource acquisition. In multicellular organisms reproduction is further complicated by sex and life histories, and the trade-offs become manifest through complicated behavioral and life history adaptations. Thus, for unicellular organisms the work has focused on quantifying trade-offs related to nutrient acquisition. For multicellular organisms we have also examined reproductive strategies and life histories.

3.1.2 Bacteria. Traits for carbon turnover in the marine environment

Aim: Quantify the trade-offs for bacterial substrate utilization.
Process: The project had one PhD student, Sachia Jo Traving (OL at KU). She defended her PhD degree successfully in June 2016.
PIs: Lasse Rieman (KU), Colin Stedmon (DTU Aqua), Uffe H. Thygesen (DTU Aqua).

Central results: Experimental quantification and theoretical model of the trade-offs related to extracellular enzymes in bacteria; a key trait in the biological control of dissolved organic matter.

Unicellular organisms are particularly well suited for a trait-based approach because in many instances the species concept is not applicable, and the taxonomic diversity of bacterioplankton is not consistently linked to community function. Bacteria are then better characterized by their functional traits than by their taxonomy. The main purpose of the experimental and theoretical work with bacteria was to use a trait-based approach to understand the biological control of the oceanic pool of dissolved organic material (DOM) and its significance in global carbon budgets. DOM is the largest pool of organic material in the ocean (> 90 %) and is only utilized by bacteria. A key trait of a bacterium is therefore the types of extracellular enzymes it can produce and the exclusive resources it thereby can access; and the key trade-offs relates to enzyme ability and the cost of enzyme production. Our hypothesis was that the biologically controlled turnover of DOM in marine environments can be predicted from: i) characteristics of DOM that define its susceptibility to degradation and ii) bacterial extracellular enzymes and their intrinsic energetic trade-offs; i.e. consequences of enzyme production for bacterial growth efficiency. Central work modelled enzyme deployment strategies in free-living bacteria, providing new mechanistic insights to decades of experimental enzyme activity measurements (Traving et al. 2015). In compliment, experimental field work was carried out to identify and quantify the occurrences and impact of bacterial enzymes in different coastal ecosystems, which lead to the identification of biological and environmental drivers of bacterial enzymes (Traving et al. 2016), and their biogeochemical role in future climate scenarios (Traving et al. submitted). A study has also been carried out on evaluating the selectivity of bacterial communities in degrading DOM, which found that the uptake of low molecular weight compounds was ubiquitous whereas the ability to consume molecules of high molecular weight was a functional trait less widely distributed amongst populations (Logue et al. 2015). Finally, the work inspired a theoretical analysis of the biogeochemical fate of DOM in the oceans which address one of the big mysteries of biological oceanography, viz. why most of the DOM in the ocean appears to be refractory and has turnover times on the order of 1000 years (Traving et al. in prep). This work proposes a mechanistic approach to biologically driven DOM turnover, and discusses the unique potential of bacterial extracellular enzymes for understanding key mechanisms controlling the DOM pool. The presented work represents an important advancement in our understanding of the organic carbon flow mediated by bacteria.

3.1.3. Phytoplankton. Mixotrophy trade-offs

Aim: Quantify the trade-offs of investments into phototrophy, nutrient harvesting and phagotrophy and understand which environments (light, nutrients and food) favors a mixotrophic strategy.
Process: The project was initiated by Terje Berge (OL post doc at KU), later supplemented by Starrlight Augustine (FNU and HCØ funded post doc at DTU Aqua). Terje Berge's background is experimental plankton ecology, but he has invested into acquiring modeling skills, and has managed to develop a generic framework. The work is continued Subhendu Chakraborty (HCØ/Ocean Life funded post doc at DTU Aqua).
PIs: Per Juul Hansen (KU), Thomas Kiørboe, Ken H. Andersen (both DTU Aqua)
Central results: Experimental quantification of the trade-offs related to mixotrophy; models describing how mixotrophic strategies depend on environmental conditions and organism size.

The traits and associated trade-offs characterizing resource acquisition (light, nutrients, inorganic carbon) in phytoplankton are pretty well understood. However, many eukaryotic unicellular organisms in the ocean photosynthesize and take up food simultaneously, i.e., they are mixotrophic. Thus, our work has focused on mixotrophy and the costs and benefits of being mixotrophic with the overarching aim to understand the spatio-temporal distribution and significance of mixotrophy in pelagic food webs. The advantage of mixotrophy is the dual source of nutrition, and the trade-off is the investment in machineries for both photosynthetic and food uptake and degradation. Mixotrophy is a continuum from almost complete autotrophy to almost complete heterotrophy, occasionally even within a species. We have discovered that mixotrophy in principle applies to almost all marine free-living flagellates and has identified several distinctly different mixotrophic strategies (Flynn et al. 2013; Hansen et al. 2013; Mitra et al. 2014, 2016; Stoecker et al. 2016), which make generalizations more difficult than originally anticipated. Through laboratory experiments we have characterized the mixotrophic life strategy for selected types and we have demonstrated that heterotrophy and autotrophy are not fully complementary strategies, but are dependent on one another (Berge et al. 2012; Berge and Hansen 2016; Hansen et al. 2016).

The insight was used to develop a trait-based model of mixotrophy (Berge et al. 2016) that characterizes a cell by three traits: investments in phototrophy, nutrient uptake, and phagotrophy. We used experimental work on two mixotrophic organisms to parameterize the trade-offs. With that in place, the model was used to explore optimal investment strategies. We showed how mixotrophy was a favored strategy during summer conditions in temperate ecosystems.

Another avenue has been to relate mixotrophic strategies to the size of organisms. From theoretical arguments and empirical data-analyses we have knowledge of how size influences an organisms' affinity for diffusive uptake of dissolved nutrients, affinity towards light and the clearance rate for predation on other organisms. Putting these together demonstrates that it is optimal (from a resource acquisition perspective) for small heterotrophic plankton organisms to supplement the carbon uptake from predation with carbon from photosynthesis (Fig. 3; (Andersen et al. 2014, 2016a). This simple analysis is among the first general arguments explaining why mixotrophs are ubiquitous among unicellular plankton in the ocean and was used as the starting point for Subhendu Chakraborty's post doc project.

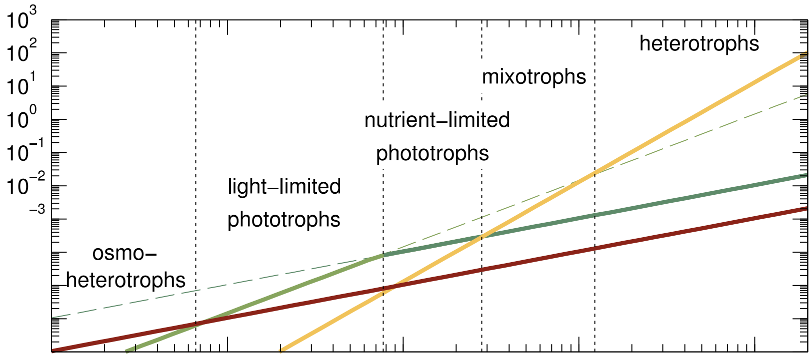

Fig 3. Encounter rates of uni-cellular organisms as a function of the trait "body size" (Equivalent Spherical Diameter, ESD) for four different resource acquisition mechanisms and resource types: diffusive uptake of dissolved organic matter scaling with diameter as l^1 (dark red), uptake of carbon through photosynthesis scaling as l^2 (light green), diffusive uptake of dissolved inorganic nutrients (dark green), and active encounter of prey organisms scaling as l^3 (yellow). The combined uptake of carbon and nutrients by phototrophs is limited by Liebig's law and shown with solid green lines; light green for light-limited conditions and dark green for nutrient-limited conditions. From (Andersen et al. 2016a).

Subhendu Chakraborty generalized the trait-based mixotrophy model (Berge et al. 2016) to account for cell size in addition to the three traits characterizing uptake of nutrients, light and phagotrophy.

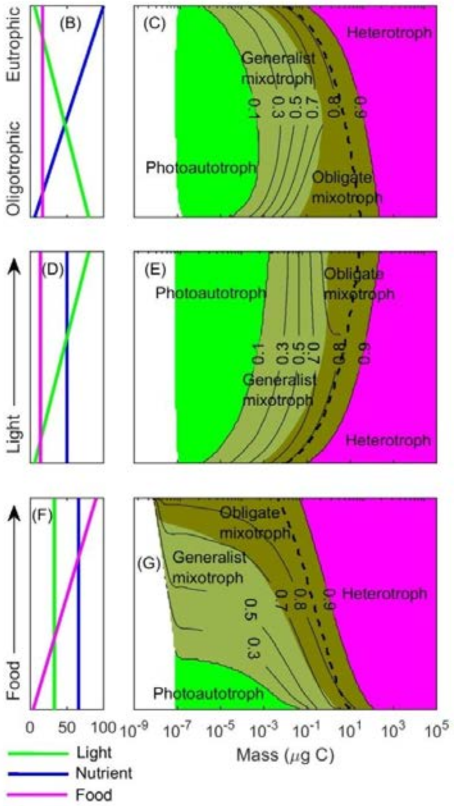

Fig 4. Demonstration of how mixotrophic strategies vary with environmental conditions (y-axes) and cell size (x-axis). Top: variation between oligotrophic and eutrophic conditions; middle: Variation in light (depth); bottom: variation with food. In all cases a large fraction of the size range of unicellular organisms are predicted to adopt one of two mixotrophic strategies. From Chakraborty et al. (2016).

This provided further insight into mixotrophy, and we were able to characterize two mixotrophic strategies: generalist mixotrophs that invest in all three traits, and obligate mixotrophs investing in only light harvesting and phagotrophy. Further, we have demonstrated how mixotrophic strategies change with environmental conditions (see Fig. 3).

3.1.4 Protozoa and zooplankton: Feeding and life history traits

Aim: Quantify the trade-offs of feeding traits in zooplankton.
Process: The project was initiated by Navish Wadhwa (OL PhD at DTU Fys) later replaced by Julia Dölger (OL PhD at DTU Fys), later supplemented by Lasse Tor Nielsen (post doc at DTU Aqua, co-financed by OL and N5T), Rodrigo Almeda (Post doc at Aqua financed by FNU and Marie Curie) and Hans van Someren Gréve (OL PhD at aqua).
PIs: Thomas Kiørboe (DTU Aqua), Anders Andersen (DTU Fys), Tomas Bohr (DTU Fys)

Central results: Experimental quantification of the trade-offs and life history implications related to feeding and swimming in zooplankton; mechanistic underpinning of prey size spectra

Zooplankton are sandwiched between the need to eat and the risk of themselves being eaten: Finding and capturing prey implies elevated exposure to predators. Zooplankton have to ascend to the surface ocean to feed on phytoplankton and hence face the risk of being eaten by visual predators (fish larvae), and feeding and swimming generates fluid signals that attracts rheotactic predators. Our work has focused on quantifying these trade-offs for various feeding strategies and for diverse protozoa and zooplankton and we have attempted to produce taxa-transcending mechanistically underpinned generalizations that allow utilization in population and ecosystem models (Theme II). We have also attempted to predict and demonstrate life history implications of feeding trade-offs. Finally, we have examined feeding mechanisms in some forms in which it is poorly understood to provide a mechanistic underpinning of prey size spectra.

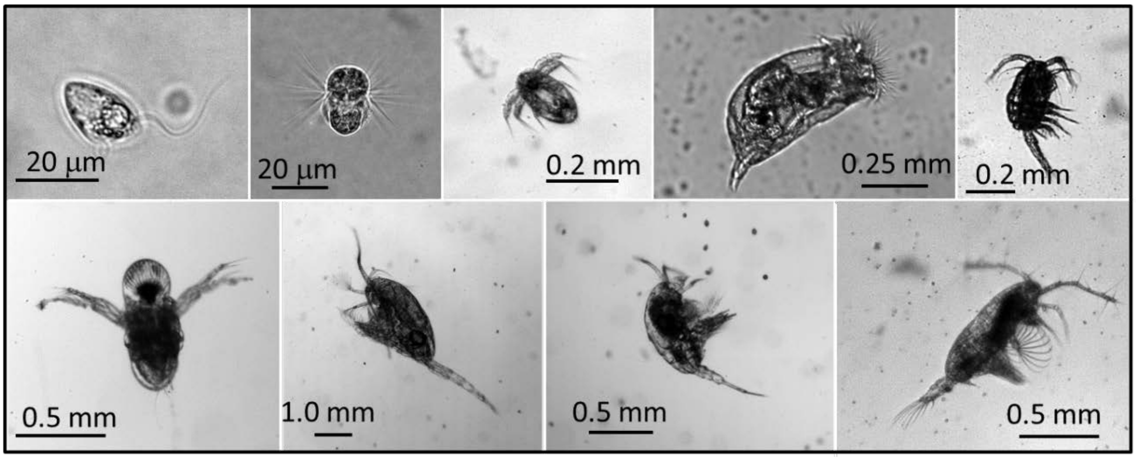

Fig.5. Zooplankton are morphologically diverse and span a large range of sizes; they also have diverse propulsion machineries and feeding modes. The trait-based approach aims at defining a few taxa-transcending traits that captures most of this diversity in a simple manner. From (Kiørboe et al. 2014).

Feeding strategies and trade-offs: Zooplankton feed in one of three ways: They can be ambush feeders that wait for prey to pass by; they can cruise through the water and capture encountered prey; or they can generate a feeding current from which they can harvest prey. This classification applies across all zooplankton taxa. Through observations of behavior and simple models we have quantified the efficiencies of the various feeding behaviors and the associated predation risks and metabolic costs. We have used high speed video recordings and flow visualization to describe the flows generated by feeding and swimming zooplankton ranging in size from 10 micron sized flagellates to > mm sized copepods (Fig. 5) (Kiørboe 2013; Kiørboe et al. 2014; Wadhwa et al. 2014; Nielsen and Kiørboe 2015). The spatial extension of the fluid disturbance generated by swimming and feeding zooplankton is a measure of the 'predator encounter cross section' and is proportional to the risk of being detected by a rheotactic predator and thus allows us to quantify predation risk (Fig. 6). We have developed simple fluid mechanical models of feeding and swimming that accurately predict bulk properties of the observed flow fields, which has provided an understanding of the underlying physics and, hence, allowed us to generalize our results into taxa-transcending quantifications of the predation risk associated with the three feeding behaviors (Kiørboe et al. 2014; Andersen et al. 2015a).

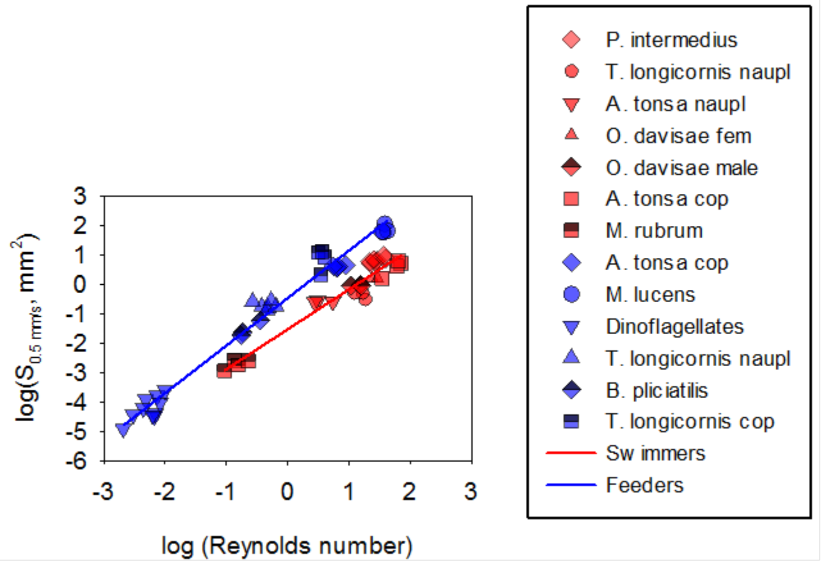

Fig 6. Feeding, swimming, and predation risk in zooplankton. The spatial extension of the fluid disturbance created by swimming and feeding zooplankton as a function of the Reynolds number (size x speed/viscosity). Blue symbols refer to hovering and cruising zooplankton; red symbols to breast stroke swimmers and zooplankton that swim-by-jumping. The latter create a fluid signal with a spatial extension about 10 times less the former and, hence, have a correspondingly lower risk of encountering a rheotactic predator. From (Kiørboe et al. 2014).

Further, the models of feeding and swimming flows have made it possible to quantify the efficiency (in terms of clearance rates) of the different feeding modes, and even to make estimates of the metabolic costs of generating these flows (Kiørboe and Jiang 2013a). By thus quantifying the main trade-offs associated with the three different feeding modes, we have been able to make predictions about optimal foraging in different environments and to successfully estimate the resulting clearance rate and swimming speed magnitudes and size scaling for zooplankton (Fig. 7).

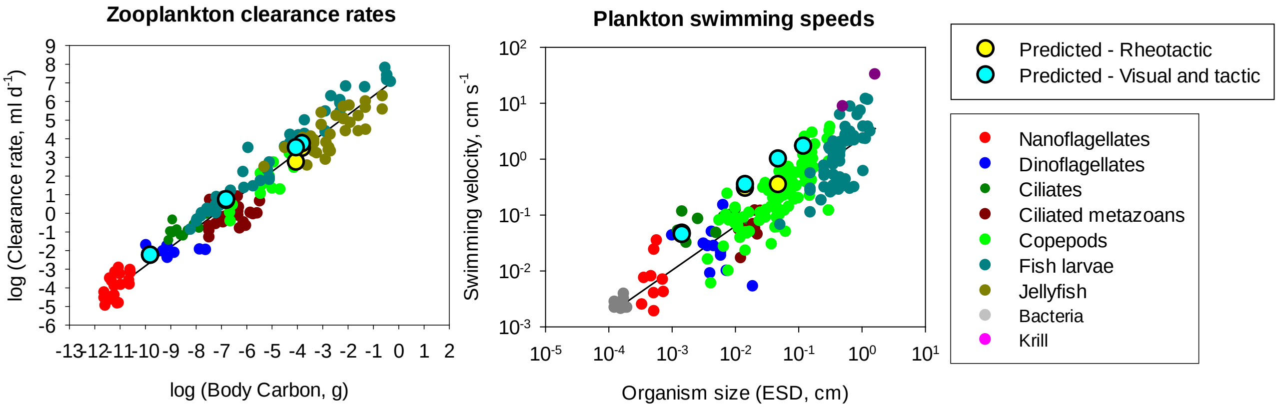

Fig. 7. Observed (small symbols) and predicted (large symbols) zooplankton clearance rates and swimming speeds as a function of size. From (Kiørboe and Jiang 2013b).

We have finally experimentally tested the predation risk and metabolic rate implications of the different behaviors that is predicted from the fluid dynamical observations and models (Almeda et al. in press; van Someren et al. accepted). This involves incubation experiments and directly measuring the predation mortality of zooplankton with the different feeding (and mate finding) behaviors when exposed to relevant predators. The results are in accordance with predictions, and confirm that mortality risk vary by up to an order of magnitude depending on the feeding mode (Fig 8).

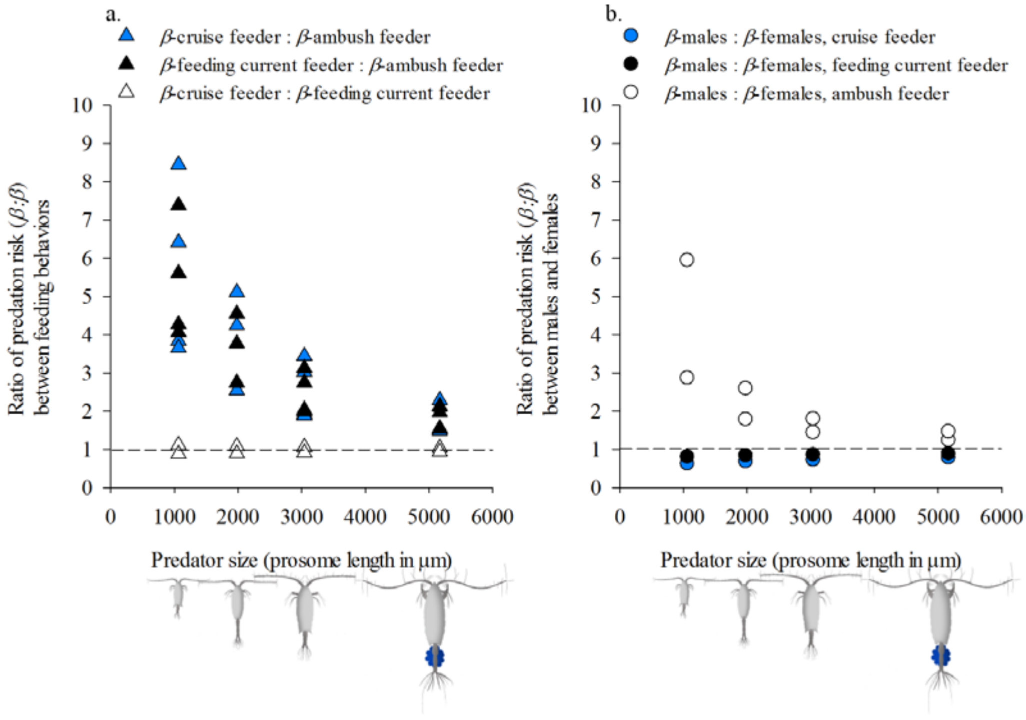

Fig 8. Observed predation risk ratios of prey combinations as function of predator size, illustrating how feeding and mate-finding behavior can lead to almost an order of magnitude difference in predation risk, as predicted by theoretical models. The risk ratio is the ratio of predicted volumetric encounter rates. a) Predation risk ratio on species exhibiting contrasting feeding behavior. b) Predation ratios between male and female copepods of the three main feeding types. The dashed line indicates a ratio=1, i.e., the predation risk is equal between prey types (Someren et al. in press)

Feeding behavior and life history trade-offs: The mortality rates implied by the different feeding (and mate finding) behaviors also have implications for the optimal allocation of energy between growth, reproduction, and maintenance at the level of the individual. Theory predicts that under certain conditions, a high external mortality rate favors investment in growth and reproduction over maintenance, and vice versa, and thus, differences in feeding behavior have implications for longevity and ageing rates. We have experimentally tested this idea in protected lab environments and found that zooplankton with low-risk ambush feeding behavior age slowly and have low fecundity compared to zooplankton with more risky feeding behaviors (Fig. 9). Thus, feeding, survival, and reproduction are interrelated through trade-offs in a quantifiable manner, and the general principles that we have developed feed directly into trait-based models of plankton communities and ecosystems (see theme II).

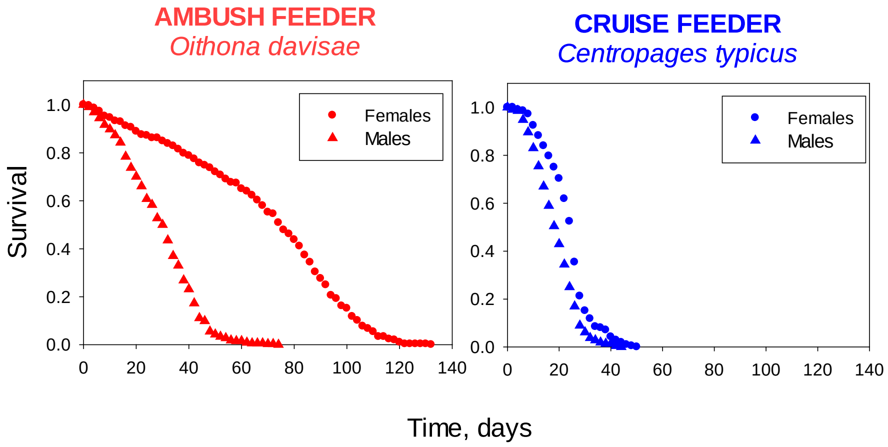

Fig. 9. Example to illustrate differences in survivorship in predator-free lab environment between copepods with different feeding and mate finding behaviors. The low-risk ambush feeder lives much longer than the high-risk cruise feeder; and males of the ambush feeder have a very risky female-searching behavior and lives much shorter than the females. The apparent larger investment in maintenance (survival) in the ambush feeder is traded off against a much lower fecundity as compared to the cruise feeder. Modified from (Kiørboe et al. 2015)

Another project, not part of the Centre's original agenda, yet relevant to understand life histories and model population dynamics, is our studies of sexual selection through mate choice in copepods (Heuschele et al. 2013; Ceballos et al. 2014), which is mediated through chemical signals (Selander et al. 2011; Heuschele et al. 2013; Heuschele and Selander 2014). Sexual selection has implications for the evolution of sexual size dimorphisms (Hirst and Kiørboe 2014) and risk taking behavior. Importantly, we have demonstrated, in lab and field studies, that it is a rather small fraction of a copepod population that contributes to population growth. 'Super males' and 'super females' account for the majority of the matings and consequent reproductive output and a large fraction of the population never mate and reproduce (Ceballos et al. 2014; Sichlau et al. 2015). The exact implications to the population biology of this finding, as well as the generality of it, have yet to be explored.

Zooplankton feeding mechanisms and prey size spectra: While feeding mechanisms in zooplankton are well studied for most species, it is still unclear for some important forms how they perceive and capture prey. In the context of the development of size-structured trait-based models it is, for example, important to know the prey size spectra of zooplankton and to understand the underlying mechanisms. We have explored the fluid dynamical constraints on resource acquisition in small aquatic organisms (i.e., at low Reynolds numbers) (Kiørboe 2016a) and have examined the feeding mechanisms and prey size spectra in three important groups, i.e., copepods, dinoflagellates, and choanoflagellates. We have employed high speed video micrography and micro-PIV to study mechanisms and visualize feeding currents (Fig. 10) and simple models to reveal mechanisms (Dölger et al. 2016 and submitted).

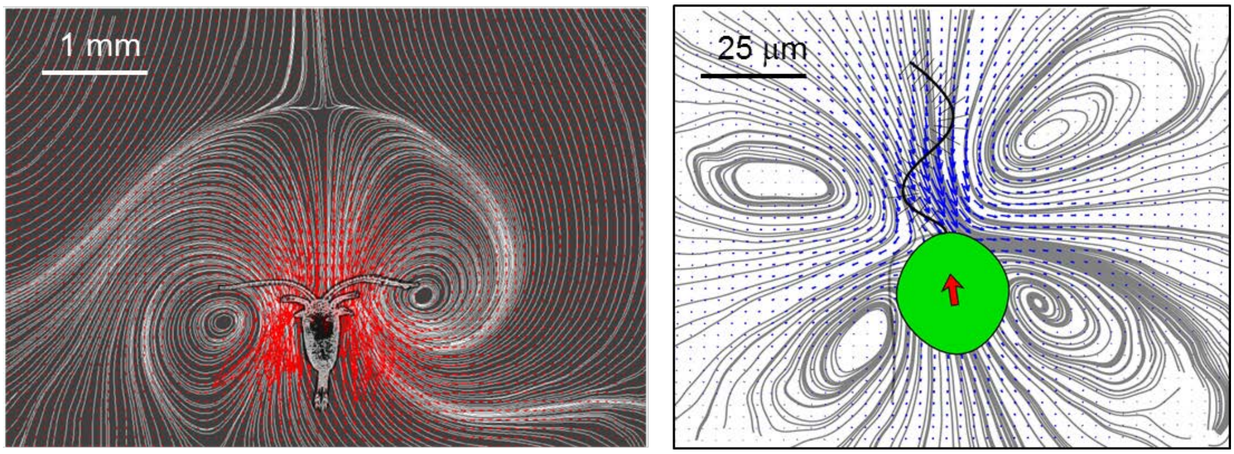

Fig. 10. The feeding current flows generated by copepod (*Temora longicornis*, left) and a flagellate (*Fibrocapsa japonica*, right). The flows are recorded using Particle Image Velocimetry. From Wadhwa et al. poster (left) and Nielsen & Kiørboe (unpublished) (right).

Hitherto it has been assumed that feeding-current feeding copepods perceive prey remotely by means of chemical cues. However, simple model calculations of signal transmission suggests that this is not possible, and we have for a variety of copepod species now discovered that the prey is perceived only when it is touched by the setae of the feeding appendages (Bruno et al. 2012; Kjellerup and Kiorboe 2012; Marc et al. 2012; Tiselius et al. 2013; Gonçalves and Kiørboe 2015; Kiørboe et al. 2016) and provided a mechanistic explanation of the prey size spectrum observed in copepods with different foraging modes(Gonçalves et al. 2014; Kiørboe 2016b). This is utilized in the sized based zooplankton models that we are developing.

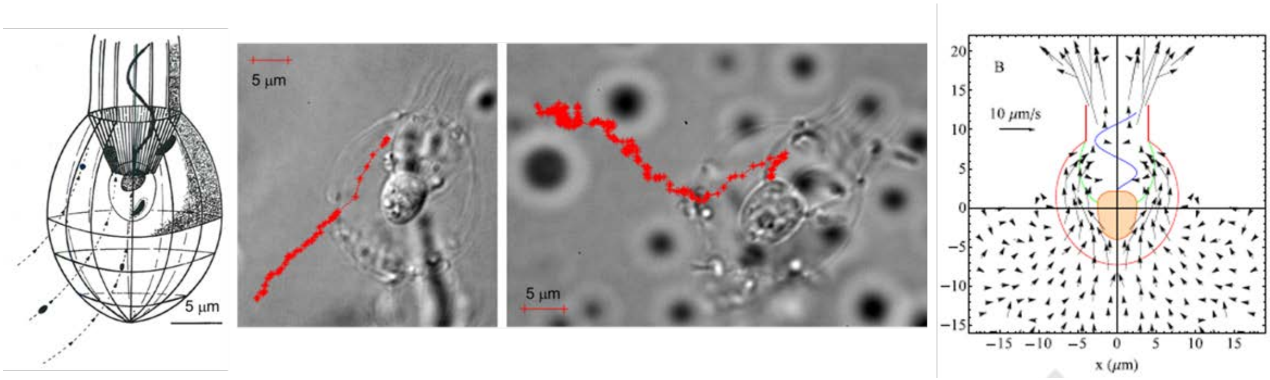

Fig. 11. Choanoflagellates are equipped with a single flagellum that drives a feeding through a fine-meshed ‘collar’ and bacterial prey are retained on the collar (typical prey trajectories are shown on the microscope images). Based on observed flagellum kinematics and slender body theory, we have computed that the force generated by the flagellum is two orders of magnitude less that required to drive water though the filter at the required rate. We have solved this apparent paradox by suggesting a novel flagellar pumping mechanism that can explain nearly all observed clearance rates reported in the literature. Left panel is from Andersen (1988/89 Mar Microb Food Webs 3: 35-50). Right panels from Nielsen et al. submitted

We have further examined feeding mechanisms in heterotrophic flagellates as their interception with prey remains poorly understood (Fig. 11. In fact, simple interception feeding in flagellates should not be feasible; a flagellate approaching a prey should push the prey away due to the viscous boundary layer surrounding the flagellate. Using high speed video-microscopy and micro-PIV we have, however, discovered how various dinoflagellates can generate feeding flows that allow them to overcome the viscosity problem, and some species are even adapted to produce ‘quiet’ flows that cannot be perceived by their evasive prey (Fig. 12). These feeding flows also significantly increase the flux of inorganic nutrient molecules to the cell, thus serving the dual purpose of supplying both prey and nutrients to these mixotrophic organisms (Nielsen and Kiørboe 2015).

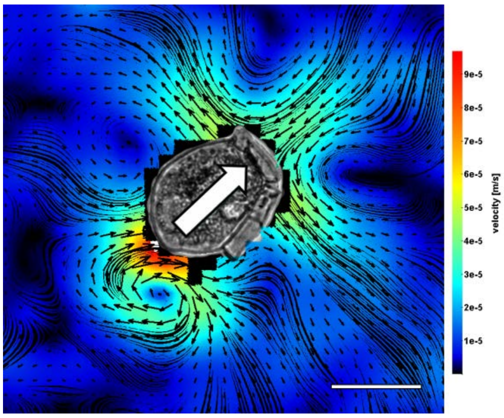

Fig. 12: The feeding and swimming flows produced by a dinoflagellate, Dinophysis. A trailing flagellum produces vortex structures in the wake of the flagellate, while a transverse flagellum generates an incoming feeding current in front of the cell. The strain rate of the feeding current is too weak to be discovered by its prey, the mixotrophic ciliate *Mesodinium*. The white arrow shows the swimming direction of the flagellate and the scale bar is 50 µm. Modified from (Nielsen and Kiørboe 2015)

3.1.5 Protistan defense mechanisms

Aim: Quantify the costs and benefits of suspected defense mechanisms in unicellular plankton
Process: The project was initiated by Jiayi Xu (Chinese funded PhD scholarship at DTU Aqua), and recently supplemented by Marina Pancic and Agnethe Hansen (both OL post docs at DTU Aqua). Jiayi and Marina both are biologists by training doing experiments, while Agnethe has an engineering degree and is developing the models.
PIs: Per Juul Hansen (KU), Thomas Kiørboe, Ken H. Andersen (both DTU Aqua)
Central results: Description of the response of individual copepods to toxic algae; review of defense trade-offs and initial model development.

While the above reported work on feeding in zooplankton demonstrates clear and quantifiable trade-offs between feeding efficiency and mortality risk, many protists have developed mechanisms with a suspected defense function that are likely to trade off against growth efficiency. Possible defense mechanisms – often inducible by the presence of grazers - have in particular been suggested for phytoplankton that may have hard external shells (diatoms, cocolitophores) and spines (diatoms) or may produce toxic substances that may function as grazer deterrents. Defense trade-offs are often assumed for the development of phytoplankton models; without such trade-offs, phytoplankton communities may reduce to one or a few species, demonstrating the competitive exclusion principle. Thus defense trade-offs is one important mechanism to explain the diversity of phytoplankton communities. However, reviewing the literature (Pancic in prep) reveals a striking lack in our knowledge: the efficiency of suspected defense mechanisms has been demonstrated only in very few instances, and quantifications of trade-offs have been made even more rarely.

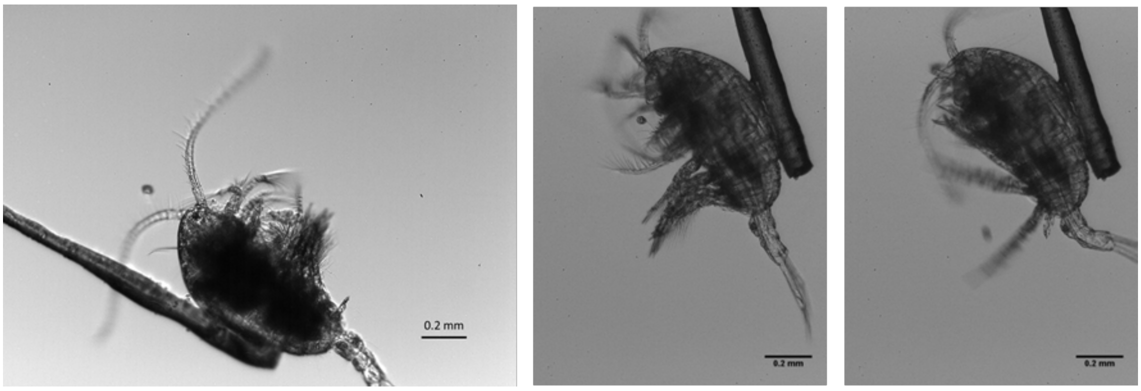

Fig. 13. By tethering a copepod in front of a high speed camera it is possible to examine the response of individual copepods to individual cells of (toxic) algae. Left: a cell arrives in the feeding; mid: the cell is captured; right: a cell is rejected (upon capture). From Xu et al. (2017)

We have initiated this work by first examining the response of individual copepods to the toxins produced by various strains of a dinoflagellate (*Alexandrium*) (Fig. 13, Xu et al. 2017). Depending on the strain, the copepod may either (i) continue to feed normally, (ii) initially eat the cells, but after a while cease feeding, (iii) continue to eat the cells, but after a while regurgitate ingested cells, or (iv) initially capture and eat the cells, but after a while reject captured cells. While responses 2-4 all eventually lead to reduction in grazing rate on cells, only the latter response can be interpreted as a result of real defense mechanism and an evolutionary stable strategy. Response 2 and 3 require toxic cells to sacrifice their life in order to benefit other cells in the population (both response) as well as their competitors (response 2), and so it is difficult to understand how the production of costly chemicals that elicit such responses have evolved as defense mechanism. These studies of individual behavioral responses to multiple strains of the same species help resolve the considerable confusion in the literature as regards grazer response to toxic algae. We have recently initiated a more systematic exploration of defense mechanisms in phytoplankton, beginning with modelling of the trade-offs associated with chemical defenses, as well as theoretical and experimental quantification of trade-offs related to exoskeleton in diatoms. We envisage that this work will continue well into next period of the Centre that we are applying for.

3.1.6 Reproduction trade-offs

Offspring size is a central trait for all multicellular organisms. Broadly speaking, the trade-off that a female faces is choosing between producing few, large offspring with good survival prospects or many small offspring, few of which are likely to reach adulthood. Evolution is expected to select the strategy that yields the greatest number of surviving offspring.

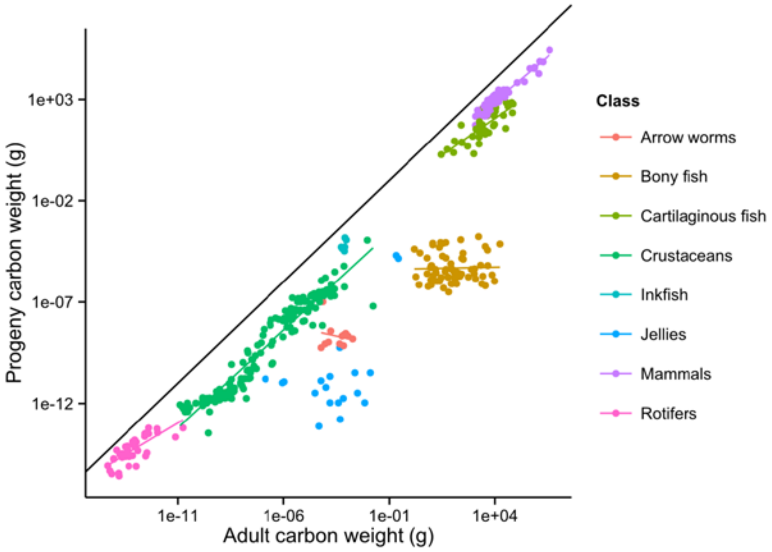

Fig.14. Offspring size as a function of adult size for different groups of organisms. Most groups have an offspring size roughly a factor 100 smaller than the adult size. Notable deviations are fish and jellyfish. From Neuheimer et al. (2015).

The majority of fish species have opted to produce large numbers of small eggs, regardless of the adult size. However, we have shown that some fish species deviate from this pattern and make offspring that are roughly a factor 100 smaller than the adults ("proportional strategy"), notably elasmobranchs (sharks, skates, rays) and also a number of small, live-bearing teleosts (bony fish) species. We have extended this analysis to other marine organisms and have found that bony fish are special as they are the largest group employing the "many-small" eggs strategy, while most other groups follow the proportional strategy (Fig. 14; Neuheimer et al. 2015, 2016).

To explain this remarkable pattern we have employed optimization modelling. Simple optimization of life-time reproductive output reveals that it always advantageous to make as many small eggs as possible. This argument has two problems: 1) it does not explain the "proportional" strategies; 2) it ignores density dependent effects in the population regulation. To address both problems we have made an "adaptive dynamics" type of model and used it to find evolutionary stable (and unstable) strategies for offspring size. The analysis essentially shows that both strategies ("many-small" and "proportional") are able to coexist (Olsson and Andersen 2016; Olsson et al. 2016).

We have also examined the trade-offs related to the trait maturation size in fish. The trade-off is that a large maturation size leads to a high reproductive output at the cost of a lower chance of survival to maturity. Life-history theory suggests that small short-lived species should allocate more energy relative to size to current reproduction than large longer-lived species that are likely to spawn several times during their lifespan, but observations do not follow the predicted size scaling of reproductive output (Olson & Gislason 2016). More work is obviously necessary to account for the costs associated with spawning migrations and courtship behavior.

3.1.7 Synthesis

We have strived to identify key traits that within life forms transcend taxonomy and to quantify trade-offs such that they can be generalized beyond the species examined and be formulated mathematically. Yet, further simplification may be necessary, particularly for attempts to develop so-called end-to-end models that describe complete ecosystems. The simplification that emerges from our work with individual traits and trade-offs is the identification of three life-form transcending traits that together captures the fitness of any organism, be it a bacterium, a copepod, or a fish: body size, resource acquisition mode, and defense. Body or cell size is the main determinant of most vital rates (growth, feeding, metabolism, mortality risk, etc.) and has clear trade-offs that we now have a good handle on quantifying; resource acquisition is a fundamental property of any organism that comes at a metabolic cost and a risk of predation that we have aimed at quantifying for different life forms; and defense is the means by which an organism can improve its likelihood of reaching maturation and perform its ultimate Darwinian mission of reproducing itself but again comes at a cost in terms of lost feeding opportunities (e.g., diurnal vertical migration, see below) or investments in defense mechanisms. Predation and predator defense is an important mechanism for generating diversity and solving the ‘paradox of the plankton’, but to our surprise poorly understood for protistan plankton and, hence, should be a focus for the continued work with developing the trait based approach to ocean life.

3.2 Theme II: trait-based modeling

The aim of theme II is to develop and apply trait-based models based on trade-offs formulated at the individual level, partly developed in theme I. The end results of the models are *trait-distributions*. A trait-distribution describes the number of individuals $N(\theta)$ with a given trait combination θ, irrespective of their species. We have worked with both continuous trait-distributions, e.g., the abundance of individuals as function of size, and discrete trait-distributions, e.g., abundance of individuals with a given feeding strategy.

As described in the application for the Centre, we mainly use three model systems: the GOTM vertical water column model, the MIT Global Circulation Model (GCM) and the fish size spectrum model. We have achieved the milestones for the completion of the model systems that we set for the first three years (see section 9).

In the following we will first describe the general modelling paradigms (section 3.2.1). Then we describe the models grouped into “project groups”: models of uni-cellular plankton, copepod models (seasons & size and foraging traits), fish models, and finally models based on life-history optimization. Some projects are directly tied to theme I where the fundamental trade-offs have been developed (in particular the various copepod models) and some are matched by similar projects in theme III (copepod models and fish models).

3.2.1 Modelling principles

We describe three types of modelling techniques: unstructured models, size-structured models, and optimization models. The core principle in all models is a description of the bio-energetic budget of an individual organism (Fig. 15). The bio-energetic budget describes how the organism acquires energy and how that energy is allocated between fundamental tasks, such as respiration, growth, reproduction and activity. The description of an individual through these (or similar) processes is a fairly standard procedure. The novelty is to connect these processes to fundamental traits such that the parameters describing each process are connected via trade-offs.

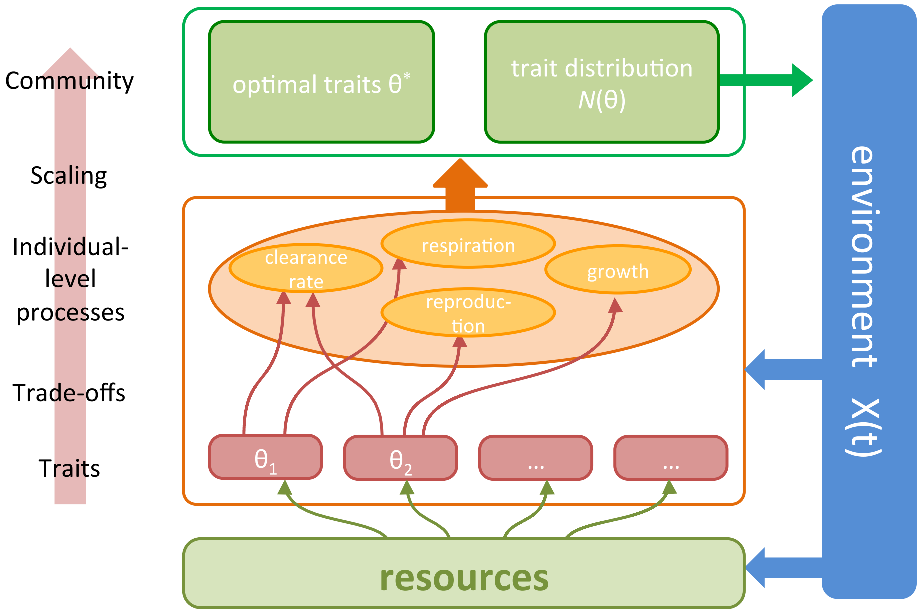

Fig. 15. Illustration of the principles in trait-based models. The aim of the model is either to derive the trait distribution N(θ) or the trait combination θ^* which is optimal under certain conditions (upper green box). These macroscopic properties are derived from a description of individual-level processes, here illustrated by the processes determining food capture (clearance rate), respiration, growth and reproduction (orange box). The scaling from individual-level processes to macroscopic patterns is performed using standard methods (see text). The crux of the trait-based approach is the description of how individual-level processes are linked to traits (red boxes) through trade-offs (red arrows).

The traits θ determine the individual level processes through the trade-offs, leading to a description of the available energy $G(\theta)$ and mortality $m(\theta)$. The available energy and the mortality $m(\theta)$ are used to scale from the individual level to the trait distribution $N(\theta)$, which is the abundance as a function of the set of trait values. This scaling follows standard procedures from theoretical ecology. In its most simple form the scaling is performed as:

$$\frac{\mathrm{d}N(\theta)}{\mathrm{d}t} = [\epsilon_r G(\theta) - m(\theta)]N(\theta) \qquad (1)$$

This equation states that the growth rate of abundance of individuals (the term in the square brackets) equals the difference between reproductive output $\epsilon_r G(\theta)$ and losses due to mortality $m(\theta)$, with ϵ_r being the reproductive efficiency.

The available energy $G(\theta)$ can be broken down into the fundamental processes from Fig. 15:

$$G(\theta) = \epsilon_a f(V(\theta)R(N(\theta))) - S(\theta)$$

where $V(\theta)$ is the clearance rate, $f(\cdot)$ is a function representing processing capacity (the "functional response"), $S(\theta)$ is the respiration and ϵ_a is the efficiency of assimilation. $R(N)$ is the concentration of the resource, which has to be specified separately for each particular model. Since the resource concentration $R(N)$ depends on the trait-distribution of predators, Eq. (1) is non-linear and has to be solved numerically in most cases.

The type of model in Eq. (1) is valid when somatic growth can be ignored, i.e., when the ratio between offspring size and adult size is small (uni-cellular organisms). For multi-cellular organisms the ratio between offspring size and adult size is large and therefore growth of individuals has to be explicitly resolved. This can be performed either through agent-based simulations or through structured models. We use size-structured models solved by application of the classic McKendric-von Foerster conservation equation:

$$\frac{\partial N(\theta)}{\partial t} + \frac{\partial (g(\theta)N(\theta))}{\partial w} = -m(\theta)N(\theta) \qquad (2)$$

Here $g(\theta) = \epsilon_g G(\theta)$ is the growth in size w of individuals with ϵ_g being the growth efficiency. This efficiency can be a complicated sub-model describing the internal energetics of the organisms (see Hartvig and Andersen 2013). The equation has to be supplemented with a boundary condition at the smallest size describing the reproductive output from the adults.

The last means of scaling is through fitness optimization. Fitness optimization does not lead to a trait-distribution but only provides information about which trait (or trait combination) is optimal under specific external circumstances. Fitness optimization is simple in principle, but fraught with subtleties that should be addressed and kept in mind when the results are interpreted. Such subtleties are related to the selection of the correct fitness proxy or the issues of density dependence and frequency dependent selection. We have applied various optimization techniques (simple fitness optimization, dynamical programming and adaptive dynamics), acknowledging their limitations and well knowing that they are no substitute for the results of dynamical simulations with the type of models described above (Eq. 1 and 2). Nevertheless, optimization techniques are a simple way to obtain some insights with a smaller investment than what is required to formulate and simulate full dynamical systems.

Fitness optimization requires an appropriate fitness measure. The optimal fitness measure is the one which leads to the largest population growth (in most cases, but see Mylius & Diekmann. "On evolutionarily stable life histories, optimization and the need to be specific about density dependence" *Oikos* (1995): 218-224, and follow-up works by the same authors). In the absence of a perfect measure for fitness optimization, proxies are used. For a uni-cellular organism the population growth rates is given by the term in the angular brackets of eq. (1), so the fitness optimization is:

$$\theta^* = \sup_{\theta}\{\epsilon_r G(\theta) - m(\theta)\}, \qquad (3)$$

i.e., the difference between reproductive output and mortality. For an organism with ontogenetic growth, the population growth rate is given by the largest eigenvalue of eq. (2). If it is not possible to find this, a suitable proxy is provided by “Gilliam’s rule”. This rule states that the organism should strive to maximize the ratio between available energy and mortality $G(\theta)/m(\theta)$:

$$\theta^* = \sup_{\theta}\left\{\frac{G(\theta)}{m(\theta)}\right\}. \qquad (4)$$

We have made a general theorem showing that Gilliam’s rule indeed is the correct proxy for an organism under steady state conditions, and a good approximation under (some) non-steady conditions (Sainmont et al. 2014).

3.2.2 Ecosystem models: seasons and size

Aim: What is the seasonal dynamics of the size-distribution of the entire ecosystem?

Process: The project started as a collaboration between DTU Compute and DTU Aqua, with Irene Heilmann (Ph.D. at DTU Compute) and Erik Martens (Post Doc. at DTU Aqua and weekly visitor at DTU Compute). The full realization of the project was hampered by Erik Martens leaving prematurely for a permanent position at KU, and by Irene Heilmann working only part time and with a long leave of absence due to health issues. With Irene Heilmann back and with a new supervisor (Mads Peter Sørensen, DTU Compute) the project is on track with one publication. It has now become a center-wide project involving most young researchers. Finally, a new post doc is just starting on the project, Floor Soujdin (HCØ funded, DTU Aqua), who will focus on the role of ontogenetic growth of copepods.

PIs: Ken H. Andersen (DTU Aqua); Jens Starke (DTU-Compute); Mads Peter Sørensen (DTU Compute); André Visser (DTU-Aqua); Thomas Kiørboe (DTU Aqua); Uffe H. Thygesen (DTU-Aqua).

Central results: In a simple unstructured trophic chain, the seasonal fluctuations become stronger in higher trophic levels. Such a model is therefore unsuited to describe the seasonal forcing of the ocean ecosystem. Organisms adapt their overwintering strategies to the degree of seasonality according to their body size.

Large parts of the ocean are strongly forced by the seasonal variation in sunlight that drives the lowest trophic levels. The aim of this project is to understand how this forcing shapes the strategies by organisms of different size. Two avenues have been followed: 1) development of a seasonally forced model of the size-distribution in the ocean. 2) modelling optimal overwintering strategies by organisms of different body size.

Our size-based model show that the concentrations of trophic levels are weakly declining with the trophic level (Fig. 16). Further, fluctuations due to the seasonal forcing are amplified in the higher trophic levels. This is a problematic result; it predicts that higher trophic levels should fluctuate even more than lower trophic levels during the season. This is hardly realistic, and we conclude that a realistic description of how the seasonal forcing propagates through the trophic levels requires a description that resolves the entire life history of each species. The simple unstructured trophic chain is therefore not an applicable model. We believe that the problem can be solved by accounting for the ontogenetic growth of higher trophic levels, and have therefore formulated a model that incorporates this (Heilmann et al. 2016).

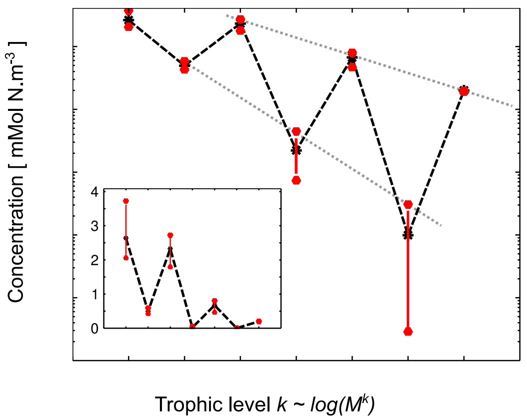

Fig. 16. The concentration of nutrients, phytoplankton and zooplankton as a function of trophic level from the trophic chain model. The red error bars show the range of the fluctuations driven by the seasonal forcing on the 1st trophic level (phytoplankton).

We have developed a large collaborative project to describe which strategies organisms follow to deal with the seasonal variability in the environment. The project is built around an optimization model that predicts optimal seasonal routines: to survive winter as eggs resting or spores; to build reserves to survive the winter, possibly combined with hibernation; or to make seasonal migrations to lower latitudes (Fig. 17). The model is complete and the second part of the project, collection of data is in the final stages. We expect the project to result in several publication similar to our earlier very successful project “size in the ocean”.

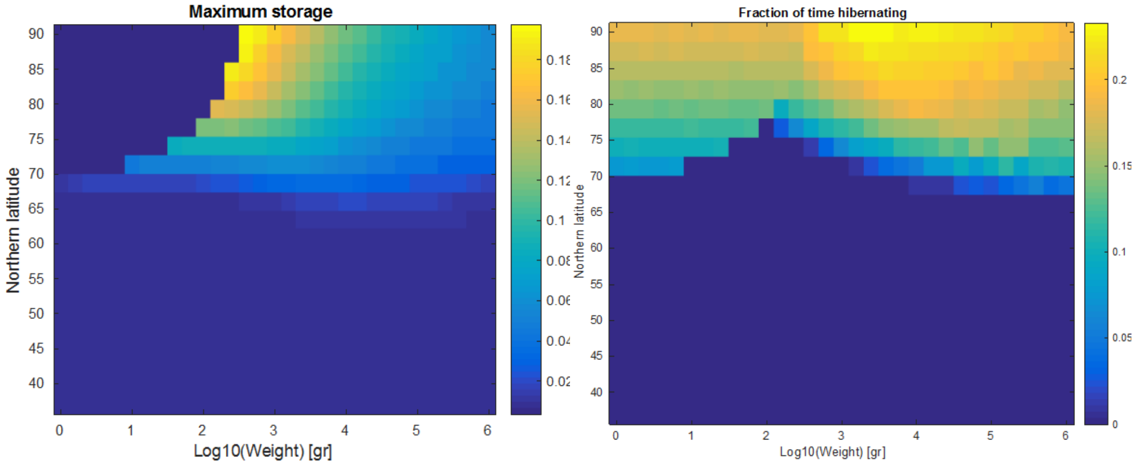

Fig. 17. Optimal seasonal routines as a function of body size (x-axis) and latitude (y-axis). The left panel shows the amount of reserves (storage) that an individual builds. In the top left corner (very small organisms in high latitudes) organisms give up trying to survive the winter and instead makes eggs or resting spores that survive the winter. Right: the fraction of the time spent in hibernation.

3.2.3 Copepod models: foraging traits

Aim: what determines the foraging-trait distribution of zooplankton, globally and seasonally?

Process: The work has been primarily driven by Friederike Prowe (Post doc., DTU Aqua). Due to the high ambitions (building, for the first time, a complex zooplankton food-web model on top of a global circulation model), the project was initiated early in the center's life. The project was ready for being written up into one or two publications around summer 2013. At that time Friederike went on maternal leave. At the end of her leave (summer 2014) she has continued in a tenure track position in Kiel. Her main project in Kiel is to keep working on the global circulation model and we have an active collaboration to finalize the publications. To further develop the project we made two hires ultimo 2014 (Ph.D. Nicolas Azaña Schnedler-Meyer and post.doc Kasia Kenitz).
PIs: Patrizio Marini (DTU-Aqua); Andre Visser (DTU-Aqua); Thomas Kiørboe (DTU-Aqua);
External collaborators: Mick Follows and Stephanie Dutkiewicz (MIT)
Central results: Established seasonal and global circulation model predictions of phytoplankton and zooplankton feeding trait distributions.

The aim of this project has been to make predictions about when and where in the global ocean one feeding trait dominates over the other. This is realized by employing the trade-offs between fundamental feeding traits of zooplankton – cruising and feeding-current feeders vs. ambush feeders - established in Theme I to formulate dynamical models. The trade-offs involve the physical environment, in particular turbulence that determines encounter rates, and light that determines the risk of feeding. We have implemented these trade-offs in two model systems: a water column model and a global circulation model.

Water column model of zooplankton behaviour: From the mechanistic description of feeding modes as described in section 3.1.4 we have developed trait-based models of copepods' behavior, which

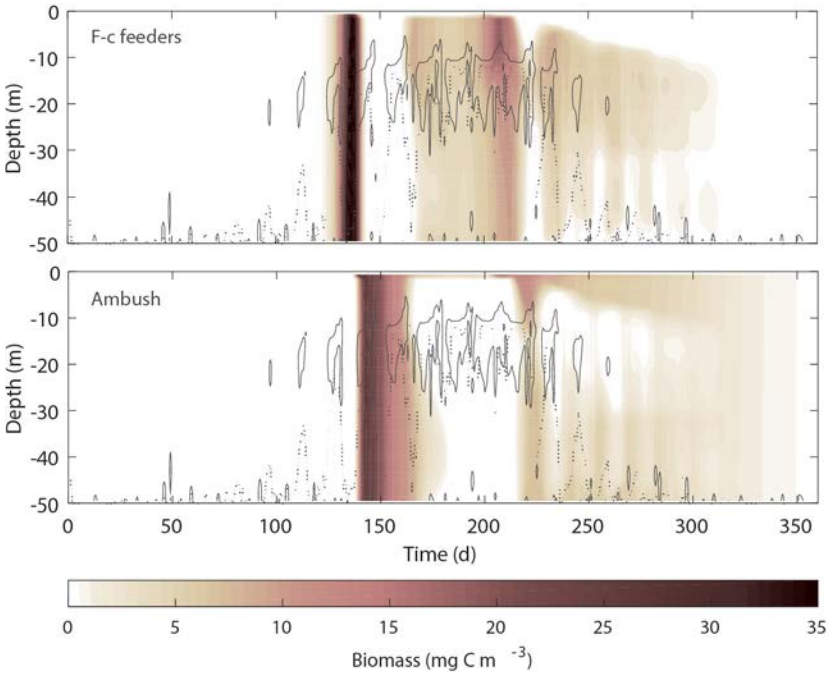

Fig. 18. Results of the trait-based model of copepod behavior in a water-column, showing the biomass of feeding-current feeding and ambush feeding copepods over the season (from Kenitz et al. 2016).

are used to simulate the seasonal succession of cruising and ambushing copepods (Mariani et al. 2013). The model has been extended to a full dynamic model (Kenitz et al. 2016). The model employs a combination of dynamic simulations of the trait distribution (Eq. 1) with an optimization of the copepod's feeding behaviour (Eq. 3). The model was embedded in a vertical water column model (GOTM) forced by climatology characteristic of a temperate ecosystem (wind, temperature, light). This simple model robustly reproduces one of the most salient features of the seasonal succession of phytoplankton in temperate oceans, viz., the transition from a spring bloom dominated by non-motile phytoplankton (diatoms) to a system dominated by motile species in summer (flagellates) (Fig. 18). Further , we have made data analyses of the trait distribution of copepod feeding modes in the North Sea (Kenitz et al. 2016) and in the Southern California Current to test model predictions.

Global Circulation Modelling: The approach developed above formed the basis for a trait-based incorporation of zooplankton grazing in global models. The basis was the trait-based "Darwin model" of phytoplankton developed at MIT. To enable a focus on zooplankton corresponding to the model described above, we simplified the phytoplankton model and described it through four fundamental trait-groups (large and small combined with motile and non-motile). Likewise the zooplankton is described as large and small combined with ambushers and cruiser (Fig. 19). The parameters of each of the eight groups are determined by the traits - size, feeding type, and trophic type (phytoplankton/zooplankton) – that are interrelated through trade-offs.

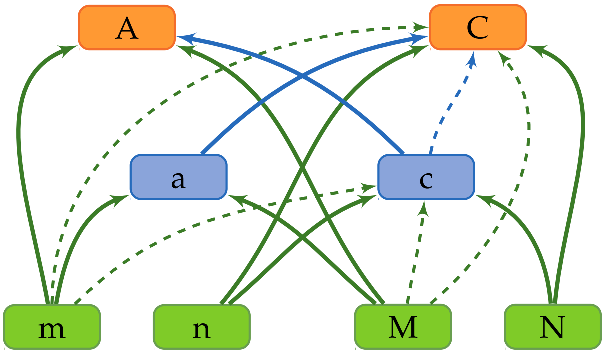

Fig. 19. Illustration of the interactions between the different trait-types in the model: motile and non-motile phytoplankton (green; "m" and "n" for small and "M" and "N" for large), and ambushing and cruising zooplankton ("a" and "c" for small (unicellular) and "A" and "C" for large (copepods)).

The model is implemented in the MIT global circulation model through collaboration with Mick Follows and Stephanie Dutkiewicz at MIT. Analysis and sensitivity analyses of the model results are ongoing. The model predicts a dominance of ambushing zooplankton in strongly seasonal environments (high latitudes), while cruising zooplanktons are dominating a-seasonal (tropical) environments (Fig. 20). Preliminary tests of model predictions against observations are promising, and we are currently compiling more observational data (Theme III).

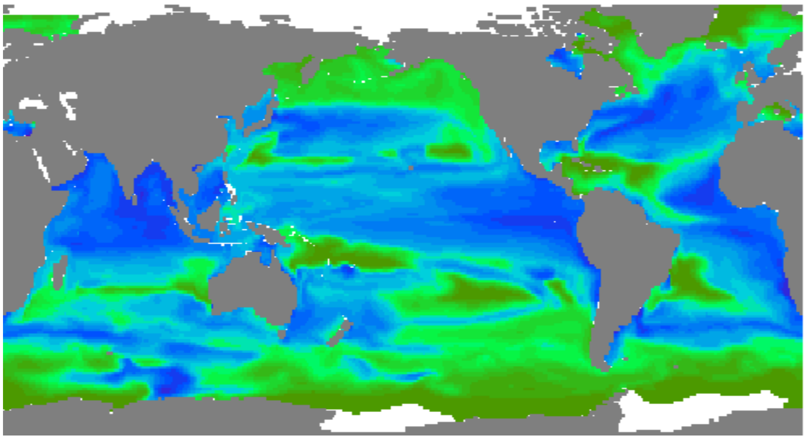

Fig. 20. Result of the default run with the trait-based phytoplankton/zooplankton model showing the ratio of annual biomass between large zooplankton being dominated by ambushers (green) and cruisers (blue).

Another line of the effort to understand which conditions favours different foraging modes has focused on the difference between jellies (tactile predators) and small fish (visual predators). The work has resulted in a trait-based model of how the interplay between primary productivity and fishing pressure determines the susceptibility of ecosystem to jelly blooms (Fig. 21).

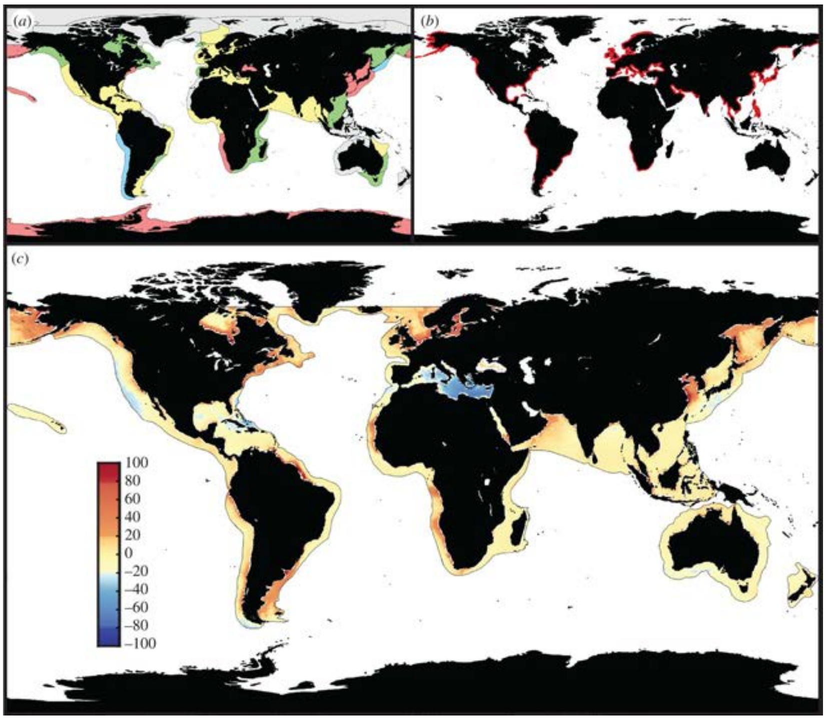

Fig. 21. Observed (a, b) and predicted (c) distribution of jellyfish in ‘Large Marine Ecosystems’. A: Trends in jellyfish populations in Large Marine Ecosystems. Colours represent areas with increasing trends and low uncertainty (red), increasing trend and high uncertainty (yellow), stable or fluctuating biomass (green), decreasing trend (blue) or no data (grey). B: Reported global occurrences of coastal jellyfish blooms (red AREAS). (c) Jelly susceptibility index for the Large Marine Ecosystems, as generated by our model. Positive values indicate that jellyfish are more likely to be present than forage fish, negative numbers the opposite. From (Schnedler-Meyer et al. 2016).

3.2.4 Size-spectrum models: Fish & fishing

Aim: What is the impact of fishing on the trait distribution of size and asymptotic size?
Process: Progress in this project was initially driven by Nis Sand Jacobsen (OL Ph.D. student) and Lise Marty (OL post doc) – both are now finished. It is continued by Ph.D. student Rob van Gemert (on EU Marie Curie funding). Progress is satisfactory and the work has received much attention.
PIs: Ken H. Andersen, Henrik Gislason (DTU Aqua)
External: Tim Essington (UW); Robert Arlinghaus (Berlin)
Central results: 1) Establishment and application of trait-based model for ecological impact assessment of fishing on an entire fish community. 2) Establishment and application of a trait-based model for ecological and evolutionary impact assessment of fishing on a single fish stock.

Size-spectrum models describe the abundance of fish populations and fish communities as a function of size of individuals. In these models, size is considered a “state” which changes throughout life as the individual grows. The fundamental trait for fish is therefore not the size, but rather the asymptotic (maximum) size that an individual may reach. The fundamental bio-energetic model describing the trade-offs was developed before the Centre started but was further refined in (Andersen and Beyer 2015). The end results of the models are the size-distribution of a population with a given asymptotic size, which is found by solving Eq. (2). We have realized this general framework in two models: a model of a single fish stock and a model of an entire fish community, both of which are applied to fundamental problems of direct relevance to fisheries management.

Single-species model: In the single-species model, acquired food and mortality are functions of individual size, and they are either maintained constant in time or dynamically emerging from an explicit model of the resource dynamics. This model has been implemented as an online simulation, available at https://www.stockassessment.org/spectrum.

The model has been used to calculate fisheries reference points, such as the fishing mortality that gives the maximum sustainable yield or the fishing mortality where the population collapses as a function of the asymptotic size (Andersen and Beyer 2015). These results were surprising: The largest species tolerate as high a fishing mortality as smaller species. This is at odds with common “metabolic” rules of thumb stating that smaller species would be able to tolerate much higher mortalities than larger species. We have shown that our results are consistent with fisheries reference points used in selected European fisheries and are currently undertaking a global analysis. Beside these main results, the model has been used to examine the importance of the “BOFFs” (Big Old Fecund Females) in a population (Calduch-Verdiell et al. 2014).

The model has further been applied to calculate rates of fisheries induced evolution. Fishing usually targets the largest individuals in a population. Fishing is therefore selective, and when there is selection there is also an evolutionary response. Size selective fishery induces an indirect selection on traits associated with growth: size at maturation, growth rate, and allocation of energy to reproduction. However, fishing is also selective towards fish behavior: ‘bold’ individuals feed more and grow faster but are also more exposed to fishing gear. We have extended the trait-based fish population model with a behavioral trait related to boldness and examined the selection response on this trait to fishing (Fig. 22). The results show that fishing will produce an evolutionary response of fishing towards producing less bold individuals.

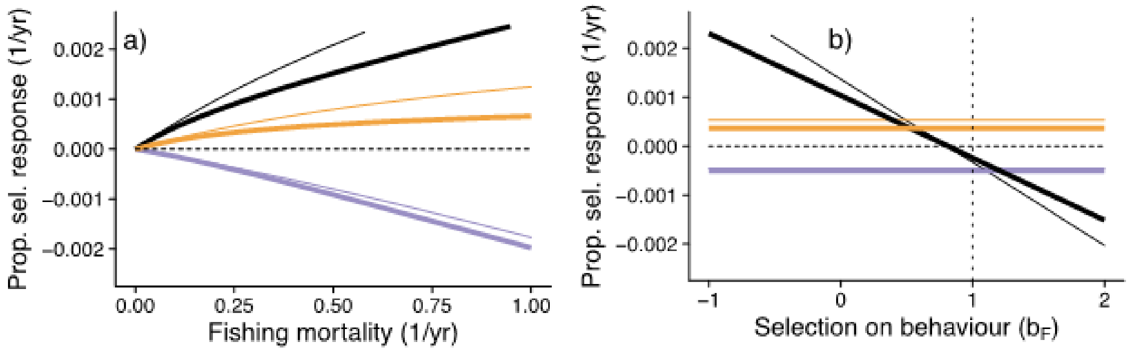

Fig. 22. Proportional selection responses as a function of fishing mortality without selection on behavior ($b_F = 0$) (a) and as a function of the strength of selection on boldness for $F_0 = 0.3$ yr^{-1} with a trawl-type size selection. Line width represents asymptotic size; thin: 140 g, thick: 14,000 g. Traits under selection: reproductive investment (orange), boldness τ (black) and maturation size (magenta). From Andersen et al. in revision).

Finally the single-species model has been applied to examine the importance of one of the fundamental assumptions in fisheries science: that the density dependent regulation of the population occurs early in life, and not within the adult or the fished part of the population (Andersen et al. 2016d). Using the model, we have been able to provide a theoretical justification to one of the fundamental assumptions of almost all demographic models of fish populations: that density dependence occurs predominantly early in life. We show that this is indeed a good assumption in large ecosystem (such as marine system), but not in lakes. We also outline cases where the assumption of early-life density dependency may break down, thus explaining some of the puzzling special cases observed. These cases have important implications for one of the most common regulations used in fisheries, namely regulation of mesh size in fishing gear (Fig 23). These plots show which mesh size (the x-axis) and fishing mortality (y-axis) leads to the highest fisheries yield. The right-hand panel shows standard theory where the highest yield is achieved by a large mesh size which allows all immature fish to pass through the mesh. The left panel shows that the opposite case is also likely: fishing on the largest individuals will lead to a significantly smaller yield that what could potentially be achieved.

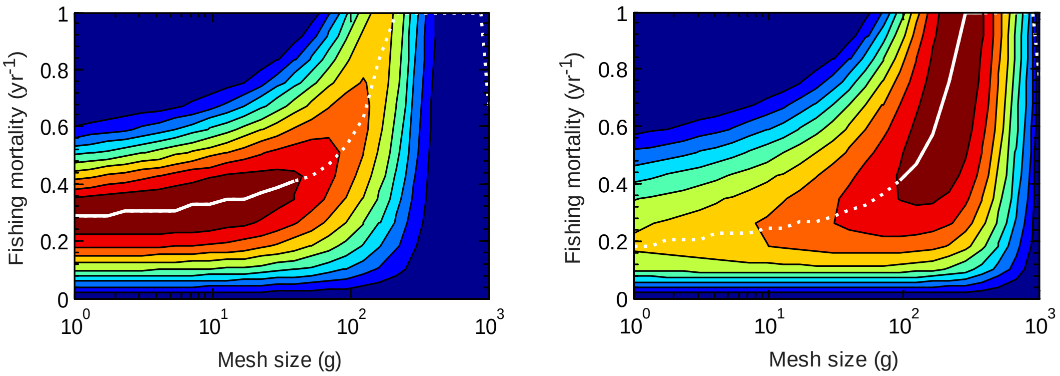

Fig.23. Yield from trawl-fishing with different mesh sizes (x-axis) and fishing mortality (y-axis). To the left our model shows that the highest yield is achieved with a mesh size that retains very small fish (around 1 g). This result is in contrast to traditional models (right) which predicts the highest yield with large mesh sizes (around a few hundred gram). Asymptotic size: 1 kg.

The significance of these results on selectivity of fishing gears for fisheries science and current good practice in fisheries management can hardly be overstated. They challenge conventional wisdom that only the largest fish should be targeted by fishery, a practice which have been implemented through mesh size regulation since the mid of the 20th century. Other influential groups in the world have also begun realizing similar results, however only for specific cases. Our trait-based framework makes it possible to generalize the calculation beyond single specific population to be valid for fish stocks in general by just varying the trait asymptotic size. Our general statements are bound to have a very strong impact – they have already created controversy (Andersen et al. 2016b).

Fish community model: The fish community model is built upon the same principles as the single-species model described above, with two important additions: it includes a continuum of species along the trait-axis “asymptotic size”, and the amount of food and predation mortality on individuals is determined by the available food and abundance of predators (Fig. 24). The advantage of the trait-based model is that it is not tied to a specific ecosystem and can therefore be used to make general statements about the expected impacts of fishing on an ecosystem. We have documented the theoretical basis of the model in an invited review to one of the main fisheries journals (Andersen et al. 2016c) and made an open-source implementation of the model (“Mizer”; Scott et al. 2014). The open-source implementation of the model is now being used by other groups throughout the world.

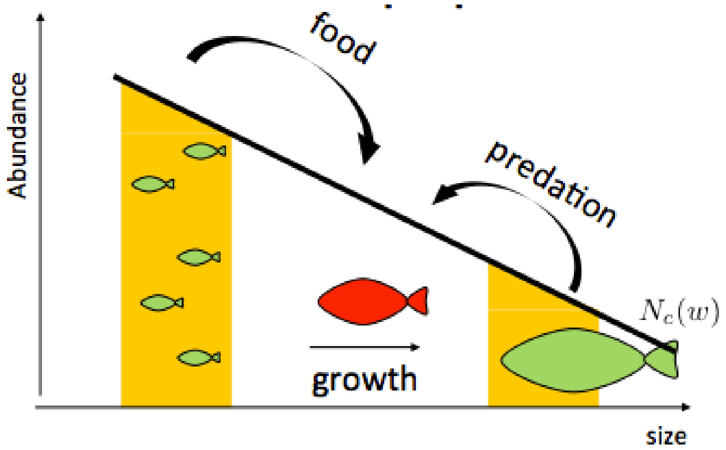

Fig. 24. Illustration of the principles in the trait- and size-based fish community model. The growth and reproductive rate of an individual (red fish) is determined by the abundance of smaller individuals. The same process determines the predation by larger individuals (large green fish). Once growth and mortality is known, the size distribution can be found by solving Eq. (2). Since growth and mortality are part of the solution, these are formulated as integrals over the solution itself, and Eq. (2) becomes a partial-integro-diffential equation.

The model has been applied to evaluate the community impacts of fishing. When one part of the fish community is fished (one species or a specific size range), it has implications for the rest of the community. Fishing of small fish species removes prey for larger species, which reduces their growth and therefore their productivity for the fishery. Conversely, fishing of large fish species removes predators on smaller species, which increase their productivity. The model provides a means of quantifying the importance of these indirect effects of fishing. We have used that to evaluate various aspects of the "Ecosystem Approach to Fisheries Management". For example, we have examined the consequences of implementing a 'balanced harvesting' fishing strategy with the trait-based model (Jacobsen et al. 2014). The central results is that while balanced harvesting might provide slightly higher yield that current exploitation, small individuals with a limited economic value will dominate the yield. We have also used the model to examine the potential conflicts between various management objectives, e.g. maximization of yield, conservation of fish stocks and maximization of economic benefit of fishing (Andersen et al. 2015b), and describe the "efficiency frontier" of fishing (Jacobsen et al. 2016).

Besides these applications of the trait-based model framework we have performed some technical evaluations of the framework. We have performed an analysis of the asymptotic stability of solutions and how they depend on fundamental parameters (Zhang et al. 2013). This analysis demonstrates how the trait-diversity inherent in the model acts to stabilize the model solution in comparison to earlier non-trait-based version of the model, which are very unstable. Finally we have compared the types of predictions of the model with those from a classic unstructured food-web model (Jacobsen et al. 2015).

3.2.5 Optimization modeling: Reproductive traits & vertical migration

Aim: use optimization models ("fitness maximization") to predict reproductive traits and vertical migration strategies.
Young researchers: Julie Sainmont (OL/project financed PhD students), Karin Olsson (OL Phd), Lise Marty (OL post doc)
PIs: André Visser, Thomas Kiørboe, Henrik Gislason, Ken H Andersen, Uffe H Thygesen (all DTU Aqua)
External collaborators: Øystein Varpe (University Centre of Svalbard)
Process: Optimization models have been central to the work of Karin Olsson and Julie Sainmont. Karin has moved beyond simple optimization towards "adaptive dynamics", which bypasses some of the inherent problems with defining a fitness measure by explicitly including density-dependent processes. Julie Sainmont's work has formed the basis of the work now being initiated in 3.2.2, where Floor Soudjin will study similar problems, but now using full dynamic models.
Central results: Optimality model of zooplankton size and reproductive traits (capital vs. income breeding) as a function of the seasonal environment (latitude); Optimality model of vertical behavioural traits; Optimality and adaptive dynamics models of offspring size. (See also section 3.1.6)

The work involving optimization models is used to gain ecological insights without needing to formulate complete dynamic models. Thematically, the use of optimization models lies at the interface between theme I (establishing trade-offs) and theme II (models). We have applied a large palette of specific methodologies: simple optimization, dynamic programming ("functional optimization") and "adaptive dynamics". The work centers on understanding behavior (to feed or not to feed) and to understanding reproductive strategies: offspring size, income vs. capital breeding and understanding the competitive abilities of jellyfish.

Vertical migration behavior: An important adaptation to the feeding-predation risk trade-off relates to vertical migration in zooplankton. Many zooplankton conduct diel vertical migration (DVM): they hide at depth during night and feed near the surface, where the food is, during day, and this is considered an adaptation to reduce mortality due to visual predators. Our observations in an arctic system has demonstrated the size dependency of vertical migration (mainly large forms migrate), which is consistent with the visual predation hypothesis (Sainmont et al. 2014), and we have developed an optimization model based on a game theory approach and on a quantification of the feeding-predation trade-off in which DVM emerges (Sainmont et al. 2013). Because DVM has important biogeochemical implications, mainly for the vertical material flux in the world's oceans, we have finally developed a simplified "myopic" approximation to the dynamic programming solution to describe DVM that captures the results very well but is computationally much less demanding and therefore better suited for incorporation in larger models (Sainmont et al. 2015).

Reproductive traits in a seasonal environment: In high latitude environments the copepod community changes between being dominated either by large copepods which reproduce in spring on fat reserves stored during the previous summer, or by smaller skinny copepods which need to feed before being able to reproduce. The larger copepods are "capital breeders", while the smaller ones are "income breeders". The trade-off involved is: making reserves makes it possible to breed early in the season to have the offspring feed on the spring bloom, but entails a risk of dying before the reserves can be used for breeding. We have modeled this pattern by characterizing copepods by two traits: reproductive strategy (discrete trait: capital or income) and body size (Sainmont et al. 2014). Fitness optimization predicts that large capital breeders dominate in short feeding seasons while small income breeders dominate in longer feeding seasons (Fig. 25). This pattern corresponds well with observations in the arctic: when the ice breaks up late in the season, the feeding season is short and the community is dominated by the capital breeder *Calanus hyperboreus* while when the ice breaks up early it is dominated by the income breeder *Calanus finmarchicus*. Our model therefore provides a mechanistic understanding of the changes in the trait distribution that may occur under climate change where the ice is expected break up earlier.

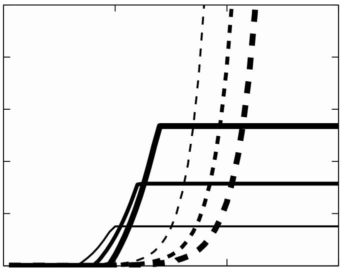

Fig. 25. Fitness of copepods with different reproductive traits (line type) and size (line width) as a function of latitude (here represented with the length of the feeding season). The reproductive traits are "capital breeding" (solid lines) and

"income breeding" (dashed lines). The figure shows that we can expect to see large capital breeders dominating the copepod community when the feeding season is short (high latitudes) while when the feeding season is long (lower latitudes), communities will be dominated by small income breeders. From Sainmont et al. (2014).

Reproductive traits of invasive jellyfish: As part of our efforts to explore the 'jelly-trait' and to be able to predict the occurrence of gelatinous plankton, we are using life history optimization to understand the biology of invasive jellyfish, specifically the multiple invasions of the voracious box jelly *Mnemiopsis leidyi* from the US east coast into European waters (Jasper et al. 2013 and submitted,). *M. leidyi* is a perfect invader since it has an enormous reproductive potential and it is hermaphroditic and can fertilize its own eggs and is, thus, released from Allee effects. The reproductive strategies of native and invaded populations are systematically different, in that individuals in invaded populations start reproducing earlier at a smaller size than those in the native mother populations. We have documented this difference both in lab experiments and in field populations. The basic hypothesis that we have explored is that a native population in steady state should optimize its competitive abilities and its life time reproductive output (= net reproductive rate, R_0). Invading populations, in contrast, would be selected for high per capita growth rate (= r, The Malthus parameter). To test this hypothesis, we considered a size-structured population growing at a constant rate and explicitly described the trade-off between somatic growth and reproduction at the individual level. We find that per capita population growth rate is maximized for the smallest possible size at maturation, whereas lifetime reproductive success is maximized for intermediate size at maturation, consistent with the pattern observed.

Along similar lines, we have explained the very unusual population structure of another recently discovered box jelly that occurs abundantly in the Baltic Sea, *Mertensia ovum* (Jaspers et al. 2012). It normally occurs in the arctic where it reaches sizes of up to 10 cm. We discovered that individuals in the (probably relict) population in the Baltic never grows beyond 2-3 mm and reproduces in the larval stage. This very unusual strategy can be explained through life-history optimization and as a result of high juvenile mortality in the Baltic population.

3.3 Theme III: Nature

Aim: To describe trait distributions in nature
Process: The theme had a slow start due to lack of man-power, and so Martin Lindegren (OL Researcher at Aqua) was hired (February 2014) to promote and direct the theme, and three PhD students were allocated: Mark Holm (OL, RUC), Philipp Bruun (OL, Aqua), Lauréne Pécuchet (OL, Aqua), and most recently also Tim Dencker (OL, Aqua), Daniel van Denderen (DTU Aqua, HCØ post doc funds) and Esther Beukhof (Aqua, externally funded). The group also hosts a visting post doc, Anna Törnroos (funded by BONUS). All young researchers are biologists, but the supervisor team has both modelling and biological expertise.
PIs: Martin Lindegren, Mark Payne, Thomas Kiørboe (all at DTU Aqua)
Central results: Data generated trait distributions and analyses of trait diversity and ecosystem resilience in nature

The goal of Theme III is to investigate the distribution and diversity of marine organism traits occurring in nature based on available observations across local, regional and global scales. The theme serves to answer fundamental ecological questions relating to marine biogeography, e.g., the occurrence and drivers of trait variation along environmental gradients, as well as the abiotic and biotic processes shaping life-history strategies of marine organisms and community composition. Furthermore, our empirical trait-based approach aims to shed light on the underlying biodiversity-related mechanisms promoting resilience of marine ecosystems, i.e., the adaptive capacity to buffer against disturbances and retain their structure and function. This will provide not only scientific insight but also knowledge relevant to conservation and management of marine biodiversity, as called for by international agreements such as the *Convention of Biological Diversity* (CBD). Theme III is linked to Theme I ("The individual"), relying on the identification of key traits and trade-offs and to Theme II (“Models”) by providing observed trait distributions with which to test and validate the predictions of mechanistic trait-based models. The work of theme III is structured into three tasks: (i) Collecting and validating marine trait data; (ii) Mapping and investigating the biogeography of marine traits and functional diversity; (iii) Assessing the underling processes of community assembly and ecosystem resilience. Please note that work under theme III has fairly recently been initiated. Therefore, we present both the finished and ongoing activities under each task.

3.3.1 Collecting and validating marine trait data

The availability of spatially resolved data on key marine traits is a fundamental requirement to study trait biogeography and trait diversity, i.e., a measure of functional diversity, in nature. Therefore, the Centre for Ocean Life, through the “Size in the Ocean” project (see Theme I) and numerous underlying studies, currently being prepared for publication, has compiled a massive amount of trait data for zooplankton and other marine metazoans (e.g., Kiørboe and Hirst 2013a-c; Brun et al. 2016). These data have been, or will be archived in open access data depositories available to scientist within and outside the Centre. In terms of fish and benthos, large repositories of data exist, either through national surveys, regional monitoring programs, or via international data bases, such as FishBase and OBIS. Although some of these are well-known and easily accessible, many have been organized from a species centric perspective, often with the aim of monitoring the abundance or spatial distributions of ecologically or commercially important species. In order to be applicable to a trait-based approach marine trait data needs to be collected, quality controlled and organized in a format suitable for further trait analysis. Based on a collaborative effort within and outside the Centre, a number of extensive trait data bases for fish and benthos have been established. The selection of traits was based on generic principles outlined under Theme 1 (Fig. 2), but adapted to fit each specific group of organisms. Furthermore, thorough quality control, revisiting or reanalyzing primary data sources has been applied, particularly where trait values were deemed uncertain or extrapolated from empirical relationships, such as for natural mortality of fish. The resulting data bases have largely been established for specific marine ecosystems, e.g., the Baltic and North Seas. However, joint efforts under ongoing research projects within the *International Council for Explorations of the Seas* (ICES) have provided comparable species abundance and trait data for marine fishes throughout European Seas, ranging from the Mediterranean to Greenland (Pecuchet et al., in review). Furthermore, a global data set of fish traits, based on a selected number of morphological, morphometric and behavioural characteristics that are measurable and comparable across most, if not all taxa and marine ecosystems has been collected and used in further analyses.

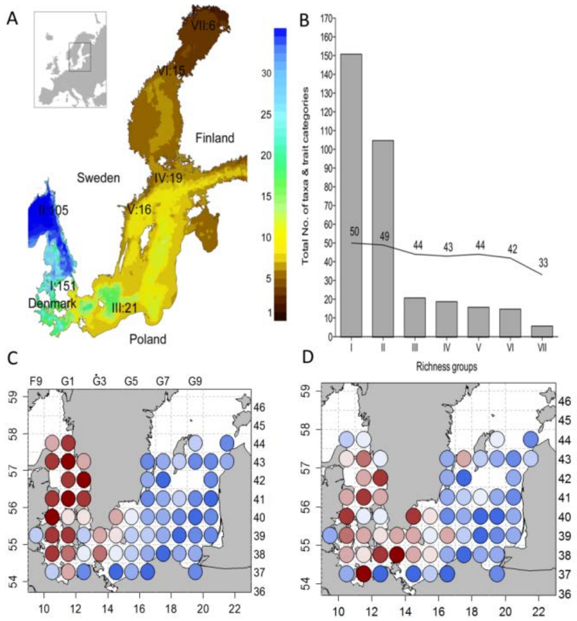

Fig. 26. (A) Map of the Baltic Sea showing the total number of species per richness group (I–VII) and mean bottom layer salinity (colour scale bar). (B) Total number of species and trait categories in respective richness group (from Törnroos et al. 2014). (C) Total number of fish species and (D) functional richness based on trawl survey data. Red and blue colours indicate high and low values, respectively (from Pecuchet et al., 2016).

3.3.2 Mapping and investigating the biogeography of traits and trait diversity

The latitudinal gradient in species richness is ubiquitous in nature and several hypotheses explaining the underlying drivers and mechanisms exist. However, the extent to which the latitudinal gradient and its suggested drivers and mechanisms apply to the number and diversity of traits, i.e., functional diversity, is largely unknown, especially in marine ecosystems where experimental insight is scarce. In order to investigate the biogeography of marine traits, the Centre and its associated partners have mapped and explained the distribution of single, or groups of traits, across multiple organisms and spatial scales. At a local scale, the Baltic Sea provides an ideal case study, demonstrating a pronounced gradient in environmental conditions (e.g., in terms of temperature and salinity), along which the number of species has been shown to change. Recently published work on fish and benthos (Törnroos et al. 2014; Pecuchet et al., 2016) has demonstrated that although the number of species decrease, primarily due to decreasing salinity, the number of traits and functional groups remains largely unchanged (Fig. 26). This contributes to maintain ecosystem function, despite a loss in individual species. Similar analyses have been initiated for other groups of organisms, including zooplankton and phytoplankton, through collaborative work with other research institutes around the Baltic Sea. This initiative will enable a novel synthesis of trait variation and functional diversity across multiple marine taxa and trophic levels, highlighted by a preliminary case study exploring temporal changes and drivers of key traits of phytoplankton, zooplankton, benthos and fish in the Central Baltic Sea (Fig. 27; Lindegren et al., in prep), as well as an ongoing comparative study on spatial patterns of life-history traits of copepods, benthos and fish in the North Sea (Pecuchet et al. in prep).

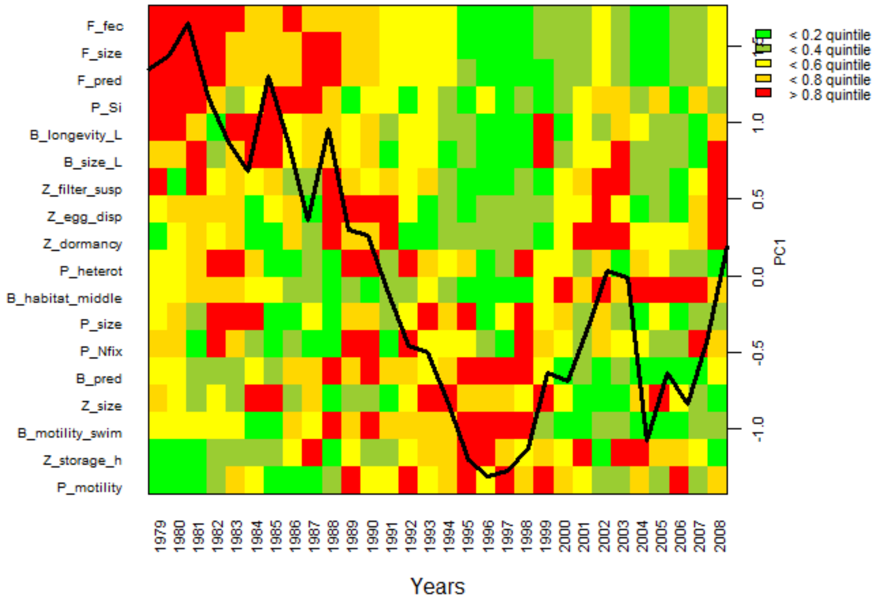

Fig. 27. Traffic-light plot representing the temporal development of functional traits in the Central Baltic Sea across all trophic levels, including phytoplankton (P), zooplankton (Z), benthos (B) and fish (F). Time-series of community weighted mean (CWM) traits are transformed into quintiles and sorted according to the first principle component of a principle component analysis (PCA) across all traits. Red represents high values while green represents low values of the respective trait. The solid black line shows the temporal dynamics of the dominant mode of variability in the traits (i.e., PC1).

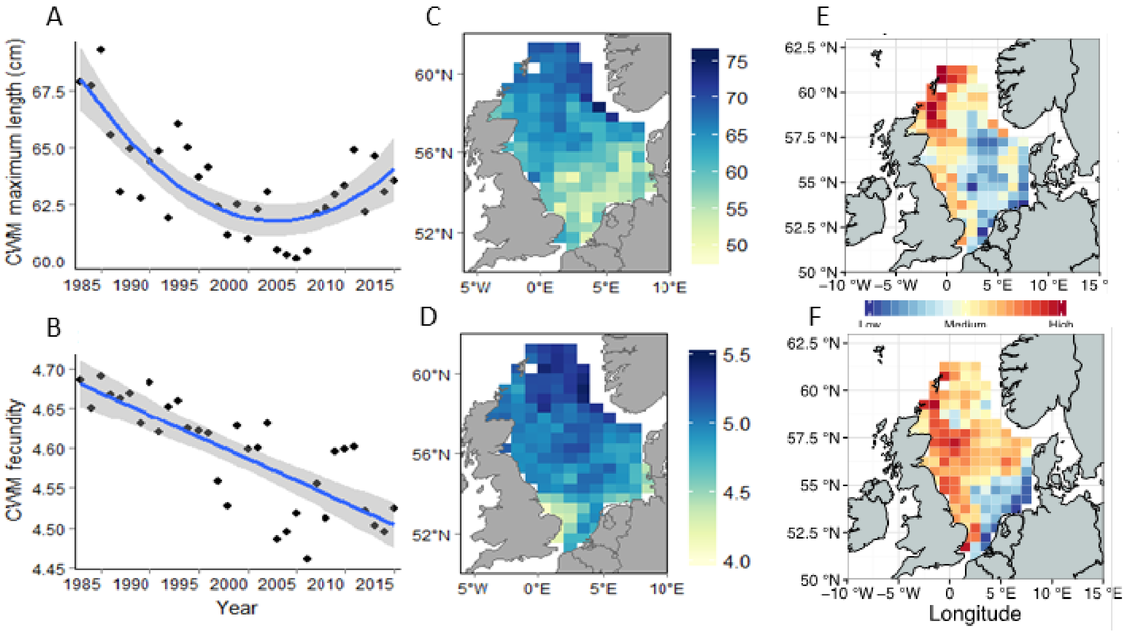

Fig. 28. Spatio-temporal patterns of fish community mean traits, here exemplified by temporal trends and spatial patterns in maximum length (A,C) and fecundity (B, D) in the North Sea, as well as spatial patterns of fish species richness (E) and functional (trait) diversity.

Furthermore, comparable analyses of fish community trait composition and functional diversity have been being conducted in the neighbouring North Sea (Fig. 28). These studies show pronounced spatio-temporal patterns in fish community traits, as well as overall indicators of fish taxonomic and functional diversity primarily related to environmental variables, such as annual variability in temperature and phytoplankton biomass, depth and salinity (Beukhof et al., in prep; Dencker et al., in prep). Similar to the local scale analysis described above, changes in trait distribution and functional diversity across regional seas, differing in species richness, community composition and abiotic conditions have been conducted. As an example, an ongoing long-term initiative conducted as part of the ICES Working Group on Comparative Analyses between European Atlantic and Mediterranean marine ecosystems (WGCOMEDA) is investigating how European marine ecosystems are structured, how they function, and which are the more sensitive ecological processes to be considered within an ecosystem-based approach to management. Scientists at the Centre are leading and coordinating a comparison of trait changes and functional diversity of demersal fish communities in a number of marine ecosystems across a pronounced gradient in temperature and productivity from the Eastern Mediterranean to Greenland (Pecuchet et al., in review). This project has successfully illustrated how traits and trade-offs shape three key life-history strategies of marine fish that vary consistently in space in response to the environment (Fig. 29). As an example of other ongoing regional activities within the Centre, a dynamic trait-based approach has been developed to understand the environmental drivers of biogeography of copepods in the North Atlantic (Brun et al. 2016b) . This study has developed and applied a statistical framework to relate key traits regarding growth, survival and reproduction to the observed distribution patterns of individual species (e.g., Fig. 30A) based on observations from the long-term Continuous Plankton Recorder (CPR). In addition to obtaining a general understanding of how key plankton traits relate to their occurrence patterns in the North Atlantic this work will allow producing distribution estimates for species, for which observational data is scarce.

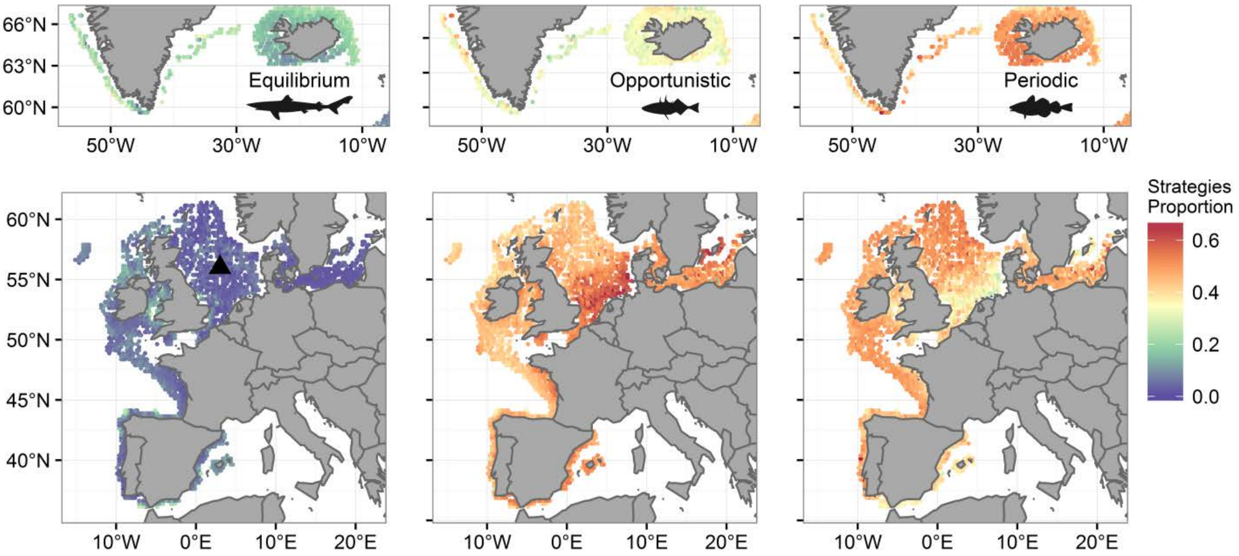

Fig. 29. The relative proportions of key life history strategies, i.e., equilibrium (left), opportunistic (middle) and periodic (right) in the marine fish assemblages of the European Seas calculated based from species abundance and trait data.

As a complement to our work on local and regional patterns of traits and functional diversity, we are also conducting global investigations on the biogeography and diversity of marine traits for several groups of organisms. In terms of phytoplankton, statistical species distribution models has been used to investigate which environmental factors control large-scale patterns and ecological niches of phytoplankton worldwide (Fig. 31B, Bruun et al., 2015). Mixed layer depth turned out to be the dominant environmental factor followed by light and temperature, suggesting that variables related to climatic conditions governs large-scale patterns in phytoplankton biogeography over nutrient availability. Furthermore, realized niches of taxa grouped by plankton functional types showed clear differences and the estimates of realized niches roughly matched the predictions of mechanistic trait-based models (Brun et al., 2015).

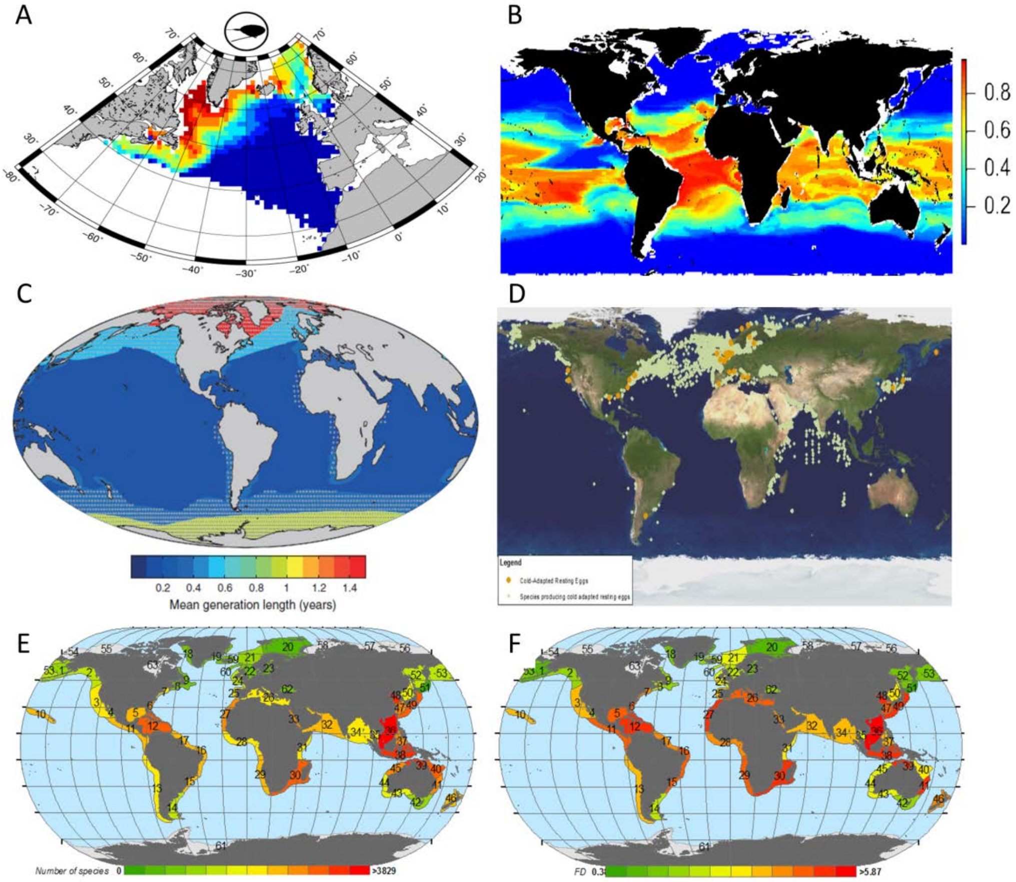

Fig. 30. Selected examples of our regional and global studies on trait biogeography. (A) Fraction of time of presence of *Calanus finmarchicus* in the North Atlantic (from Brun et al., 2016c). (B) Habitat Suitability index of *Trichodesmium* (N-fixer) in the global ocean (from Brun et al 2015) (C) Estimated biogeographical patterns of characteristic generation length and diapause strategy for calanoid copepods (from Barton et al., 2013). (D) Distribution of copepod species producing resting eggs as a cold-adaption combined with findings of cold-adaptive resting eggs in the sediment (from Holm et al., in prep). (E-F) Global patterns of marine fish species richness and trait diversity (from Lindegren et al., submitted).

In another study, a trait-based approach was used to map the global biogeography of several key plankton traits that underlie variations in plankton communities, e.g., cell size, N2-fixation and mixotrophy among phytoplankton, and body size, ontogeny and feeding behavior for zooplankton (Fig. 30C, Barton et al. 2013). This trait based approach shed light on what structures plankton communities in the current ocean, as well as under climate change scenarios, and allowed for finer resolution of community function. Another important trait is the ability to cope with periods of adverse environmental conditions, e.g., during winter in temperate regions. To do so copepods have developed different strategies, e.g., dormancy of adults, production of resting eggs, and starvation resistance. There is generally a lack of understanding of which ecosystems support these traits worldwide. In a recent contribution, published literature on resting eggs of marine copepods, and presence data on these species was used to examine the occurrence of resting eggs in relation to the presence of the species (Fig. 30D, Holm et al in prep). Combined with sea surface temperature data it seems that resting eggs are produced to cope with both high and low temperatures, presumable related to the thermal tolerance of the adults, as findings of resting eggs are on the boards of the species geographical distribution.

Finally, several studies on global trait biogeographies of higher trophic levels are finished or underway (Fig. 31). These include a global mapping and investigation of copepod traits (e.g., size) and their relationships to strong environmental gradients in temperature and primary production using a combination of global abundance data and statistical modelling (Brun et al. 2016b), as well as an investigation of the underlying causes of the shifting dominance of large pelagic fish predators (e.g., tunas, marlin and swordfish) to large demersal predators (e.g., gadoids and flatfish) at higher latitudes (van Denderen et al., in prep). Finally, a global study on trait biogeography of marine fish is underway (Lindegren et al., in prep). This study investigates the spatial patterns, drivers and match-mismatch of species richness and functional diversity across 64 Large Marine Ecosystems (LME) worldwide. Our results show similar global patterns and a pronounced latitudinal gradient for species richness and functional diversity (Fig. 30E-F). Based on a number of potential covariates, sea surface temperature (SST) was found the best predictor explaining these global patterns. However, the shape of the SST relationship differs, illustrated by a log-linear response for species richness, but a non-linear response for functional diversity. Hence, increasing temperatures seems to favor species richness, likely through an increased rate of evolution, but not necessarily lead to an equal increase in the number of functional groups. The resulting saturating relationship between species richness and functional diversity (Fig. 32-33) leads to increased functional redundancy, a fundamental mechanism contributing to ecosystem resilience (see the following section).

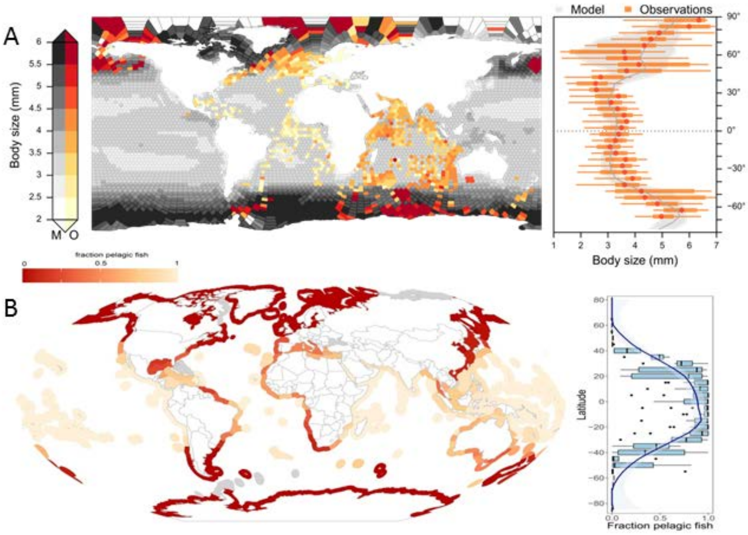

Fig. 31. (A) Global distributions of community-weighted mean body size of copepods from observations (color) and model predictions (grey-scales). The panels on the right shows aggregated patterns per latitude. (B) Weight fraction of large pelagic fish compared to large demersal fish in fisheries landings between 1970 and 2012. Large pelagic fish are by far the dominant group of fish in most tropical and subtropical areas, while large demersal fish are dominant in temperate regions and the exclusive group at the poles. Grey areas in the map are excluded from the analysis due to limited data availability.

3.3.3. Assessing the underling processes of community assembly and ecosystem resilience

The Baltic Sea is one of the most studied seas in the world. However, there is still a knowledge gap regarding the underlying mechanism shaping community composition. In a recently published paper, we investigate the relative importance of a number of suggested mechanisms of community assembly, i.e., niche filtering, neutral selection or limiting similarity, using the Baltic Sea fish community as a case study (Pecuchet et al. 2016). Our hypothesis is that due to the strong salinity gradient the primary mechanism influencing community composition is “environmental filtering”, i.e., that coexisting species are functionally more similar (in terms of their traits) than expected by chance. To assess the Baltic fish community composition bottom trawl survey data and a trait database of fish species occurring in the area was used. At a spatial scale of 0.5°x1° a co-occurrence index and functional dissimilarity was calculated for each pair of species. Our results show that the fish composition followed an environmental filtering pattern, with the species co-occurring in a community having a significantly higher functional similarity than expected by chance (Fig. 33). Therefore, due to strong environmental pressure, species with similar traits – enabling them to endure the environmental forcing - are filtered.

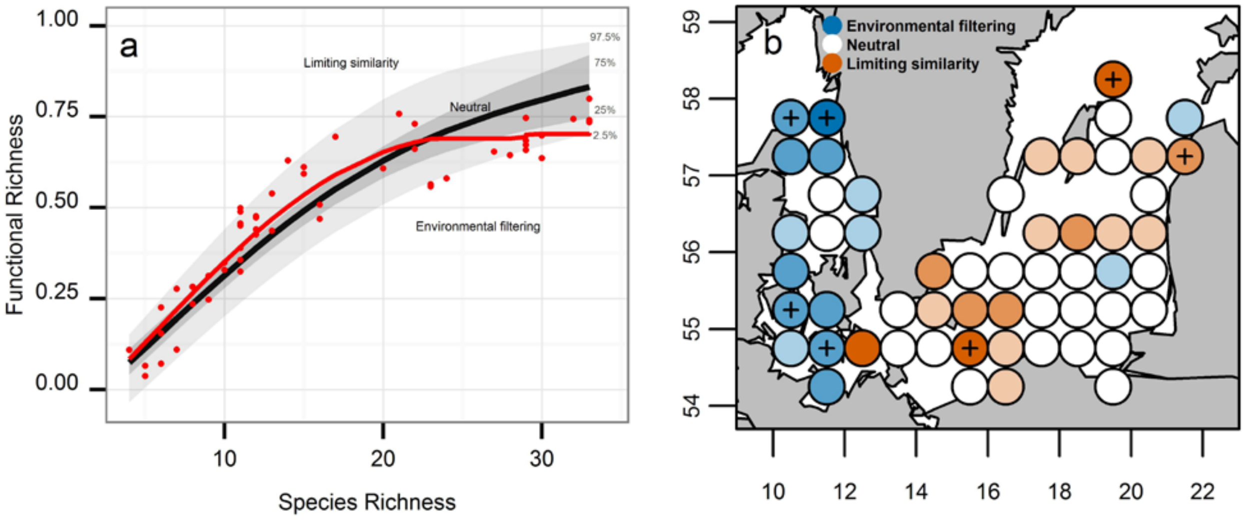

Fig. 32. Modes of community assembly in the Baltic Sea fish community. (A) The deviation of observed patterns of functional richness vs species richness (red) relative to a null model (black line) shows that the fish community has a lower functional richness than expected at random. (B) This is consistent with environmental filtering as the primary mechanism shaping community assembly, primarily in the western Baltic Sea where the sharp decline from high to low salinity act as a filter, while in the eastern Baltic Sea neutral or biotic processes are at work.

A primary rationale for protecting biodiversity is its positive effect on resilience. However, it is not species richness *per se*, but the amount of functionally similar species within communities, the functional redundancy that promotes resilience and stabilizes ecosystem function. This is caused by multiple pathways for ecosystem processes that may compensate for any changes in function due to the decline or loss of individual species. Theory and experiments have provided key insight into these issues, yet our ability to understand and assess resilience and its underlying factors in nature is limited, especially in open marine ecosystems. In an ongoing study we use global data on fish species distribution and a data base on functional traits to empirically assess the resilience and vulnerability of marine ecosystems to biodiversity loss (Lindegren et al., in prep). This is accomplished by quantifying the degree of functional and phylogenetic redundancy and singularity across marine ecoregions of the world (Fig. 34). Furthermore, our results highlight a potential trade-off between achieving simultaneous protection of biodiversity, resilience and ecosystem services within a protected area. This issue may arise if focusing conservation efforts in areas of high biodiversity, compared to areas with low biodiversity and high vulnerability to biodiversity loss, e.g., in the North Atlantic and North Pacific. These boreal areas currently provide a wide range of important ecosystem services and are, partly due to the exploitation of these services, exposed to a high degree of anthropogenic impact. Our empirical trait-based approach illustrates the need for a holistic perspective when designating appropriate protection and management measures across areas, varying in their degree of redundancy, resilience and vulnerability to biodiversity loss.

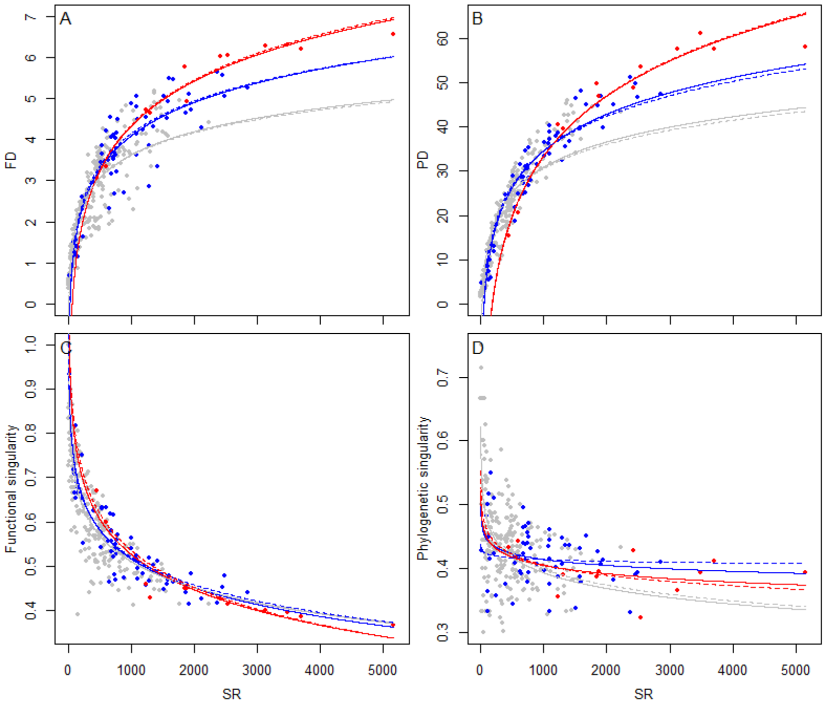

Fig. 33. Functional redundancy and singularity across spatial scales. The saturating relationship between species richness (SR), functional diversity (FD) (A) and phylogenetic diversity (PD) (B), indicating an increasing degree of functional and phylogenetic redundancy at high levels of SR. Functional and phylogenetic singularity expressed as the proportion of functional groups or clades occupied by a single species in each area. (C, D). The points denote each ecoregion (gray), province (blue) and realm (red). The solid and dashed lines represent fitted relationships when including or excluding areas with poor taxonomic completeness, respectively.

4. The daily life of the Centre (activities)

The Centre is cross-disciplinary and a meeting point for students and scientists with very diverse backgrounds: mathematics, biology, physics, chemistry, and engineering. Each discipline speaks its own language and has its own scientific traditions. While exciting discoveries and true scientific progress is often made at the interface between disciplines, it also requires a constant and major effort to develop a common language, to define the common questions, and to make the group feel and function as a coherent unit working towards a common goal. We have installed a number of instruments aimed at achieving this and find that we have been largely successful in accomplishing this goal:

4.1 Weekly science meetings

Key to the coherence of the Centre is the weekly meetings where all students and post docs meet with PIs to discuss progress of their work and other topics of mutual interest. Attendance to these meetings is mandatory. The format of these meetings has developed over the life time of the Centre, from being mainly top-down controlled and dominated by discussions among seniors, to become the responsibility of the Young Researchers (YR) to organise and lead the meetings. This has led to a much more active meting participation. The YR group has developed a set of guidelines for meeting organisation and presentations and ideas for format and content, and in practice every meeting is rather different. We aim at NOT having slick PowerPoint presentations, but rather have open presentations that invite for discussion, and we have been partly successful in implementing this. We have spent considerable effort communicating across scientific disciplines. It is a continuous learning experience for all and it has trained the mathematicians and physicists to formulate their ideas verbally, and the biologists to phrase their thoughts such that they can be translated to equations and made suitable for modelling. Communication across disciplines continues to be a challenge since new members are continuously added to the group.

4.2 Annual retreats:

We have had annual 2-day science retreats at the field station ‘Søminestationen’ at the Isefjord. The annual retreats serve the same purpose as the weekly meetings, however, with more time to discuss, network, and socialize. Young Researchers that have left the Centre are also invited in order to develop and maintain the Young Researcher network. These retreats are organized by the YR group. Each retreat has had about 40 participants, which include all YR and senior scientists hired by or associated the Centre, as well as members of our scientific board. In addition to presentations given by all young scientists and students we have had a few tutorials given by invited scientists.

4.3 Working and study groups

Ad hoc working groups, involving relevant YRs and PIs, exploring specific problems have been established, e.g., ‘*Evolving Food webs*’, ‘*Food chain modelling*’, ‘*Feeding in choanoflagellates*’, ‘*Size in the ocean*’, and ‘*The jelly trait*’, ‘*Zooplankton fluid dynamics*’, '*Adaptive ecological-evolutionary modelling*', ‘*Mixotrophy*’ ‘*Seasons in the Ocean*, ‘*Zooplankton modelling*’, ‘*Trait biogeography*’, and others. These groups have also been a means to advise (groups of) students and post docs in their work, and an attempt is made to bring different disciplines into each of these groups. Some groups have had a short life, others are almost permanent, and many of the working groups are focused on producing joint science and papers. Two group in particular – *Size in the Ocean* and *Seasons in the Ocean* - have worked on big joint project, which has involved most of the Young Researchers, all disciplines represented in the Centre, and several of the PIs. Size in the Ocean has resulted in several papers, as reported on above.

4.4 Researcher visitors Centre

We have from the start of the Centre had an active 'Researcher visitors Centre', which is a rather informal structure that provides seed funds (when occasionally necessary) for visiting scientists and students, and also actively seek funds to invite visiting professors for longer stays (3 successful applications). We have also organized to have a DTU adjunct professor associated the Centre (Dr. Andre Hirst, Queen Mary University of London). We have a constant flux of short-term visitors, several per month, that come to give seminars and interact with us for a few days. Longer-term visiting scientists and PhD students that come work with us or conduct part of the PhD at the Centre have been quantified in Table 3.

4.5 Miscellaneous

We have established a WIKI on the Centre home page with all kinds of information relevant to newcomers in the Centre. We also organize various social events, such as excursions, BBQs, and dinners.

5. Training of students and early career scientists

Training of students and early career scientists (collectively referred to as young researchers, YR) in cross-disciplinary marine research is an important delivery of the Centre. Currently there are about 20 students and post docs associated the Centre (Appendix 1) and their research and other activities have been described in individual reports (Appendix 6). Students of course follow the standard requirements of the University where they are enrolled (course work, teaching, etc), but cross-disciplinarity is a special asset of the training we offer. The crossing of disciplines is a major challenge to most students, and we try to emphasize that aspect of the training by typically having two advisors from different disciplines for each YR. We also try to have YRs from different disciplines work together, cf. the working groups described above. The installation of cross-disciplinarity in YRs is not always equally successful – also because it is not a given for all advisors – but we have had many very positive experiences.

The Centre offers an international environment. The YRs are of many different nationalities, as is the PI-group, and the many international visitors that interact with YRs further add to this. We have experienced that the international and vibrant atmosphere developed at the Centre is conducive to both research and teaching

In addition to traditional academic training we emphasize a number of additional skills. First, we delegate responsibilities to YRs for various activities, such as weekly meetings, annual retreats, maintenance of home page etc. This not only strengthens their ownership to the Centre and helps us have some jobs done, but it also makes them good citizens (we hope). Secondly, we encourage YRs to take active part in public outreach (see below). We consider this important in two ways. First, public outreach, whether in the form of lectures, popular articles, or otherwise, forces the YR to put his/her maybe nerdy research into a broader context that is appealing to the general public. This, in fact, is important for the project itself. Secondly, almost whatever the future career of the YR, s/he will be forced to communicate expert knowledge to non-experts. Thus, training in public outreach is an important educational component. We organized an internal course on ***'Ocean Literacy'*** for students and post docs, taught by visiting scientist Diana Payne. The course focused on two topics: (i) How to place your research in a societal context, and (ii) How to explain your research to non-experts.

Finally, we encourage YR networking, and invite former YRs to the annual retreat and other activities. The network of YRs associated the Centre may be of lasting significance.

6. Scientific dissemination

We reach out to the scientific community through an active website (www.Oceanlifecentre.dk) and a twitter (Twiter: @oceanLifeCentre) and Face book accounts as well as through publications in international journals, presentations at seminars and conferences, through PhD summer schools, and through the organization of international workshops and conference sessions:

6.1. Publications and presentations.

We use the normal channels for scientific dissemination: scientific papers and presentations at conferences and seminars. So far about 144 papers, entirely or mainly funded by the Centre, have been published. In addition, 113 papers have been 'contributed' to the Centre; i.e., papers that are relevant to the Centre but funded by other means. We have given several hundreds of presentations. List of papers and presentations are in Appendices 2 and 3.

6.2 Workshops and conference sessions

We have organized or co-organized a number of international workshops and conference sessions where the Centre and its research get international exposure (for a list: see appendix 5). The flagship event was the International *Workshop on Trait-based approaches to Ocean Life* that took place at the Royal Danish Academy of Sciences and Letters in Copenhagen 26-28 August 2013. A report on the workshop can be found here www.oceanlifecentre.dk/International_workshop. The workshop was vastly oversubscribed (about 200 applicants to the 60 participants we had planned; we expanded to the 80 participants that the facility could accommodate) so we had to turn away many relevant participants.

Fig. 26. *Participants at the Copenhagen workshop on Trait-based approaches to Ocean Life, August 2013 at The Royal Danish Academy of Sciences and Letters.*

The workshop in Copenhagen jhas been followed up by the 2nd Workshop on trait-based approaches to Ocean Life in New England in the fall of 2015 (http://www.oceanlifecentre.dk/international-workshops/2nd-workshop-2015), and the 3rd workshop is planned in Bergen, 2017 (https://traitbased.b.uib.no/). Thus, the Copenhagen workshop was the first in a continued series of international workshops on Trait-based Ocean Ecology.

6.3 Summer Schools

We have co-organized and contributed to a number of PhD summer schools, where YRs from the Centre have participated, as students or instructors, see appendix 6

7. Public Outreach

Our public outreach has taken multiple forms (see Appendix 4 for a complete list). We write popular science articles to both newspapers and to popular science magazines and popular science web pages; we visit high schools and elementary schools on 'science days' to give lectures on Ocean Life; we give popular lectures at science cafes, to various societies, and through 'Folkeuniversiteterne' (Århus, Copenhagen, Odense); we have organized a lecture series on Ocean Life offered through 'Selskabet til Naturlærens Udbredelse' (Society for the dissemination of natural sciences); and we encourage our students and post docs to produce popular 'pitch videos' on their research (see http://www.oceanlifecentre.dk/people) . The Centre also had a very strong presence at the Euroscience Open Forum (ESOF) Science Festival in Copenhagen 2014: during 3 days we had more than 4500 visitors at our Ocean Life stands on DTUs research vessel (DANA), where we demonstrated ecological models, live plankton, ocean physics, 3-dimensional real-time video observations of live plankton (a major hit), and gave lectures to high school students on how it is to be a scientist. About 15 YRs and PIs from the Centre contributed to this event. Finally, through a grant from the 'Tipsmidlerne', we have produced a children's bedtime e-book on Ocean Life ('*Otto the copepod'*, www.heuschele.com/otto/) that in different 'layers' have stories and information appealing to 3-year old kids, their teenage siblings, and their parents (Fig. 27), and though a grant from the Research Council we organized an **International Workshop on**

'Transatlantic Ocean Literacy'(jointly with the European Environment Agency), 24-25th Sept 2015 in Copenhagen (http://www.conferencemanager.dk/TOL2015).

Fig. 27. *A children's bedtime picture e-book on ocean life. Information to kids and adults are available in different layers. The book is animated, so this still image does not reproduce the appeal of the book. The book has been made by scientist and artist Jan Heuschele, a former post doc at the Centre.*

In addition, our research has often led to media coverage in both Danish (various newspapers, Radio and TV stations, Videnskab.dk) and international media (Radio, TV, newspapers), including *Nature*, *Science*, and *Scientific American*.

8. Management and leadership

8.1 The Centre leadership

The management structure and leadership of the Centre is very much as described in our proposal: A Centre Leader (T Kiørboe), a deputy Centre leader (KH Andersen), and a PI-group consisting of additionally 8 senior scientists representing the 5 participating institutions (i.e., L Riemann, Institute of Biology, University of Copenhagen; BW Hansen, Department of Environmental, Social and Spatial Change, Roskilde University; and from the Technical University of Denmark (DTU): C Stedmon, AW Visser, H Gislason, and M Payne, National Institute of Aquatic Resources (DTU Aqua), T Bohr, Department of Physics (DTU Fysik), and J Starke, Department of Mathematics (DTU Compute)). Additional senior scientists help advise students and post docs and are, thus, in practice members of the PI-group that are involved in all major decisions regarding the Centre, while the day-to-day operation is managed by the leader and deputy leader together with relevant PIs. The PI group has met formally twice a year, as planned, but meets frequently at the weekly meetings. Scientific leadership is implemented through the weekly and annual meetings, study groups, and YR supervision, as described above, and through hiring of YRs.

8.2 International advisory board

We have established an International advisory board to advice on research directions. The board members are:

Prof. Markus Pahlow, IFM-Geomar, Kiel, Germany
Associate Professor Michael Follows, MIT, Cambridge, USA
Associate Professor Christopher Klausmeier, Michigan State University, USA
Associate Professor Elena Litchman, Michigan State University, USA
Professor Øyvind Fiksen, University of Bergen, Norway
Professor Tim J. Pedley, University of Cambridge, England
Senior Scientist Jorn Brüggeman, Plymouth Marine Laboratory, England

The board meets at our annual retreats and/or workshop, and we have developed active collaboration with several board members. Thus, interaction with the board has also been through mutual research visits and student exchange and has been relatively intense. The main formal advice from the board is through an annual report that comments on the progress of the Centre and suggests changes in strategy. Informal advice is provided through collaboration.

8.3 Hiring strategy

The original strategy (see proposal) of intensive hiring of students and post docs at the initiation of the Centre, followed by less intense 'maintenance hiring', could only be partly fulfilled due to shortage of qualified applicants. While we receive many applications to open positions, we initially experienced a shortage of applicants that were sufficiently qualified and with the right skills. In addition, the best applicants also often received independent post doc grants (see below), allowing us to stretch Centre funding. We therefore applied for, and were granted, a 1-year no-cost extension of the Centre, thus allowing us to pick only the best candidates. With the increasing international visibility and reputation of the Centre, we now attract plenty of highly qualified applicants with the right skills.

8.4 Funding

We have been quite successful in using Centre funding to attract additional external funds. This has mainly been for post docs through the HC Ørsted fellowship program (8 stipends), The Carlsberg Foundation (1), The Danish Council for independent Research (2), and the Marie Curie program (1), as well as for visiting professors through the Marie Curie program (1), and VKR visiting professor program (1). We have also received some external funding for workshops arrangement, outreach activities, travel, housing of visitors, etc.

9. Have the goals been accomplished?

Have we accomplished our goals, as they were formulated in the project proposal? Considering that we still have one year left, and based on what we have described above, we would argue that for the most part we have. Below we first briefly qualify this statement by summarizing the extent to which we have met milestones and completed the specific projects that we described in the proposal, and by providing some statistics on student production, publications etc. We thereafter discuss the ‘added value’ of the Centre.

9.1. Milestones, projects, and other deliverables

The project proposal promised a number of concrete deliverables in the form of projects, milestones and PhD and post doc fellowships, and below we compare those with what we did:

Project #	Short title	Status	Section	Appendix
1.1	Bacterial traits	Completed	3.1.2	6.1
1.2	Mixotrophy	Completed	3.1.3	6.2, 6.3, 6.27
1.3+1.4	Virus; Ph effects	Cancelled (to extend 1.2)		
2.1	Zooplankton feeding and motility trade-offs	Completed	3.1.4	6.4,6.5,6.6
2.2	Zooplankton fitness optimization	Completed	3.2.5; 3.1.4	6.7
2.3	Global zooplankton patterns	Expanded and partly completed	3.2.3;3.3.2	6.8, 6.16, 6.19, 6.20
2.4	Zooplankton feeding mechanisms	Completed	3.1.4	6.9, 6.10, 6.11
2.5	Prey size spectra	Completed	3.1.4	6.28
3.1	Trait-based modelling fish communities	Completed	3.2.5	6.17
3.2	Operationalization of fish model	Expanded and completed	3.2.4	6.13, 6.18
3.3+3.4	Fish trait distribution	Expanded and completed with slightly changed scope	3.3.3	6.14, 6.15, 6.30, 6.31, 6.33
3.5	Stability analysis	Ongoing; delayed	3.2.2	6.24
4.1	Marine megafauna	Cancelled		
5.1	Seasonality and fish life histories	Ongoing, slightly changed focus	3.2.2	6.22, 6.31
5.2	Zooplankton overwintering	Ongoing, expanded, but delayed	3.2.2	6.19, 6.16
6.1	Trait-based pelagic ecosystem	Completed	3.2.3	6.20, 6.21, 6.23, 6.25, 6.34
6.2	Small-scale heterogeneity	Not initiated		
6.3	Anthropogenic impacts	Completed in changed form	3.3.3	6.15, 6.20, 6.25
6.4	Biological pump	Completed and continued with expanded scope	3.2.5	6.7, 6.25

Table 1. Comparison of planned and executed projects. Project numbers refer to the proposal; ‘Section’ and refer to where in this report the project has been described; and ‘Appendix’ refers to the reports of the young researchers in Appendix 6. Projects in grey were planned potential projects to possibly be initiated late in the lifetime of the Centre. Many more projects than those planned were completed, as described in Appendix 6.

Potential concrete projects were outlined in the proposal (for the entire duration of the Centre), some to start initially, and others later. In the proposal we allowed for flexibility in project content and in distribution of tasks between projects. Table 1 compares the project list with what we have actually done so far.

The proposal also provided a list of *milestones* for the first 3 years, mainly for the modelling activities, see Table 2.

Month	**Scientific milestones from proposal**	**Comments on completion**
6	Implementation of GOTM vertical water column model	Completed. Used in Mariani et al (2013), Kenitz et al (2016) and other projects (3.2.3 and on-going work in 3.1.3)
12	Implementation of Global Ocean Circulation model (GCM)	Implemented in collaboration with MIT (3.2.3).
18	Model of DOM & microbial ecophysiological traits Simple general trait-based zooplankton feeding and motility model with mechanistic underpinning	Completed (Traving et al. 2015) (3.1.2) Marini et al (2013) and Kenitz et al (2016) and implemented in the MIT GCM (3.2.3).
30	Operational fish model	Implemented as single-species and ecosystem model (3.2.4), and as a community model in an open-source framework (Scott et al. 2014) and used in multiple publications.
36	Mechanistic underpinning of predictive mixotrophy model Global zooplankton-phytoplankton model Compilation and model of Latitudinal pattern in zooplankton winter strategies Fish life history model Trait-based pelagic ecosystem model	Implemented (3.1.3) Implemented (3.2.3) Almost complete (3.3.2) Implemented as a part of the 'operational fish model' (section 3.2.4). On-going. Based on the work with optimization models in (3.1.3).

Table 2. *Completion of milestones for the model systems.*

Finally, the proposal promised various output, in the form of PhD students, post doc fellowships, publications (implicit), and the arrangement of workshops. Table 3 compares the promises (for the entire project) with what we have done until now.

Item	Proposal	Realized
PhD fellowships	11	18
Post Doc man-years	14	32
Publications by Centre (incl. submitted)	Not specified	144
Publications contributed to Centre	Not specified	113
International workshops	1	6
Conferenced sessions organized	Not specified	7
PhD schools organized or taught	1	16
Visiting scientists (> 1 month), man-months	Not specified	148

Table 3. *Comparison of promised and realized output from the Centre. Post docs and PhDs include contracts that reach beyond the reporting period and the first period of the Centre.*

Of the total of 18 PhD students, only 5 have so far graduated (see Appendix 1), none have (so far) failed, and most of them are delayed due to parental leave or other factors but are all expected to finalize successfully.

9.2 Added value

Has the grant made a difference, other than funding more of what would have happened anyway? We would like to highlight the following that would not have happened without the grant:

- Promotion of trait based approaches in marine ecology, including applications to fisheries management, conservation, and environmental impact assessment, with the Centre developing into an international hub for such activities.
- Development of mechanistic underpinning of trait based methods, and development of trait based trophic models
- Establishment of a fruitful environment for cross-disciplinary training of young researchers in quantitative marine ecology. The societal need for ‘Ecological engineers’ is very high.
- Magnet for further funding and visitors and promotion of international cooperation.
- Establishment of a young researcher network that is likely to be of significant value long beyond the lifetime of the Centre.
- New scientific discoveries at the border between disciplines, mainly physics and biology.

10. Challenges

There are several challenges to make the Centre of Ocean Life a success:

- The cross-disciplinarity of the Centre is its strength, but also its weakness. Communication across disciplines and departments is challenging and the lack of cross-disciplinary skills in YRs sometimes makes progress slow. We address this by having advisors for YRs coming from complementary disciplines.
- The breadth of the specific research topics of the Centre challenges the coherence of its research profile, but this diversity also allows synergies between different disciplines and makes the Centre a dynamic and attractive working place. While senior researches have a better overview of the links and coherence of our activities, YRs may at times be overwhelmed by the complexity of topics and approaches and feel uncomfortable operating outside their scientific comfort zones. We address this mainly through the establishment of focused working groups to supplement the more widely embracing Centre meetings.
- Our post docs are highly qualified and attractive candidates for fixed tenure track positions internationally. Although this highlights the success of our YR training activities within the Centre the premature loss of three post docs, as well as periodic maternal/paternal leaves, has seriously delayed some key modelling activities. We address this by strengthening the group through new/recent hires
- Post docs often arrive with a backlog of unfinished projects. We need to respect that they are developing a career and need to dedicate efforts to finalize such projects.

- Multiple locations of the researchers is a challenge because the daily and informal contact is important. However, it also adds to the diversity in advisor skills and to cross-disciplinarity. We combat this problem by (i) having one location being the hub of the network (Aqua), and (ii) by having advisors from different environments to most YRs, and (iii) by having YRs working at different locations, either for extended periods, or 1 or 2 days a week throughout their employment.

Awards:

Navish Wadhwa received the *Young Scientist Award*, European Fluid Mechanics Conference, Copenhagen, Denmark, 2014, and the *Best poster award*, DTU Physics Conference, Kgs. Lyngby, Denmark, 2013

Julie Sainmont received *DTU young researcher award* 2014 for her Ph.D. thesis.

Julia Dölger received the Best poster award at the Microscale Ocean Biophysics workshop in Eilat, Israel 2016

Martin Lindegren was nominated as a PEW fellow (2014), and was awarded a Villum Young Investigator grant (2016)

Thomas Kiørboe received the EB 2014 Open data award and the Hageman Gold Medal 2015

Philipp Brun Best Early Career Scientist Presentation for Brun, Kiørboe & Payne: The predictive potential of ecological niche models for plankton in the North Atlantic. International symposium on “Effects of Climate Change on the World’s Oceans”, Santos, March 2015.

APPENDICES

Contents

Appendix 1. Personnel

Students and post docs: We have made the following hires on Centre funds (sometimes co-financed by other programs):

1. **Friederike Prowe** (WP 2.2-3, Post doc, hired February 2012, on maternal leave from October 2013, terminated June 2014)
2. **Terje Berge** (WP 1.2, Post doc, February 2012-February 2015)
3. **Erik Martens** (WP 6.1,Post doc, hired August 2012, terminated October 2013)
4. **Sachia Jo Traving** (WP 1.1, PhD student, Graduated, February 2012 – February 2016, on maternal leave from March 2014-March 2015)
5. **Karin Olsson** (WP 5.1, PhD student, Graduated, March 2012- March 2015)
6. **Navish Wadhwa** (WP 2.1, PhD student, Graduated, August 2012-August 2015)
7. **Nis Sand Jacobsen** (WP 3.2, PhD student, Graduated, November 2012-November 2015)
8. **Julie Sainmont** (WP 2.2, PhD, Graduated, fall 2014, co-funded by Climate Centre, Nuuk)
9. **Irene Heilmann** (WP 6, PhD, expected graduation 2017; works only 75 % time. Long-term leave of absence summer 2014-summer 2015)
10. **Philipp Brun** (WP 4, PhD, Expected graduation January 2017, December 2013-December 2016)
11. **Laurén Pécuchet** (WP 3.4, PhD, Expected graduation February 2017, December 2013-February 2017)
12. **Martin Lindegren** (WP 3, post doc -> Senior scientist, February 2014-December 2016; co-financed by NorMER)
13. **Mark Wejlemann Holm** (WP 5.2, PhD student, Expected graduation summer 2017, April 2013-November 2016; Paternal leave 6 months 2015)
14. **Lise Marty** (WP 5.1, Post doc hired July 2013-March 2015)
15. **Lasse Tor Nielsen** (WP 2.4, Post doc, March 2013-December 2017; paternity leave December 2013-January 2014)
16. **Hans van Someren Gréve** (WP 2.1, PhD student, Expected graduation May 2017, May 2014-May 2017)
17. **Kasia Kenitz** (WP 6, Post Doc, September 2014- February 2017)
18. **Nicolas Azaña Schnedler-Meyer** (WP 6, PhD student, September 2014-September 2017)
19. **Sofia Piltz** (WP 6, Post doc, September 2014-December 2015, co-financed by HC Ørsted Postdoctoral fellowship; terminated prematurely)
20. **Julia Dölger** (WP 2.4, PhD student, December 2014-December 2017)
21. **Agnethe Hansen** (WP 6, PhD student, December 2015; Maternal leave since February 2016)
22. **Tim Dencker** (WP3, PhD student, August 2015-August 2018)
23. **Marina Pančić** (WP 1, PhD student, November 2015-November 2018)
24. **Subhendu Chakraborty** (WP 1.2, Post Doc, November 2014-December 2017, co-Funded by the HC Ørsted program)

Other students and post docs: A number of additional post docs, funded by other sources, are working partly or entirely within the Centre and participate in the weekly and annual meetings:

25. **Erik Selander** (WP 2, Post Doc, January 2012-December 2013, Funded by Danish Council for Strategic research)

26. **Jan Heuschele** (WP 2, Post Doc, February 2012-June 2014, Funded by Danish Council for Strategic research)
27. **Samuel Hylander** (WP2, Post Doc, March 2011-February 2013, Funded by The Carlsberg Foundation and the HC Ørsted Post Doc program)
28. **Starrlight Augustine** (WP1, post doc, July 2013-February 2015, co-funded by a HC Ørsted Fellowship and the Danish Council for Independent Research).
29. **Anna Törnroos** (WP6, Post doc, visiting 2014-2017, Funded by BONUS)
30. **Rodrigo Almeda** (WP2, Postdoc, May 2014-December 2017, co-Funded by the Danish Council for Independent Research and The EU Marie-Curie program)
31. **Sofia Xu** (WP 1 and 2, PhD student, December 2014-Decemeber 2017, co- Funded by Chinese Fellowship and DTU-Aqua PhD school)
32. **Marc Andersen Borg** (WP 2.1, Post Doc, finished Sept 2012, Funded by the Swedish Research Council)
33. **Anna Katharina Meisner** (WP 6, PhD student, September 2016- September 2018, Funded by EU project)
34. **Esther Beukhof** (WP 3, PhD student, March 2016-Marh 2019, Funded by EU ITN network)
35. **P. Daniel van Denderen** (WP5, Post doc, October 2015-December 2017; Funded by HC Ørsted program)
36. **Floor Soudijn** (WP6, Post doc, September 2016-September 2018, Funded by HC Ørsted program)
37. **Rob van Gemert** (PhD Student, November 2015- November 2018, Funded by EU ITN network)

Appendix 2. Scientific publications

We list here only those of our publications that are related to Centre for Ocean Life. We distinguish between papers that are mainly funded by the Centre (marked with an *), and those contributed to the Centre. We include papers that are submitted or '*in press*', since a large fraction of our work is at that stage only.

2016

1. Albertsen CM, Nielsen A, Thygesen UH (2016) *Choosing the observational likelihood in state-space stock assessment model.* Canadian Journal of Fisheries and Aquatic Sciences DOI: http://dx.doi.org/10.1139/cjfas-2015-0532

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Appendix 3. Presentations at scientific meetings and institutions

2016

1. Almeda R, van Someren Gréve H, Kiørboe T. *Trade-offs in zooplankton feeding behaviour.* ICES/PICES 6th Zooplankton Production Symposium. Bergen, Norway. May 2016.
2. Almeda R, van Someren Gréve H, Kiørboe T. *Behaviour-dependent predation risk in marine zooplankton: an experimental and modelling approach.* ASLO-Ocean Sciences Meeting. New Orleans, USA. Feb., 2016
3. Andersen A. *Hydrodynamics of Choanoflagellate Feeding.* Poster presentation at workshop on Microscale Ocean Biophysics, Eilat, Israel, 30 October – 4 November 2016.
4. Andersen A. *Hydrodynamics of Microbial Filter-Feeding.* Talk at "The 69th Annual Meeting of the American Physical Society's Division of Fluid Dynamics", Portland, USA, 20-22 November 2016.
5. Andersen KH. *Is fisheries management able to deal with stock recovery?* Invited talk at the British Ecological Society annual meeting, 12 December 2016.
6. Andersen KH. *Size- and trait-based modelling for ecosystem-based fisheries management.* Lab. Meeting, Drogo Lab, Princeton University, 17 February 2016.
7. Andersen KH. *Size in the Ocean.* Seminar (invited) Princeton University, 10 March 2016.
8. Andersen KH. *Size in the Ocean.* Seminar (invited) Rutgers University, 14 April 2016.
9. Andersen KH. *Size in the Ocean.* Seminar (invited) University of California, Irvine, 13 January 2016.
10. Andersen KH. *Trophic strategies of plankton.* Invited seminar at the Geophysical Fluid Dynamics Laboratory, Princeton University. 28 January 2016.
11. Beukhof E, Dencker TS, Pécuchet L, Lindegren M. *Spatio-temporal changes in life-history traits of the North Sea fish community under climate change and fishing.* ICES Annual Science Conference, Riga, 19-23 September 2016.
12. Brun P, Kiørboe T, Payne M. *A trait biogeography of marine pelagic copepods*. International workshop "PlankDiv" on "Impact of climate change on the distribution of plankton phylogenetic and functional diversity", Villefranche sur mer, March 2016.
13. Dencker TS, Payne M, Lindegren M. *Three decades of spatio-temporal patterns of taxonomic and functional diversity in the North Sea fish community.* ICES Annual Science Conference, Riga, 19-23 September 2016.

14. Dencker TS, Lindegren M, Richardson K, Payne MR (2017) *Temporal and spatial mismatches and matches between taxonomic diversity and trait diversity in the North Sea fish community.* ICES Annual Science Conference, September 2016, Riga.
15. Dölger J. *Feeding and Swimming in Biflagellated Haptophytes.* Talk and poster presentation at workshop on Microscale Ocean Biophysics, Eilat, Israel, 30 October – 4 November 2016.
16. Dölger J. *Hydrodynamics of freely swimming flagellates.* Talk at "The 69th Annual Meeting of the American Physical Society's Division of Fluid Dynamics", Portland, USA, 20-22 November 2016.
17. Hirst AG (Invited) *Frills and spills: the interplay of body size, shape and oxygen in aquatic organisms.* Eawag, Zurich, Oct 2016
18. Hirst AG, Lilley MKS, Glazier DS, Atkinson D. *New model to explain the body mass scaling of diverse biological rates in aquatic invertebrates.* American Society for Limnology and Oceanography, Santa Fe, USA, June 2016.
19. Jacobsen NS. *Size based models as tools for an ecosystem approach to fisheries management*, Quantitative Seminar, University of Washington, Seattle, March 2016.
20. Jacobsen NS. Size structured multispecies models to evaluate indirect effects of fishing. ISEC, Seattle, USA, June 2016.
21. Kiørboe T. *A trait-based approach to zooplankton ecology*. Seminar (invited) ETH, Zürich 18 January 2016.
22. Kiørboe T. et al *The functional response in zooplankton*. ICES/PICES Zooplankton Symposium, Bergen, 9-13 May 2016.
23. Kiørboe T. *Fluid mechanical constraints on planktonic life*. Invited seminar at Inter-University Institute for Marine Sciences in Eilat, Israel, 30 October – 4 November 2016.
24. Kiørboe T. *Fluid mechanical constraints on planktonic life*. Observatoire Océanologique de Villefranche sur mer, France, 29 February 2016 (Invited)
25. Kiørboe T. *Small-scale turbulence and organism-organism interactions in the ocean*. Workshop on Microorganisms in turbulent flows, Lorenz Center, Holland, 8-12 February 2016 (Invited)
26. Kiørboe T. *Zooplankton: Can we describe the many species with a few traits*. PlankDiv Euro Marine Workshop, Villefranche sur mer, France, 15-18 March, 2016 (Invited key note lecture)
27. Lindegren M. *Understanding long-term changes in ecosystem functioning: the Central Baltic Sea as a case*. ICES/HELCOM Working Group of Integrated Assessment in the Baltic Sea (WGIAB) Annual meeting, Helsinki, 18-22 April 2016.
28. Lindegren M. *A trait-based assessment towards understanding long-term changes in ecosystem functioning: the Central Baltic Sea as a case.* ICES Annual Science Conference, Riga, 19-23 September 2016.

29. Mariani P. *Group formation and efficiency of migratory species*. Animal movement international Symposium, Lund University, Sweden, 16-17 February 2016 (poster)
30. Mariani P. *Swimming under the risk of predation: plankton encounter rates and self-overlap in calm and turbulent conditions*. Workshop on Microorganisms in turbulent flows, Lorenz Center, Holland, 8-12 February 2016 (Invited)
31. Miesner, AK , Payne, MR. *Forecasting the spawning distribution of blue whiting (Micromesistius poutassou).* ICES Annual Science Conference, Riga, 19-23 September 2016.
32. Nielsen LT, Dölger J, Andersen A & Kiørboe T. (Oct-Nov 2016) *Prey Capture at Low Reynolds Number.* Oral presentation at Microscale Ocean Biophysics. Eilat, Israel.
33. Payne MR. *How skilful are projections of plankton distribution shifts in a changing climate?* ICES Annual Science Conference, Riga, Latvia.
34. Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzon A, Solmundsson J, Payne MR. *From traits to life history strategies: deconstructing fish community composition in European Seas.* ICES Annual Science Conference, Riga, 19-23 September 2016.
35. Pecuchet L, Reygondeau G, Beauchard O, Beukhof E, Brun P, Cheung W, Dencker T, Van Dendere D, Licandro P, Törnroos A, Payne MR, Lindegren M. *Spatial structuration of life history traits: congruence between multiple taxa and environmental drivers in the North Sea*. (poster) ICES Annual Science Conference, Riga, Latvia, September 2016
36. Schnedler-Meyer NA, Mariani P, Kiørboe T. 2016. *Modelling global ecosystem susceptibility to jellyfish blooms* (talk). Fifth International Jellyfish Symposium, Barcelona, Spain.
37. Thygesen UH, Albertsen CM, Berg CW, Kristensen K, Nielsen A, Pedersen MW. *Validation of state space models.* Presented at International Statistical Ecology Conference, June, Seattle, USA.
38. Thygesen UH, Patterson TA. *Inference in dynamic models of fitness optimization based on observed aniumal behaviour.* Presented at International Statistical Ecology Conference, June, Seattle, USA.
39. Thygesen UH. *What's on a tuna's mind? Confronting dynamic optimization models of behavior with tracking data.* Invited plenary presentation at Animal Movement International Symposium, Lund, February, 2016
40. Törnroos A. *Introduction to trait modelling*. The Ocean's Seafloor – One Bio-Geo System. Hannover, Germany, 12-14.10.2016.
41. Törnroos A. *Describing key traits and trade-offs of marine benthos: towards a mechanistic trait-based approach*. Trait-based approaches to Ocean Life, an international workshop. Waterville Valley Resort, New Hampshire, USA 5 8.10 2016, poster.

42. Traving SJ. *Microbial marine ecology – the role of marine heterotrophic bacteria in the carbon cycle.* Invited talk at Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Neuglobsow, Germany, 25-26 September 2016.

43. van Denderen PD, Lindegren M, MacKenzie B, Watson R, Andersen KH. *Global patterns in the feeding ecology of large marine fish Gordon research conference and seminar "Unifying ecology across scales"*. University of New England, Biddeford, Maine, July 2016

44. van Gemert R, Andersen KH. *Late-in-life density-dependence: catching smaller fish for higher yields.* ICES Annual Science Conference, Riga, Latvia, September 2016.

45. van Someren Gréve H, Almeda R, Kiørboe T. *Behavior as key trait in zooplankton predation risk.* Poster presentation, NAEM Netherlands Annual Ecology Meeting, Lunteren, The Netherlands, February 2016

46. van Someren Gréve H., Almeda, R., Kiørboe T. *Behavior-dependent predation risk in marine zooplankton. DTU PhD course: 'Aquatic Science and living resources'*, Feb 2016, Charlottenlund, Denmark

47. van Someren Gréve H, Almeda R, Kiørboe T. *Behavior-dependent predation risk in marine planktonic copepods - an experimental and modelling approach.* ICES/PICES 6th Zooplankton Production Symposium, Bergen, Norway, May 2016

48. Xu JY, Hansen PJ, Nielsen LT, Kiørboe T. *Feeding behavior and prey selection of Temora longicornis fed on toxic dinoflagellates, Alexandrium spp (poster).* ICES/PICES 6th Zooplankton Production Symposium, Bergen, Norway, May 2016.

2015

1. Almeda R, van Someren Gréve H, Kiørboe T: *Behaviour-dependent predation risk in marine zooplankton: an experimental and modelling approach*. 2016 ASLO-Ocean Sciences Meeting. New Orleans, USA. February 2016 (submitted).
2. Almeda R, van Someren Gréve H, Kiørboe T: *Trade-offs in zooplankton feeding behaviour*. ICES/PICES 6th Zooplankton Production Symposium. Bergen, Norway. May 2016 (submitted).
3. Andersen A, Wadhwa N, Kiørboe T: *Quiet swimming at low Reynolds number*, 68th Annual Meeting of American Physical Society's Division of Fluid Dynamics, Boston, November 2015
4. Andersen KH: *Characteristic sizes of life in the ocean.* Mini-symposium, Wageningen, 3/8-2015
5. Andersen KH: *The theory behind fisheries reference points.* University of Washington, 28/4-2015
6. Andersen KH: *Size- and trait-based modelling for ecosystem-based fisheries management*. Princeton, 23/4-2015.
7. Andersen KH: *Size as a Master Trait*. Session at Trait-based approaches to Ocean Life (http://www.whoi.edu/workshop/traitworkshop2015). Waterville valley October 5-8

2015.

8. Andersen, Nielsen, Haaning, Aagaard & Kiørboe: *Hydrodynamics of Choanoflagellate Feeding*. Complex Motion in Fluids Summer School, Krogerup Højskole, August 2015 (poster)
9. Brun, Kiørboe & Payne: *The predictive potential of ecological niche models for plankton in the North Atlantic*. International symposium on “Effects of Climate Change on the World’s Oceans”, Santos, March 2015
10. Chakraborty & Andersen: *Correlation between organism size and trophic strategies*. Trait-based Approaches to Ocean Life, Waterville Valley, New Hampshire, USA, October 2015
11. Dölger, Andersen, Kiørboe & Bohr: *Optimal design of salps as gelatinous filter feeders,* DANSIS Research Seminar, Campus Lyngby, May 2015
12. Dölger, Nielsen, Kiørboe, Bohr & Andersen: *Feeding and Swimming of Flagellates,* Complex Motion in Fluids Summer School, Krogerup, August 2015
13. Dölger, Nielsen, Kiørboe, Bohr & Andersen: *Feeding and Swimming of Flagellates,* 68th Annual APS DFD Meeting, Boston, November 2015
14. Hirst A.G. et al.: *New insights from body surface area: A major trait in pelagic invertebrates*. Trait-Based Workshop: exploring traits of marine organisms, organised by Princeton / MIT, October 2015
15. Hirst A.G. et al.: *Body size patterns in contrasting ecological systems*. University of Saint Andrews, September 2015 (Invited)
16. Hirst, Horne, Atkinson & Kiørboe: *Upscaling phenotypic plasticity and physiological responses*. ASLO Aquatic Sciences Meeting, Granada, February 2015
17. Hylander, Kiørboe, Snoeijs Leijonmalm, Sommaruga & Nielsen: *Is there a trade-off between feeding and UV-exposure in Calanus species during the arctic spring bloom?* ASLO Aquatic Sciences Meeting, Granada, February 2015
18. Jackson GA, Visser AW: *Implications of zooplankton feeding type on particle fate as determined by individual based models.* Aquatic Sciences Meeting ASLO, Granada Spain. February 2015
19. Jacobsen NS, Andersen KH: *Size based models predict efficiency frontiers in large marine ecosystems.* American Fisheries Society, Portland, August 2015.
20. Jacobsen NS: *Can you catch a fish before it is mature?* Naturskyttsforeningen, Stockholm, Sweden. April 2015 (Invited)
21. Jonasdottir SH, Visser AW: *Calanus and the biological carbon pump.* Aquatic Sciences Meeting ASLO, Granada Spain. February 2015
22. Kenitz, Andersen, Mariani & Visser: *Vertical distribution of motile and non-motile phytoplankton and implications for the optimal feeding mode of zooplankton*. ASLO Aquatic Sciences Meeting, Granada, February 2015
23. Kenitz, Mariani, Visser & Andersen: *Optimal zooplankton feeding mode in a seasonally-stratified shelf sea*. Workshop on Trait-based Approached to Ocean Life, New Hampshire, October 2015

24. Kiørboe: *Microscale Ocean Biophysics* – Kick off lecture at Aspen Center for Physics winter workshop, 10-16 January (Invited)
25. Kiørboe: *invited lecture at Trait-based approaches to Ocean Life (http://www.whoi.edu/workshop/traitworkshop2015)*. Waterville valley October 5-8 2015.
26. Kiørboe & Goncalves: *Detecting the algae: How copepods detect their prey*. ASLO Aquatic Sciences Meeting, Granada, February 2015
27. Lindegren M: *A general note on functional biodiversity and why it matters using global fish data as an example.* Workshop on Functional Diversity of Baltic Zooplankton (FUNBAZOO) and other trophic levels, Hamburg, Germany, 23-25 November 2015.
28. Mariani: *Group formation and efficiency of migratory species* (talk). *Living systems: from interaction patterns to critical behavior*, Venezia, 16-19 September 2015
29. Mariani: *Group formation and efficiency of migratory species* (Poster presentation). Trait-based Approaches to Ocean Life international workshop, 5-8 Oct. 2015, Waterville Valley USA
30. Nielsen, Andersen & Kiørboe: *Dinoflagellates create flows that mediate feeding and nutrient uptake*. ASLO Aquatic Sciences Meeting, Granada, February 2015
31. Payne M: *Addressing uncertainty in projecting climate change impacts in marine ecosystems*, 3rd International Symposium on Effects of Climate Change on the World's Oceans, 21-27 March 2015, Santos, Brazil
32. Payne M: *A statistical approach to model uncertatinty*, 3rd International Symposium on Effects of Climate Change on the World's Oceans, 21-27 March 2015, Santos, Brazil
33. Payne M: *The roles of plasticity and adaptation in spawning time of Atlantic cod (Gadus morhua): Explaining phenology and making predictions in a changing climate*, 3rd International Symposium on Effects of Climate Change on the World's Oceans, 21-27 March 2015, Santos, Brazil
34. Payne M: *Climate change in the seasonal domain: Impacts on the phenology of marine ecosystems and their consequences*, 3rd International Symposium on Effects of Climate Change on the World's Oceans, 21-27 March 2015, Santos, Brazil
35. Payne M: *A Cascade of Warming Impacts Brings Bluefin Tuna to Greenland Waters*, 3rd International Symposium on Effects of Climate Change on the World's Oceans, 21-27 March 2015, Santos, Brazil
36. Payne M: *Towards Decadal Predictions of Marine Ecosystems: The NACLIM Experience*, Application of Seasonal to Decadal Climate Predictions for Marine Resource Management Workshop, 4 June 2015, Princeton, USA
37. Payne M: *Making and using predictions of species distribution to improve survey design*, ICES Annual Science Conference, 21-25 September 2015, Copenhagen, Denmark
38. Payne M: *Can we understand and predict the distribution of pelagic fish?* ICES Annual Science Conference, 21-25 September 2015, Copenhagen, Denmark
39. Pécuchet, Hidalgo & Lindegren: *Taxonomic and functional diversity patterns of fish assemblages in the European Seas* (poster). ICES Annual Science Conference, Copenhagen, Denmark, September 2015.

40. Pécuchet, Törnroos & Lindegren: *Environmental filtering drives functional diversity of fish assemblages in a temperate system.* ICES Annual Science Conference, Copenhagen, Denmark, September 2015.
41. Pécuchet, Törnroos & Lindegren: *Environmental filtering drives functional diversity of fish assemblages in a temperate system.* Third international Symposium on the Effects of climate change on the world's Oceans, Santos city, Brazil, March 2015.
42. Piltz S: *Are plankton discontinuous, smooth, or slow-fast (&furious)?* Invited minisymposium talk at the Society for Industrial and Applied Mathematics (SIAM) Applications of Dynamical Systems Conference, Snowbird, Utah, USA, May 2015
43. Piltz S: *Are plankton discontinuous, smooth, or slow-fast (&furious)?* Invited seminar talk at the BioComplexity Wednesday meeting, Niels Bohr Institute, University of Copenhagen, Denmark, May 2015
44. Schnedler-Meyer, Mariani & Kiørboe: *A model of fish and jellyfish competition*. Trait-based approaches to ocean life, New Hampshire, October 2015
45. Sichlau, Kiørboe, Nielsen & Thygesen: *Mating success and sexual selection in a pelagic copepod, Temora longicornis – Evidence from paternity analysis*. ASLO Aquatic Sciences Meeting, Granada, February 2015
46. Starke: *Equation-free analysis of collective behavior in particle models,* talk on invitation by Y. SUGIYAMA (Nagoya University, Japan), Symposium Group formation and control of collective bio-motions, Meiji Institute for Advanced Mathematical Science, Meiji University, Japan, October 2015
47. Starke: *Coarse analysis of complex systems by implicit methods,* talk on invitation by K. PAKDAMAN and P. BOURGINE, e-session "Mathematical modeling in biological complex systems" of the Complex Systems Digital Campus 15 World e-Conference (CS-DC'15), September 2015
48. Starke: *Numerical bifurcation analysis of the macroscopic behavior in multi-scale systems*,talk on invitation by R.Abgrall (Zürich), W. Hundsdorfer (Amsterdam), A. Meister (Kassel), T. Sonar (Braunschweig), Oberwolfach Workshop "Recent Developments in the Numerics of Nonlinear Hyperbolic Conservation Laws", September 2015
49. Starke: *Continuation for situations with noisy data*, talk on invitation by B. KRAUSKOPF (University of Auckland, New Zealand) and J. SIEBER (University of Exeter, UK), minisymposium Continuation methods and applications at EquaDiff 2015, Lyon, France, July 2015
50. Starke: *Non-standard traveling waves in traffic and pedestrian flow models*. SIAM Conference on Applications of Dynamical Systems, Snowbird, Utah, USA, invited talk in minisymposium The Behavior of Autonomous Agents in Diverse Applications on invitation by P. CARTER and A. VOLKENING (Brown University, USA), May 2015
51. Stedmon CA: *Shedding light on Life's leftovers: persistence of dissolved organic matter (DOM) in the ocean*. Microscale Ocean Biophysics – Aspen Center for Physics winter workshop, January 2015 (Invited)
52. Traving SJ, Bentzon-Tilia M, Knudsen-Leerbeck H, Mantikci M, Hansen JLS, Markager S, Riemann L: *Dynamics in microbial composition and functionality over a season in*

two contrasting estuarine systems. SAME Aquatic Microbial Ecology - EMBO conference, Uppsala, Sweden, 23-28 August 2015

53. Traving SJ, Bentzon-Tilia M, Sørensen H, Knudsen-Leerbeck H, Mantikci M, Hansen JLS, Markager S, Riemann L: *Dynamics of microbial functions and communities over a season.* Danish Microbial Society, Denmark, 9 November 2015
54. Traving SJ, Bentzon-Tilia M, Sørensen H, Knudsen-Leerbeck H, Mantikci M, Hansen JLS, Markager S, Riemann L: *Dynamics of microbial functions and communities over a season in two estuarine systems*. PhD day, University Of Copenhagen, Denmark, 12 November 2015
55. Törnroos A: *Describing key traits and trade-offs of marine benthos: towards a mechanistic trait-based approach*. Trait-based approaches to Ocean Life, an international workshop, Waterville Valley Resort, New Hampshire, October 2015 (poster).
56. Törnroos A, Olsson J, Gårdmark A, Pécuchet L, Blomqvist M, Lindegren M, Bonsdorff E: *Long-term functional trends in Baltic Sea coastal macrofauna and fish.* ICES Annual Science Conference, Copenhagen, September 2015.
57. Törnroos A, Bonsdorff E: *Interpreting ecological functioning in coastal waters: spatial and temporal trait patterns across the Baltic Sea.* 10th Baltic Sea Science Congress, BSSC, Riga, June 2015.
58. van Someren Gréve, Almeda & Kiørboe: *Behaviour-dependent predation risk in marine planktonic copepods*. ASLO Aquatic Sciences Meeting, Granada, February 2015
59. Wadhwa N, Martens EA, Jacobsen NS, Lindemann C, Andersen KH, and Visser A: *Size matters: The interplay between sensing and size in aquatic environments*, Complex Motion in Fluids Summer School, Humlebæk, August 2015
60. Wadhwa N: *Hydrodynamics of swimming in zooplankton*, Dansis Research Seminar, Kongens Lyngby, May 2015
61. Wadhwa N: *Physical ecology of swimming in plankton*, University of Cambridge, Cambridge, March 2015
62. Wadhwa N: *Some hydrodynamic aspects of zooplankton ecology*, MPI for Terrestrial Microbiology, Marburg, February 2015

2014

1. Andersen A, Nielsen LT, Kiørboe T. *Hydrodynamics of Filter Feeding in Choanoflagellates*. 10th European Fluid Mechanics Conference. Kgs. Lyngby, Denmark. 15 September 2014.
2. Andersen KH. *Trait based models of plankton*. Copenhagen area algal seminar, DTU, February 6 2014.
3. Andersen KH. *Towards ecosystem-based fisheries management - a size- and trait-based modelling approach*. Invited presentation at Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Germany, March 6, 2014

4. Andersen KH. *Size- and trait-based methods for end-to-end models of intermediate complexity.* Invited presentation at the Working Group on Integrative Physical-Biological and Ecosystem Modelling, the Netherlands, March 18, 2014
5. Andersen KH. *Tools for ecosystem-based fisheries management - a size- and trait-based modelling approach*. Institute of Marine Research, Bergen, Norway, June 18, 2014
6. Andersen KH, Berge T, Goncalves R, Hartvig M, Heuschele J, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer A, Olsson K, Palacz A, Payne A, Prowe F, Sainmont J, Traving SJ, Visser A, Wadhwa N, Kiørboe T. *Characteristic sizes of life in the oceans from bacteria to whales*. Institute of Biology, University of Bergen, June 19, 2014
7. Andersen KH. *Tools for ecosystem-based fisheries management - a size- and trait-based modelling approach*. Invited keynote at the symposium on size based models of aquatic systems at the 2014 American Fisheries Society meeting, Quebec City, Canada, Aug 17-21, 2014
8. Andersen KH. *Size- and Trait-Based Model of a Single Stock*. Poster at the 2014 American Fisheries Society meeting, Quebec City, Canada, Aug 17-21, 2014
9. Andersen KH. *Conflicting objectives for ecosystem based fisheries management*. Invited keynote at the EcoPath 30 conference, Barcelona, November 11, 2014.
10. Andersen KH, Simmonds J. *Defining the biomass to deliver MSY*. Invited presentation at the PEW workshop on biomass reference points for fisheries. Brussels, October 13, 2014
11. Augustine S. *Comparing energy budgets of a comb jelly (Mnemiopsis leidyi) and a pelagic medusa (Pelagia noctiluca).* Invited speaker at Seminar, Mediterranean Institute of Oceanography, Marseilles, France, October 2014
12. Augustine S, Nielsen LT, Riisgard K, Andersen KH, Mariani P. *Modelling the growth, division and starvation of D. acuminata in fed-batch cultures*. 2nd International Conference on Algal Biorefinery, Tecnical University of Denmark, Lyngby, Denmark, 27-29 Aug 2014
13. Augustine S, Andersen KH, Berge T, Nielsen LT. *Quantifying cellular investment in autotrophic and heterotrophic machineries for Dinophysis and Karlodinium*. Invited speaker at Algae Seminar, DTU Env, Lyngby, Denmark, 6 Feb 2014
14. Brynnum KM, MacKenzie BR. *Warming impacts on fish species composition in the Kattegat-Belt Sea*. Ecosystem Studies of Sub-arctic Seas Annual Conference, Copenhagen, April 5-7, 2014.
15. Ferreira ASA, Hátún H, Counillon F, Payne MR, Visser AW. *Phytoplankton bloom and subpolar gyre induced dynamics in the North Atlantic*. Ocean Sciences Meeting. Honolulu, Hawaii USA, 2014.
16. Ferreira ASA, MacKenzie BR, Butenschön M, Payne MR. *How can we distinguish between competing explanations of year class strength?* Johan Hjort Symposium. Bergen, Norway, 2014.

17. Ferreira ASA, Hátún H, Counillon F, Payne MR, Visser AW. *Phytoplankton bloom dynamics in the North Atlantic*. Ecosystem Studies of Sub-Arctic Seas. Copenhagen, Denmark, 2014
18. Gislason H. *Size spectra and species diversity in the sea*. Mini symposium on size-based approaches to fish and fisheries. Copenhagen, June 2014
19. Gislason H. *Biodiversity and species abundances in the North Atlantic Ocean*. CMEC, University of Copenhagen, October 2014
20. Gislason H. *Marine fish species richness in the north and north-eastern Atlantic*. World Conference on Marine Biodiversity. Qingdao, China, October 2014
21. Gislason H. *Patterns in marine fish species richness in the north and north-eastern Atlantic*. EU VECTORS Final Meeting. La Grand Motte, France, November 2014.
22. Glazier DS, Hirst AG, Atkinson D. (Invited) *Shape-shifting predicts ontogenetic changes in metabolic scaling in diverse aquatic invertebrates.* Gordon Research Conference, USA, Jul 2014 (Poster)
23. Hirst AG. (Invited) *The interplay of body size, shape and oxygen in aquatic organisms.* Centre for Macroecology, University of Copenhagen, Aug 2014
24. Hirst AG. (Invited) *Body size, shape and oxygen in aquatic organisms.* University of Sheffield, UK, Mar 2014
25. Hirst AG. *Shape-shifting in pelagic invertebrates resolves major contradictions in metabolic scaling.* ASLO Conference Hawaii, USA, Feb 2014
26. Hirst AG. (Invited) *Frills and spills: the interplay of body size, shape and oxygen in aquatic organisms.* University of Swansea, UK, Feb 2014
27. Horne C, Hirst AG, Atkinson D. *The temperature-size rule in arthropods: environment and body size do make a difference.* Marine Biological Association Conference, Scarborough, May 2014
28. Hylander S, Sylvander P, Gonçalves RJ, Friis Møller L, Kiørboe T, Snoeijs Leijonmalm P. 2013. *Deficiency syndromes in Baltic Sea top predators and the importance of zooplankton as producers of vitamins and pigments*. ASLO Ocean Sciences Meeting. Honolulu, Hawaii, Feb 23-28, 2014
29. Jacobsen NS, Essington TE, Andersen KH. *Comparing ecosystem models as fisheries management tools: a case study in the California current.* KBBE workshop, feature talk for the multispecies session, Wellington, April 2014
30. Jacobsen NS, Essington TE, Andersen KH. *Comparing ecosystem models as fisheries management tools – a case study in the California Current.* Symposium on size based approaches to fish and fisheries, Copenhagen, June 2014
31. Jacobsen NS, Essington TE, Andersen KH. *Comparing ecosystem models as fisheries management tools – a case study in the California Current.* American fisheries Society, Quebec, August 2014

32. Jacobsen, NS. *The consequences of balanced harvesting on fish communities.* American fisheries Society, Quebec, August 2014

33. Jacobsen NS, Andersen KH. *A reappraisal of fisheries selectivity in light of density-dependent regulation.* Balanced harvesting meeting, FAO, Rome, September 2014

34. Jacobsen NS, Kolding J, Andersen KH, van Zwieten P. *Maximizing fisheries yield, while maintaining community structure.* Balanced harvesting meeting, FAO, Rome, September 2014

35. Jacobsen, NS et al. *Identify and adapt models necessary for data-poor situations*. MYFISH yearly meeting, Nantes, April 2014

36. Jacobsen NS, Gislason H, Andersen KH. *The consequences of balanced harvesting on fish communities.* WGECO, Copenhagen, May 2014

37. Kiørboe T. Conflicting Missions. *How zooplankton feed, survive, and reproduce*. Monterey Marine Lab, Stanford University, 16 January 2014

38. Kiørboe T. *A trait-based approach to plankton ecology*. Romberg Tiburon Center - San Francisco State University, 29 January, 2014

39. Kiørboe T. *The fire of Life: How metabolism and other vital rates scale with body mass in pelagic organisms. And why*. UC. Berkeley, Dept of Integrative Biology, 3 February 2014

40. Kiørboe T. *Conflicting Missions. How zooplankton feed, survive, and reproduce*. Scripps Institution of Oceanography and UC San Diego, 6 March 2014

41. Kiørboe T. *How plankton hide: fluid dynamics of feeding and swimming zooplankton.* Invited presentation at NORDITA workshop on *Active Particles in Fluid Flows*, Ålands Islands, May 2014

42. Kiørboe T. *Fluid mechanical constraints of ocean life*. Invited key note presentation at *European Fluid Mechanics Conference*, September 2014

43. MacKenzie BR, Payne M, Boje J, Højer JL, Siegstad H. *A cascade of warming impacts brings bluefin tuna to Greenland waters*. ICES Annual Science Conference, A Coruna, Spain, Sept. 15-19, 2014.

44. McConville K, Atkinson A, Hirst AG, Fileman E, Spicer J. *Does relative water content of tissues explain growth rates in zooplankton.* ICES Conference: Sustainability in a Changing Ocean, Coruña, Spain, Sept 2014 (Poster)

45. Neuheimer AB, MacKenzie BR. *Explaining life history variation in a changing climate across a species' range*. Ecosystem Studies of Sub-arctic Seas Annual Conference, Copenhagen, April 5-7, 2014.

46. Neuheimer AB, Payne MR, MacKenzie BR. *Atlantic cod and bloom phenology: Exploring "critical period" adaptation across a species' range*. Johan Hjort Symposium on Recruitment Dynamics and Stock Variability, Bergen, Norway, 7-9 October 2014

47. Starke J. *Nonlinear Effects in Examples of Crowd Evacuation Scenarios*. Talk on invitation by W. Song (University of Science and Technology of China), special session on Pedestrian Dynamics at 17th International IEEE Conference on Intelligent Transportation Systems (ITSC 2014), Qingdao, China, 9.10.2014

48. Starke J. *Analysis of Unstable States in Particle Models for Pedestrian Flow.* Talk on invitation by L. Grüne (University of Bayreuth), mini symposium Control of Dynamical Systems in Science and Engineering at 34. Dynamics Days Europe, Bayreuth, Germany, 11.9.2014

49. Starke J. *Analysis of Unstable States in Particle Models for Pedestrian Flow*. Talk on invitation by H. Dankowicz (University of Illinois), J. Sieber (University of Exeter) and T. Sapsis (Massachusetts Institute of Technology), mini symposium Computational Methods at 8th European Nonlinear Dynamics Conference (ENOC 2014), Vienna, Austria, 8.7.2014

50. Starke J. *Analysis of particle models by implicit equation-free methods.* Talk on invitation by N. Popovic (University of Edinburgh) satellite workshop on Slow-fast dynamics: theory and application as part of the International Conference on Complex Systems and Applications (ICCSA 2014), Le Havre, France, 24.6.2014

51. Starke J. *Analysis of implicit equation-free methods and applications*. Invited MS-keynote presentation at minisymposium Multiscale, fast-slow dynamics and applications, International Conference on Structural Nonlinear Dynamics and Diagnosis (CSNDD’2014), Agadir, Morocco, on invitation by M. Belhaq (Hassan II-Casablanca University, Morocco), 20.5.2014

52. Starke J. *Multiscale analysis of the macroscopic behaviour of particle models*. Talk on invitation by M. Dellnitz, University of Paderborn, Germany, 20.11.2014

53. Starke J. *Bifurcation of Learning and Structure Formation in a Neuronal Map*. Talk on invitation by D. Avitabile, University of Nottingham, UK, 14.10.2014

54. Starke J. *Multiscale analysis of the macroscopic behaviour of particle models.* Talk on invitation by W.-A. Yong, Tsinghua University, Beijing, China, 8.10.2014

55. Starke J. *Engineering Dynamics – Using Mathematics in Engineering.* Talk on invitation by U. Staufer and F. van Keulen, Technical University Delft, The Netherlands, 30.6.2014

56. Starke J. *Implicit methods for equation-free analysis and applications to particle models.* Talk on invitation by J. Freund and U. Feudel, University of Oldenburg, Germany, 9.1.2014

57. Stedmon CA. *Why does dissolved organic matter persist in the deep ocean? Is part of the solution, dilution?* Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) Open Science Conference, Bergen Norway, 23-27 June 2014

58. Thygesen UH, Christiansen TK, Sommer L, Evans K, Patterson T, Madsen H. *Vertical Migrations of Bigeye Tuna. Predictions from a dynamic optimal foraging model.* Oral presentation at 5th Biologging Science Symposium, Strasbourg, France, September 2014.

59. Thygesen UH, Christiansen TK, Sommer L, Evans K, Patterson T, Madsen H. *Vertical Migrations of Bigeye Tuna: A time series analysis based on dynamic optimal foraging*. Oral presentation at International Statistical Ecology Conference, Montpellier, France, July 2014.

60. Thygesen UH, Christiansen TK, Sommer L, Evans K, Patterson T, Madsen H. *Vertical Migrations of Bigeye Tuna. Predictions from a dynamic optimal foraging model*. Oral presentation at 5th Biologging Science Symposium, Strasbourg, France, September 2014

61. Thygesen UH, Christiansen TK, Sommer L, Evans K, Patterson T, Madsen H. *Vertical Migrations of Bigeye Tuna: A time series analysis based on dynamic optimal foraging*. Oral presentation at International Statistical Ecology Conference, Montpellier, France, July 2014.

62. Wadhwa N, Andersen A, Kiørboe T. *How to be invisible as a microscopic swimmer* (talk). 67th Annual Meeting of American Physical Society's Division of Fluid Dynamics, San Francisco, CA, 2014

63. Wadhwa N, Andersen A, Kiørboe T. *Hydrodynamics and energetics of jumping copepod nauplii and adults* (talk). 10th European Fluid Mechanics Conference, Kgs. Lyngby, Denmark, 2014

64. Wadhwa N, Andersen A, Kiørboe T, *How plankton hide: swimming quietly at low Reynolds numbers* (talk). Active Fluids Workshop, Mariehamn, Aaland, 2014

2013

1. Andersen A, Nielsen LT, Couespel D, Haaning K, Aagaard J, Thomsen HA, Kiørboe T. *Hydrodynamics of Filter Feeding in Choanoflagellates*. Poster. International Workshop on Trait-Based Approaches to Ocean Life, Copenhagen, 26-28 August 2013

2. Andersen A. *Introduction to Flight and Propulsion of Animals*. Invited Talk. DANSIS workshop, DTU Aqua, Charlottenlund, 4 September 2013

3. Andersen A, Nielsen LT, Kiørboe T. *Hydrodynamics of Choanoflagellate Feeding*. Contributed Talk. 66th Annual Meeting of the APS Division of Fluid Dynamics, Pittsburgh, USA, 24-26 November 2013

4. Andersen KH. (Invited talk): *Trait-based approaches to ecosystem modelling* at the 2013 CNRS Thematic School on Innovative Approaches in Marine Environment Modelling, Brest, France.

5. Andersen KH: *Conflicting objectives for optimal ecosystem management of fisheries* at the 2013 Annual Science Conference in the International Council for the Exploration of the Sea, Iceland.

6. Andersen KH (Poster): *Simulate the impact of fishing on a stock* at the 2013 Annual Science Conference in the International Council for the Exploration of the Sea, Iceland.

7. Berge T, Hansen PJ. *Mixotrophy*. Poster. International workshop on Trait-based approaches to Ocean Life, Copenhagen, Denmark, 26-28 August 2013.

8. Berge T, Daugbjerg N, Moldrup M, Moestrup Ø, Mogensen SB, Poulsen LK, Hansen PJ: *Multiple roles of a mixotrophic dinoflagellate in the marine food web*. Poster. 17. danske havforskermøde. Januar 2013, Roskilde, Denmark; Øresund Plankton Meeting, November 2013, Lund, Sweden.
9. Berge T, Daugbjerg N, Jakobsen HH, Hansen PJ. Poster. *Elevated pH, intraspecific variation and laboratory selection in two red-tide marine dinoflagellates*. 15th International Conference on Harmful Algae. October 29 - November 2 2012. Changwon, Korea.
10. Gonçalves R, Kiørboe T. *Prey/predator size ratio in feeding of Temora longicornis* (poster). International workshop on Trait-based approaches to Ocean Life, Copenhagen 28/8-2013
11. Gonçalves R, Kiørboe T. *Feeding mechanisms in suspension-feeding copepods* (poster). 2nd annual meeting of Centre for Ocean Life, Holbæk. 12/12-2013
12. Hansen PJ, Nielsen LT, Johnson M**,** Berge T, Flynn KJ. *Acquired phototrophy in Mesodinium and Dinophysis – A review of cellular organization, prey selectivity, nutrient uptake and bioenergetics*. Øresund Plankton Meeting, Lund, Sweden, November 2013
13. Hansen PJ. *Mixotrofi i plankton*. Inviteret Sessionsforedrag. Dansk Havforskermøde, Roskilde, DK, 21-23. Jan 2013
14. Heilmann I, Starke J, Andersen KH, Thygesen UH, Lorenz T, Sørensen MP. *Analysis of size structured population models in marine ecosystem.* Poster presentation at SIAM conference on Applications of Dynamical Systems, Snowbird, Utah, USA, May 19-23 2013
15. Hirst AG. (Invited) *Frills and spills: the interplay of body size, shape and oxygen in aquatic organisms.* Heriot-Watt University, UK, Sept 2013
16. Hirst AG. (Invited) *Body size, shape and oxygen in aquatic organisms.* University of Nottingham, UK, Aug 2013
17. Hirst AG. (Invited) *The interplay of body size, shape and oxygen in aquatic organisms.* University of Essex, UK, June 2013
18. Hirst AG. (Invited) *Frills and spills: the interplay of body size, shape and oxygen in aquatic organisms.* Plymouth Marine Laboratory, UK, May 2013
19. Hirst AG. (Invited) *The how and the why of the temperature-size rule.* Woods Hole Oceanographic Institute, USA, Apr 2013
20. Hirst AG. (Invited) *Frills and spills: the interplay of body size, shape and oxygen in aquatic organisms.* Scripps Institute of Oceanography, USA, Apr 2013
21. Hirst AG. (Invited) *Insight into metabolic scaling in pelagic organisms.* University of Reading, UK, Apr 2013

22. Hirst AG. (Invited) *Body size, shape and oxygen in aquatic organisms.* University of California San Francisco, USA, Apr 2013
23. Hirst AG. *Changing size in a warming world*. ASLO Conference, New Orleans, USA, Feb 2013
24. Jacobsen NS. *Balanced Harvesting and size spectrum models – A multispecies approach to fisheries management.* Quantitative seminar, School of aquatic sciences and fisheries, University of Washington, Seattle, 5/4-2013.
25. Jacobsen NS, Essington TE, Andersen KH. *Comparing compartment and trait-based models in fisheries management*. (Poster), Trait based workshop in Copenhagen, August 2013
26. Jacobsen NS. *The consequences of balanced harvesting of fish communities*. ICES Annual Scientific meeting, September 2013.
27. Kiørboe T. (Invited talk) *Attack or attacked: Sensory and fluid mechanical constraints of copepod predator-prey interactions*. Invited lecture at Annual Meeting Society for Integrative & Comparative Biology, San Fransico 4-7 January 2013
28. Kiørboe T, Andersen A, Bohr T. (Invited tralk) *How to catch the interest of a friendly physicist. Microscale interactions in aquatic environments*. Ecole de Physique, Les Houches, France. 10 March 2013
29. Kiørboe T. (Invited talk) *Fluid mechanics of small animals in the Sea*. DANSIS workshop, Charlottenlund, 4 September 2013
30. Kiørboe T. (Invited) *The fluid mechanics of swimming and feeding in zooplankton*. The biomechanics group, University of California, Berkeley, 11/10-2013
31. Kiørboe T. (Invited) Conflicting missions: *How zooplankton feed, survive, and reproduce*. Department of Integrative Biology, University of California, Berkeley, 5/12 2013
32. Lindemann C, Palacz A, Prowe F. *Towards an adaptive evolutionary and ecological trait-based model.* Poster, International Workshop on Trait-based approaches to Ocean Life, Copenhagen, 26-28 August 2013
33. Marty, L, Dieckmann U, Ernande B. *Fisheries-induced neutral and adaptive evolution*. Poster, International Workshop on Trait-based approaches to Ocean Life, Copenhagen, 26-28 August 2013
34. Neuheimer AB, MacKenzie BR. *Explaining variation in life history timing across a species' range: Spawning time in an exploited marine fish*. ICES Annual Science Conference, Sept. 23-27, 2013.
35. Nielsen LT, Couespel D, Haaning K, Aagaard J, Thomsen HA, Andersen A, Kiørboe T. *Hydrodynamics of Choanoflagellate Feeding*. Poster. 2013 International Choanoflagellate Workshop, Cologne, Germany, 22-25 May 2013.

36. Nielsen LT, Andersen A, Bohr T, Kiørboe T. *Traits and trade-offs in microzooplankton feeding*. Poster. International Workshop on Trait-Based Approaches to Ocean Life, Copenhagen, 26-28 August 2013
37. Prowe F. *A new trait-based zooplankton model for the Darwin-2 framework*, MIT, USA, Feb 22, 2013.
38. Prowe AEF, Andersen KH, Kiørboe T, Visser AW. *Zooplankton feeding traits and community composition in a global ecosystem model.* Presentation, 45th International Liège Colloquium, Liège, Belgium, 16/5 2013
39. Prowe AEF, Pahlow M, Oschlies A. *Phytoplankton community effects on productivity changes in a global reduced mixing scenario.* Poster, 45th International Liège Colloquium, Liège, Belgium, 16/5 2013
40. Prowe AEF, Andersen KH, Kiørboe T, Visser AW. *Zooplankton feeding traits and community composition in a global ecosystem model.* Poster, International Workshop on Trait-based approaches to Ocean Life, Copenhagen, 26-28 August 2013
41. Prowe AEF, Andersen KH, Kiørboe T, Visser AW, Dutkiewicz S, Follows M. *Trait-based trophic interactions in a global ecosystem model.* 29th Annual Meeting of the German Limnological Society & 43rd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Potsdam, Germany, 9/11 2013
42. Sainmont J, Varpe Ø, Andersen KH, Visser AW. *Feeding season duration and the relative success of capital and income spawning copepods*. ASLO, Aquatic Sciences Meeting, New Orleans (Oral presentation), 20/02-2013
43. Sainmont J, Andersen KH, Visser AW. *Optimal foraging and diel vertical migration in a life history model.* (Poster) ASLO, Aquatic Sciences Meeting, New Orleans, 19/02-2013
44. Sainmont J, Varpe Ø, Andersen KH, Visser AW. *Income versus Capital breeders*. (Poster) Trait-based workshop, Copenhagen, 26-28 August 2013
45. Starke J. *Bifurcation Analysis of Learning and Structure Formation in a Neuronal Map*. BrainModes 2013: *Criticality, connectivity, and neural masses*, VU University Amsterdam, Plenary talk on invitation by A. Daffertshofer (VU University Amsterdam, The Netherlands) and T. Boonstra (University of New South Wales, Australia), 2.12.2013
46. Starke J. *Implicit methods for equation-free analysis. Workshop on Slow-Fast Dynamics: Theory, Numerics, Application to Life and Earth Sciences*, Centre de Recerca Matem`atica (CRM), Bellaterra, Barcelona, Spain, invited talk in minisymposium *Numerical methods for multi-scale systems* on invitation by D. Avitabile (University of Nottingham, UK) and G. Samaey (KU Leuven, Belgium), 6/2013
47. Starke J. *Continuation and bifurcation analysis of vibrations in mechanical experiments*. SIAM Conference on Applications of Dynamical Systems, Snowbird, Utah, USA, invited talk in minisymposium *Nonlinear dynamics in experiments* on invitation by J. Sieber (University of Exeter, UK) and D. Barton (University of Bristol, UK), 5/2013

48. Starke J. *Bifurcation analysis of controlled lab experiments*, talk on invitation by A. Daffertshofer, VU University Amsterdam, The Netherlands, 4.12.2013
49. Starke J. *Implicit methods for equation-free analysis and applications to particle models,* talk on invitation by I. Kevrekidis, Princeton University, USA, 7/2013
50. Starke J. *Bifurcation analysis of controlled lab experiments*, talk on invitation by V. Jirsa, CNRS and Aix-Marseille Université, France, 3/2013
51. Starke J. *Multiscale analysis of traveling waves and oscillations in particle models*, talk on invitation by T. Lorenz and P.E. Kloeden, University of Frankfurt, Germany, 2/2013
52. Starke J. *Equation-free analysis of the collective behaviour of microscopic pedestrian models*, talk, Traffic and Granular Flow ’13, Forschungszentrum Jülich, Germany, 9/2013
53. Traving SJ, Rowe OF, Paczkowska J, Lefebure R, Brutemark R, Miranda F, Lindehoff E, Stedmon CA, Båmstadt U, Andersson A, Riemann L. *The influence of increased river inflow on a coastal bacterial community in the Baltic Sea*. Poster at Dansk Havforskermøde, Roskilde, Denmark, 16 January 2013
54. Traving SJ, Thygesen U, Stedmon CA, Riemann L. *Bacterial diversity meets chemical complexity*. Talk at Nordic Environmental NUcleotide Network workshop and Microbial Ecology Theory PhD course, Swedish University of Agricultural Sciences and Uppsala University, Uppsala, Sweden, 6-10 May 2013
55. Traving SJ, Thygesen UH, Riemann L, Stedmon CA. *Extracellular enzymes – Foraging strategy for free-living marine bacteria*. Flash-talk and poster at International workshop on Trait-based approaches to Ocean Life, Royal Academy of Sciences and Letters, Copenhagen, Denmark, 26-28 August 2013
56. Traving SJ, Thygesen UH, Stedmon CA, Riemann L. *My PhD research*. Invited presentation at MSc course Marine Biology, University of Copenhagen, Helsingør, Denmark 10 October 2013
57. Traving SJ, Thygesen UH, Riemann L, Stedmon CA. *Extracellular enzymes – Foraging strategy for free-living marine bacteria*. Flash-talk and poster at BIO, PhD Day 2013, University of Copenhagen, Copenhagen, Denmark, 14 November, 2013
58. Tsoukali S, Visser AW, MacKenzie BR. *Comparative impacts of temperature on egg ecology of pelagic fish species in the north Atlantic*. ICES Annual Science Conference, Sept. 23-27, 2013.
59. Visser AW, *Behavioral traits and their trade-off in the plankton*. International Workshop on Trait-Based Approaches to Ocean Life, Copenhagen, 26-28 August 2013
60. Wadhwa N, Andersen A, Kiørboe T. *Size dependent flow structure changes in swimming copepods* (poster). Microscale interactions in aquatic environments, Les Houches, France. 10/3-2013
61. Wadhwa N. *Swimming by jumping in marine zooplankton* (talk). Fluid•DTU Summer School, Humlebæk, Denmark, 7/8-2013

62. Wadhwa N, Andersen A, Kiørboe T. *Swimming by jumping in marine zooplankton* (poster). International workshop on Trait-based approaches to Ocean Life, Copenhagen 28/8-2013
63. Wadhwa N. *Swimming by jumping in marine zooplankton* (talk). Department of Physics, DTU, Kgs. Lyngby. 2/10-2013
64. Wadhwa N. *Swimming by jumping in marine zooplankton* (invited lecture). Physical Oceanograohy, DTU, Charlottenlund. 3/10-2013
65. Wadhwa N. *Swimming by jumping in marine zooplankton* (invited lecture). Introduction to Biophysics, DTU, Kgs. Lyngby. 23/10-2013
66. Wadhwa N. *Hydrodynamics of jumping copepod nauplii and adults* (talk). 2nd annual meeting of Centre for Ocean Life, Holbæk. 12/12-2013

2012

1. Berge T. Mixotrophy. *Symposium of The Danish Microbiological Society.* Monday, Copenhagen, Denmark, November 5th, 2012
2. Berge T, Daugbjerg N, Moldrup M, Moestrup Ø, Mogensen SB, Poulsen LK, Hansen PJ: *Multiple roles of a mixotrophic dinoflagellate in the marine food web* (2012). 17. danske havforskermøde. RUC, Roskilde, Denmark
3. Berge T, Daugbjerg N, Jakobsen HH, Hansen PJH. *Elevated pH, intraspecific variation and laboratory selection in two red-tide marine dinoflagellates*. 15th International Conference on Harmful Algae. Changwon, Korea, October 29 - November 2 2012.
4. Hansen PJ, Nielsen LT, Johnson M**,** Berge T, Flynn KJ. *Acquired phototrophy in Mesodinium and Dinophysis – A review of cellular organization, prey selectivity, nutrient uptake and bioenergetics*. Changwon, Korea, October 29 - November 2 2012
5. Riemann, L. *Traits for bacterial carbon turnover in the marine environment: chemical complexity meets bacterial diversity.* Talk at the annual meeting of the Danish Microbiological Society, Copenhagen, 5 November 2012
6. Traving, S. J. *Enzymatic activities in the Baltic Sea bacterial communities.* Poster at BIO, PhD Day, Copenhagen, Denmark, 1 - 15 November 2012

Appendix 4. Public outreach activities

Popular articles 2012-2016

1. Beyer, JE: *Fiskeri for fremtiden.* Fiskeritidende, 12. november 2016.
2. Dutkiewitz S, Follows M, Fiksen Ø, Kiørboe T (2012): *Trait-based Ecosystem Models*, International Innovations, June 2012: 120-122
3. *Havets usynlige liv*, Billed-artikel i '**Ud og Se'**, Juni 2013. http://ipaper.ipapercms.dk/DSB/udogse/2013/Juni2013/ (Look at page 12)
4. Jacobsen, N.S. (2014) *Fiskeyngel er fremtidens nytårstorsk,* Aktuel Naturvidenskab 3 Juli 2014
5. Kiørboe T, Andersen A (2013) *Sirupssvømmerne*. Weekendavisen, Ideer, 19: 8-9
6. Kiørboe T, Heuschele J, Selander E (2013) *Havets dufte*. Aktuel Naturvidenskab 3: 30-33 www.aktuelnaturvidenskab.dk/fileadmin/Aktuel_Naturvidenskab/nr-3/AN_3_2013dufte.pdf
7. Kiørboe T, Hylander S (2013) Plankton beskytter sig med solcreme. Videnskab.dk 18 november. http://videnskab.dk/miljo-naturvidenskab/plankton-beskytter-sig-med-solcreme
8. Kiørboe, T., Andersen A. Bohr T (2014) *Forskning på tværs af faggrænser*. Aktuel Naturvidenskab, 1: 32-36 www.aktuelnaturvidenskab.dk/fileadmin/Aktuel_Naturvidenskab/nr-1/AN1-2014paatvaers.pdf
9. Kiørboe, T, Hylstofte Sichlau, M (2014) *Lækre lopper scorer bedst*. Aktuel Naturvidenskab 3:8-11 www.aktuelnaturvidenskab.dk/fileadmin/Aktuel_Naturvidenskab/nr-3/AN3-2014lopper.pdf
10. Kiørboe T (2015) *Planktons svømmeteknik er uovertruffen*. Videnskab.dk 28 Februar 2015. http://videnskab.dk/miljo-naturvidenskab/opdagelse-planktons-svommeteknik-er-uovertruffen
11. Kiørboe T & Nielsen LT (2015) *Hvordan fanger flagellater deres føde*? Videnskab.dk 13 juli 2015, http://videnskab.dk/miljo-naturvidenskab/forskere-afslorer-flagellaternes-hemmelighed
12. Kiørboe T, Ceballos S, Thygesen, UH (2015*) Behavior-Dependent Senescence in Pelagic Copepods*. Bulletin of the Ecological Society of America 96:651–653. http://dx.doi.org/10.1890/0012-9623-96.4.651
13. Neuheimer AB, Hartvig M, Heuschele J, Hylander S, Kiørboe T, Olsson KH, Sainmont J, Andersen KH (2015). *Offspring Size in Marine Animals*. Bulletin of the Ecological Society of America 96:662–663. http://dx.doi.org/10.1890/0012-9623-96.4.662
14. Nielsen LT, Kiørboe T (2013) *Plankton med helgardering*. Weekendavisen, Ideer, 31: 4-5
15. Olsson. K.H. (2014) *Hvorfor lægger fisk små æg?* Aktuel Naturvidenskab 5: 8-10

16. Payne MR, Kiørboe T (2013) *Immigranter sydfra på tallerkenen*. Weekendavisen, Ideer, 20: 3
17. Schnedler-Meyer, NA, Kiørboe T (2016) *Gele i verdenshavene*. Weekendavisen, 'Ideer', 49: 5 (9. December 2016)
18. Traving SJ, Stedmon CA, Riemann L, Thygesen UH (2015) *Kulstof i havet – en tynd kop te?* Aktuel Naturvidenskab 5:14-17
19. Traving SJ (2015) *The Promise and Pitfalls of Extracellular Biochemistry*. Discover Magazine October 9 2015. http://blogs.discovermagazine.com/the-extremo-files/2015/10/09/the-promise-and-pitfalls-of-extracellular-biochemistry/#.Vk2YAb8YF2w
20. Törnroos A. (2016). *Høj funktionel rigdom trods få arter i Østersøen*. Aktuel Naturvidenskab 1: 16-19.
21. Wadhwa N, Kiørboe T, Andersen A (2015) *Hydrodynamics of stealthy propulsion by plankton*. Euromech Newsletter 46, winter 2015.

Popular lectures 2012-2016

1. Andersen A. *Zooplankton hydrodynamik optaget med højhastighedsvideo*. Ingeniørforeningen, IDA. 11 November 2014.
2. Andersen KH: *Liv og død i havet*. "Hjernekassen", København 19 February 2015
3. Andersen KH: *Liv og død i havet*. Open Air Academy, Brede, 24. May 2015
4. Andersen KH: *Liv og død i havet*. Stege Rotary klub. 1. September 2015
5. Gislason H: *'Våd og usynlig'* 26/5/2016. Naturmødet, Hirtshals.
6. Hansen PJ. *Mixotrofi i plankton Dansk Havforskermøde*. Invited plenary. 16 January 2013
7. Jacobsen, NS. *Små fisk på spisebordet – et balanceret fiskeri*, Dansk selskab for marinbiologi, Naturstyrelsen, 27 marts 2014
8. Jacobsen, NS. *Babyfisk på middagsbordet – et balanceret fiskeri*, Naturvidenskabsfestival, Herlev Gymnasium, 24 september 2014
9. Kiørboe T. *To eat and not be eaten. Vandloppers kvantitative naturhistorie*. Dansk Havforskermøde. Invited plenary. 16 January 2013
10. Kiørboe T. *Havets usynlige liv.* Foredrag ved videnskabsarrangementet *HØRT* (Hovedstadsregionen) med Peter Lund Madsen 24 May 2013
11. Kiørboe T. *Livet i havet*. Rotary Club Copenhagen, 9 September 2014 på SAS hotel
12. Kiørboe T. *Oceanernes biologi*, Dansk Naturvidenskabs festival,

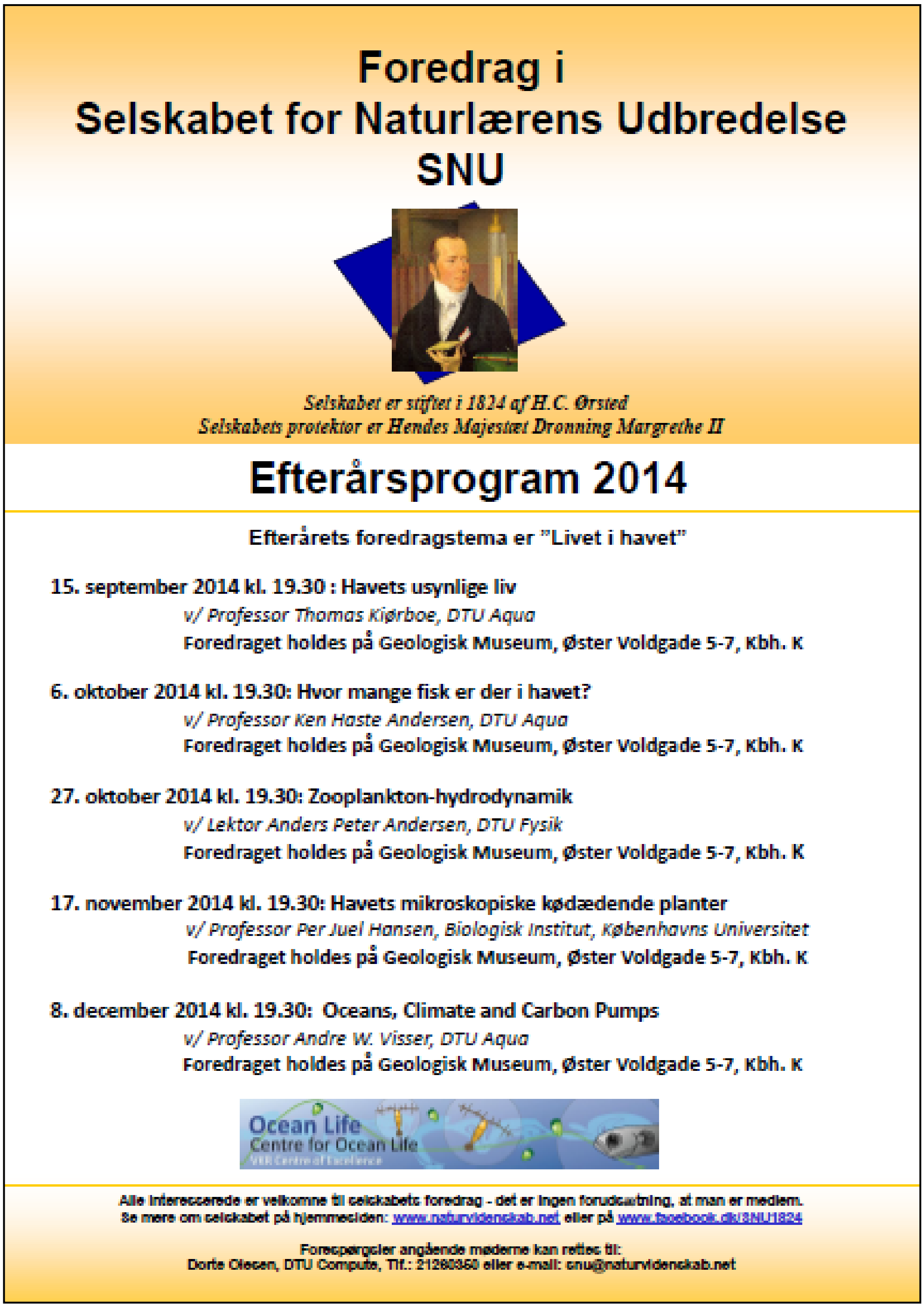
    Roskilde Gymnasium 23/9 2013
    Ørestad Gymnasium, 24/9 2013

13. Kiørboe T. *Havets usynlige liv*, Lyngby Gymnasium, 23 September 2014

14. Kiørboe T. *Oceanernes liv,* Tårnby Pædagogiske Center for 400 high school students. 25 Sept 2014
15. Kiørboe T. *Livet under vand*. Folkeuniversitetet in Århus, 25 september 2014.
16. Kiørboe T. *Verdens almindeligste dyr*. Dansk naturhistorisk forening, 26 september 2013.
17. Kiørboe T. *Havets usynlige liv*. Lecture at Folkeuniversitetet in Copenhagen, 2 October 2014
18. Kiørboe T. *Det er svært at være lille: Havets mikroskopiske liv*. Dansk Naturvidenskabelig Akademi, 28 October 2014
19. Kiørboe: *Livet i havet,* København KVUC, 23 April, 2015
20. Kiørboe: *Livet i havet,* Roskilde Gymnasium, 24 September 2015
21. Kiørboe: *Havets usynlige liv*. Folkeuniversitetet v. Odense Universitet, 18 March, 2015
22. Kiørboe: *Havets usynlige liv*. Folkeuniversitetet v. Århus Universitet/Emdrup, 25 September, 2015
23. Kiørboe: *Havets usynlige liv*. Folkeuniversitetet i Sønderborg, 5 November, 2015
24. Kiørboe: *Mysterier, myter og andre historier om havets mikroskopiske liv,* Marinbiologisk Selskab, København, 9 December 2015
25. Kiørboe T:*'Sex og død i havet'*. 27/9/2016. Nyt fra Videnskaben, KDVS populære foredragsserie.
26. Lindegren M: *Fiskeriforvaltning, klimaendringer og forsuring av havene.* Nordisk råd sommarmöte (Miljø- og naturressursutvalget), Hirtshals, Danmark, 23 June 2015,
27. Lindegren M: *Climate, Fishing, and Fluctuations of Sardine and Anchovy in the California Current Ecosystem.* "Salongen" (Science and dinner), Lund, Sweden, 22 November 2015
28. Nielsen LT, *Tales from the plankton*. Dansk Naturvidenskabsfestival, 22-28 Sept 2014: Four 2-hour presentations at high schools in and around Copenhagen.
29. Nielsen LT: Dansk Naturvidenskabsfestival, 2014-2016: Ten 2-hour presentations at high schools in and around Copenhagen. Title: *"Tales from the plankton"*. Collectively more than 400 high school students.
30. Schnedler-Meyer NA: *Jellyfish!* Lecture, at DTU Aqua for visiting German high school students. Oktober 2016.
31. Sichlau MH. Danskernes Akademi, DR2, *Har vandlopper mange elskere og deres afkom mange fædre?* 13 October 2013 http://www.dr.dk/DR2/Danskernes+akademi/Natur_Matematik/Har_vandloppehunner_mange_elskere_og_har_deres_afkom_mange_faedre.htm
32. Starke J. *Robots, Swarms and Labyrinths,* public talk at DTU for Allerød Gymnasium and Grønnemose Skole, 3/2013
33. Stedmon C: *'Havet, Klima og Kulstof: hvordan hænger det sammen*? 28/4/2016. Bestil en forsker (Folkeuniversitetet), Birkerød Skole.
34. Stedmon C: *'Havet, Klima og Kulstof: hvordan hænger det sammen*? 5/11/2016. Dansk Laborant Forening årsmøde, HK Huset, København.

35. Törnroos A. *Fish - more than just food? Their functional roles, diversity and long-term trends in the Baltic Sea.* FishBase Symposium - The Baltic Sea. Stockholm, Sweden, 17.10.2016.

36. Lecture series on ‘*Ocean Life’* offered by ’Selskabet for Naturlærens Udbredelse’ in the fall of 2014 and given by Ocean Life PIs



Foredrag i
Selskabet for Naturlærens Udbredelse
SNU

Selskabet er stiftet i 1824 af H.C. Ørsted
Selskabets protektor er Hendes Majestæt Dronning Margrethe II

Efterårsprogram 2014

Efterårets foredragstema er ”Livet i havet”

15. september 2014 kl. 19.30 : Havets usynlige liv
v/ Professor Thomas Kiørboe, DTU Aqua
Foredraget holdes på Geologisk Museum, Øster Voldgade 5-7, Kbh. K

6. oktober 2014 kl. 19.30: Hvor mange fisk er der i havet?
v/ Professor Ken Haste Andersen, DTU Aqua
Foredraget holdes på Geologisk Museum, Øster Voldgade 5-7, Kbh. K

27. oktober 2014 kl. 19.30: Zooplankton-hydrodynamik
v/ Lektor Anders Peter Andersen, DTU Fysik
Foredraget holdes på Geologisk Museum, Øster Voldgade 5-7, Kbh. K

17. november 2014 kl. 19.30: Havets mikroskopiske kødædende planter
v/ Professor Per Juel Hansen, Biologisk Institut, Københavns Universitet
Foredraget holdes på Geologisk Museum, Øster Voldgade 5-7, Kbh. K

8. december 2014 kl. 19.30: Oceans, Climate and Carbon Pumps
v/ Professor Andre W. Visser, DTU Aqua
Foredraget holdes på Geologisk Museum, Øster Voldgade 5-7, Kbh. K

Alle interesserede er velkomne til selskabets foredrag - det er ingen forudsætning, at man er medlem.
Se mere om selskabet på hjemmesiden: www.naturvidenskab.net eller på www.facebook.dk/SNU1824

Forespørgsler angående møderne kan rettes til:
Dorte Olesen, DTU Compute, Tlf.: 21280350 eller e-mail: snu@naturvidenskab.net

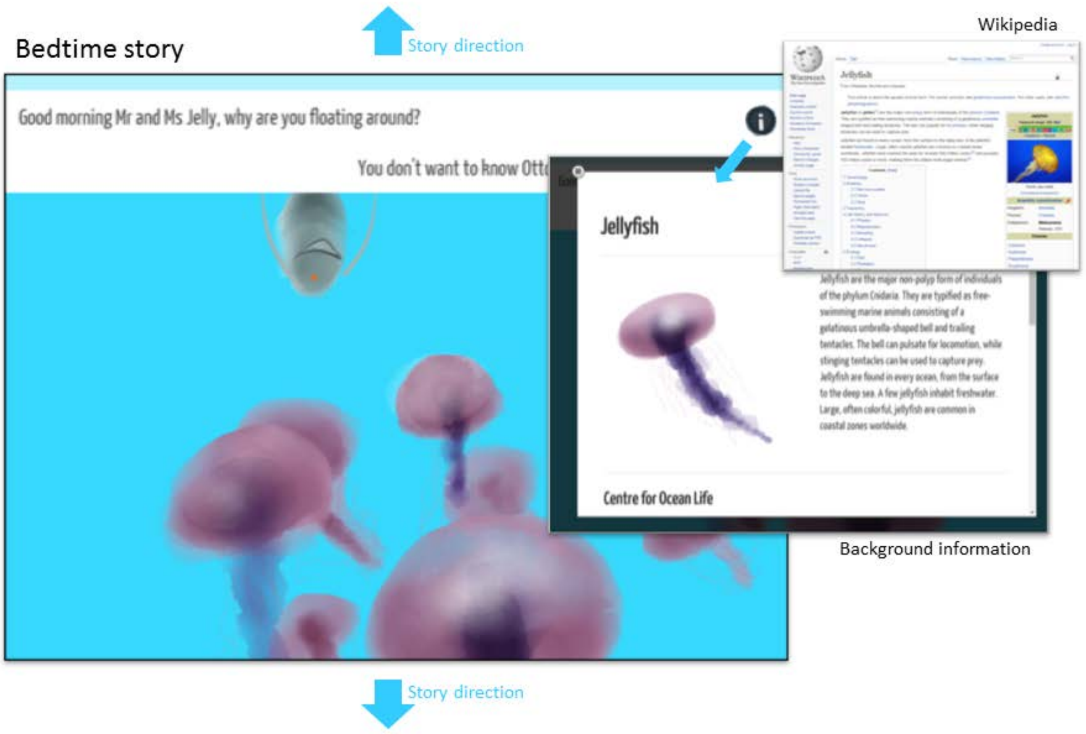
Other activities 2012-2016

Interactive website: size-spectrum simulator: https://www.stockassessment.org/spectrum/

ESOF Science Festival, Copenhagen, 23-26 August 2014: 4500 people visited the Ocean Life stand on the open ship DANA to see demonstrations of ecological models, ocean physics, 3-dimensional real-time video of live plankton, etc.

Ocean Life demonstrations during ESOF 2014

Childrens e-book on Ocean Life: Otto the copepod. Through a grant from '*Tips- og lottomidler'* from the *Ministry of Research Innovation, and Education* we have contracted a scientist and artist to develop a concept for science out-reach to small kids and to produce an e-book. All other outreach activities of the Centre target mainly adolescents and adults, and we want to extent the impact of the Centre for Ocean Life to the younger generation. Therefore we want to develop and publish a bedtime picture book that introduces kids (and their parents) to the main players and processes in the ocean and the important interactions between them. The content of the book is developed in cooperation with the researchers at the Centre for Ocean Life and a local design studio. The book will be distributed as a freely available eBook and as an interactive platform-independent website, which will allow us to add several information layers to the otherwise minimalistic picture book. On top of the basic story will be a layer that contains more information about the topic and examples of the current research at the center. We also consider adding a second layer for the interested reader where he can directly read the relevant pages on Wikipedia without leaving the book. The developing version of the book is available at http://heuschele.com/otto/index.html. Currently, the book works only properly on an Ipad, but eventually it will be platform independent.



Good morning Mr and Ms Jelly, why are you floating around?

You don't want to know Ott

Jellyfish

Jellyfish are the major non-polyp form of individuals of the phylum Cnidaria. They are typified as free-swimming marine animals consisting of a gelatinous umbrella-shaped bell and trailing tentacles. The bell can pulsate for locomotion, while stinging tentacles can be used to capture prey. Jellyfish are found in every ocean, from the surface to the deep sea. A few jellyfish inhabit freshwater. Large, often colorful, jellyfish are common in coastal zones worldwide.

Centre for Ocean Life

1. Brun P. In: Persson CP: Danske forskere gør op med darwinistisk tradition. www.videnskab.dk
2. Brun P. In: Persson CP: Scientists do away with Darwinian tradition. www.sciencenordic.com
3. Brun P. In: Kappel US: Dansk forskning udfordrer Darwin-tradition. Kristeligt Dagblad, 5.11.2016
4. Dencker T. Representing Centre for Ocean Life and DTU Aqua in the ICES working group for biodiversity, WGBIODIV in 2016 in San Sebastian, Spain.
5. Dencker T. Student PhD-representative on the PhD-committee for Life Sciences at DTU, 2016-2017, nominated for same position 2017-2018.
6. Dencker T. Guest presenter, Physical Oceanography course, DTU Aqua. Quick presentation of potential topics for Msc. thesis students.
7. Holm MW: Lecturer in “Estuarine and coastal ecology and human impacts”:
   - Shelfs Planktonic Systems
   - Estuarine Planktonic Systems
   - Coastal Fish Production

   Lecturer in “Zoology” - physiology of:
   - Acoelomata/Pseudocoelomata
   - Mollusca og annelida

   Lecturer in “An introduction to ecosystems”:

- The abiotic environment
- Energy input and primary producers
- Stream fauna and community structure

Lecturer in “Biological Production”:
- Shellfish; natural stocks, reefs, artificial reefs, relay of bycatch, physiology, interspecific competition, aquaculture’

8. Schnedler-Meyer N. In: Ida Eriksen: Hvad skal jeg gøre, når jeg bliver brændt af en brandmand? Interview for popular science article on videnskab.dk. http://videnskab.dk/krop-sundhed/hvad-skal-jeg-goere-naar-jeg-bliver-braendt-af-en-brandmand.
9. Törnroos A. Popular science Blog under the BONUS project site: “Baltic Diversity Notes” (http://www.bonusprojects.org/bonusprojects/blogs/baltic_diversity_notes)
10. van Denderen PD. Representing Centre for Ocean Life and DTU Aqua in the scientific steering committee of the ICES/PICES early career marine biology conference, Busan, Korea .

Appendix 5. Summer schools, symposia session, and workshops taught and/or organized

2016

1. *Microscale Ocean Biophysics*, Eilat, Israel, 31 Oct - 4 Nov 2016, International workshop
2. *Microbial Oceanography - Complexity vs Simplicity in Microbial Ecology*, Hjort Summer School, Bergen, August 29 – September 22, 2016: *Predation in the microbial world*
3. *Modelling biodiversity for Sustainable Use of Baltic Sea Living Resources*, BIO-C3 Summer school, Holbæk, August 22-26, 2016.
4. *Food-webs and Traits. Workshop I.* Copenhagen 9-10 June 2016.
5. *Food-webs and Traits. Workshop II.* Hamburg 15-16 September 2016.
6. *Food-webs and Traits. Workshop III.* Copenhagen 1-2 December 2016.

2015

1. Andersen KH: Trait-based approaches to Ocean Life (http://www.whoi.edu/workshop/traitworkshop2015). Waterville valley October 5-8 2015 (co-organizer)
2. Kiørboe T: Aspen Center for Physics winter workshop: Microscale Ocean Biophysics, Aspen 10-16 January, (co-organizer)
3. Kiørboe T: Geilo-School on Cooperative particles: Patchy colloids, active matter and nanofluids. Geilo 16-26 March 2015 (Instructor)
4. Kiørboe T: ASLO Granada 22-27 February) session: Small bugs with big impact: linking plankton ecology with ecosystem processes (co-organizer)
5. Kiørboe T: ASLO Granada 22-27 February) session: Life at small scale: Microscale insights into aquatic systems (co-organizer)
6. Piltz S: National Institute for Mathematical and Biological Synthesis (NiMBioS) Research Collaboration Workshop for Women in Mathematical Biology, University of Tennessee, USA, June 2015 (participation via application and through a selection process).
7. Piltz S: Organising and guest lecturing a 2-day course programme on mathematical modelling of phytoplankton populations for third-year undergraduate course Arctic Ecology and Population Biology, University Centre in Svalbard, Norway, October 2015.
8. Starke J: 4 days course, Numerical bifurcation analysis and its applications, RheinMain University of Applied Sciences in Wiesbaden, Germany, on invitation by E. GEHRIG and T. LORENZ, 3-4/2015 (Instructor)

2014

- *Small bugs with a big impact: linking plankton ecology with ecosystem processes*. Session at ASLO conference, February, Hawaii
- *Mini symposium on size-based approaches to fish and fisheries*. June 2-3, DTU Aqua, Denmark www.size-based-symposium.dk
- *Advanced Time Series Analysis, DTU Aqua, Charlottenlund, October 2-4, 2014*
- *Multiscale, fast-slow dynamics and applications, minisymposium, International Conference on Structural Nonlinear Dynamics and Diagnosis (CSNDD'2014), Agadir, Morocco*
- *Control of dynamical systems in science and engineering, minisymposium, Dynamics Days Europe, Bayreuth, Germany*
- *Diffusion in aquatic environments. University of Gothenburg, 19-23 May, 2014.*
- *DEBtox course, University of Copenhagen, 5-13 August*

2013

- *Microscale interactions in aquatic Environments*, Workshop, 11-15 March, Les Houches Physics School, France
- *Trait-based approaches to Ocean Life*, Workshop, Copenhagen, 23-26 August
- *A changing ocean*, EUR-OCEANS hot topics conference, 6-8 November, Gran Canaria, Spain.
- *Modelling and data synthesis of marine planktonic ecosystems using functional types and trait-based approaches*. Session at IMBER conference, June, Bergen
- *From Bloom to Gloom* (Iceland, August),
- *Climate-Biogeochemistry Interactions in the Tropical* Ocean (Kristineberg, Sweden, August (University of Kiel)
- *CNRS Thematic School on Innovative Approaches in Marine Environment Modelling*, Brest, August.
- *Multi-scale Analysis in Dynamical Systems*, Lyngby (DTU), 9th - 13 December
- *Dynamical models with uncertainty and constraints*, minisymposium, SIAM Conference on Applications of Dynamical Systems, (19.-23.05.2013), Snowbird, Utah, USA

2012

- *Aquatic Microbiology*. Session at the annual meeting of the Danish Microbiological Society, Copenhagen, 5. November 2012
- *Arctic Plankton Ecology* (Godhavn, Greenland, April)

Appendix 6. Young Researcher reports

All current young researchers of the Centre were asked to produce a report on progress and plans for their individual projects. Some projects have just started; others are close to completion, hence the diversity in contents of the f contributions. Also, some projects that are not financed by the Ocean Life Centre have commitments to other agencies and, hence, add to the diversity of the project portfolio.

Contents

6.1 Traits for bacterial carbon turnover in the marine environment: chemical complexity meets bacterial diversity

Sachia Jo Traving, PhD student
Employment period: 1 February 2012 - 12 March 2016 (Maternity leave 16 March 2014 – 2 April 2015).
PhD degree: 24 June 2016
Supervisors: Lasse Riemann (University of Copenhagen) and Colin Stedmon (DTU Aqua).

Description of project:

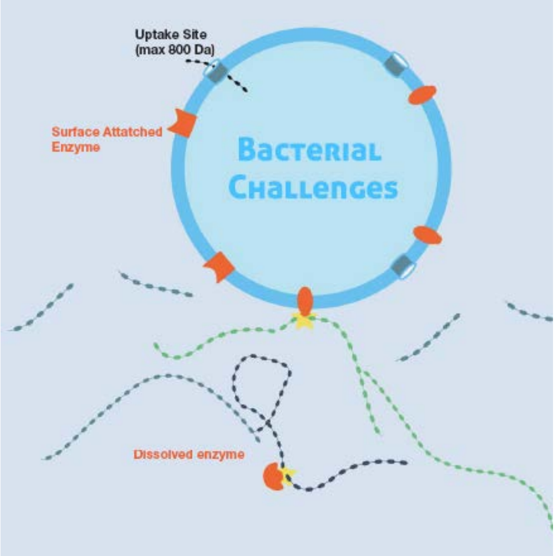


Figure 1 *bacteria produce a vast range of diverse enzymes, and how they are deployed can be grouped into two types: free or attached enzymes. Both types of enzyme deployment carry significant impact on the microscale environment, and due to microbes vast numbers, also on the global scale.*

Marine microbes represent a major pathway in the global carbon cycle by converting dissolved organic carbon (DOC) into living biomass and carbon dioxide. Degradation of DOC by enzymes produced by bacteria is the rate-limiting step for bacterial utilization of the DOC pool. These extracellular enzymes mediate the microbial degradation and recycling of detrital organic matter, which is fundamental for ocean biogeochemistry. However, how the enzymes are deployed and under which conditions, has proven hard to discern through measurements alone. This PhD project focuses on microbial degradation of marine DOC, and on how this is connected to microbial identity and diversity, and to the composition of DOC. The approaches include a theoretical project on an enzyme model for marine bacterioplankton[1], and two large field studies[2,3].

The first field study was a seasonal study, with monthly sampling for the entire year of 2012, monitoring two Danish estuaries[2]. The time-series documented a highly variable composition and function of the heterotrophic bacterioplankton communities over the year. Bacterial population was linked to specific community functions, suggesting that single bacterioplankton populations may be important in driving specific community functions such as extracellular enzyme activities. The data also revealed a large presence of parameters related to the nitrogenous dissolved organic matter, suggesting that nitrogen is an important environmental factor shaping Danish coastal bacterioplankton communities. The second field study was a food-web experiment carried out in mesocosms at Umeå Marine Science Center, Sweden[3]. The study simulated future predictions of increased inflow of allochthonous organic matter due to precipitation, and aimed at investigating the effect on a pelagic food-web from the Northern Baltic Sea. The bacterioplankton was heavily influenced by the addition of dissolved organic matter (DOM) which also induced an increased activity in key functions (i.e. extracellular enzymes). Overall, the experimental data suggest that a future elevated DOM outflow from Baltic Sea rivers will be efficiently mineralized by bacteriolankton and have large consequences for the nutrient biogeochemistry as well as primary production in the system. This story will be submitted to Frontiers in Microbiology within 2016.

The enzyme model[1] has yielded interesting results and have i) identified extracellular enzymes as a key bacterial trait, and ii) successfully modeled enzyme deployment strategies for free-living bacteria. The model clearly supports surface-associated extracellular enzymes as the most efficient strategy for a free-living bacterium. The enzyme model is broad in scope, as it can be applied to other free-living, single cells; which forage by extracellular enzymes in aqueous environments.

Furthermore, work from the enzyme model has contributed to a discussion on the biogeochemical fate of DOM in the oceans, which has resulted in an opinion paper[4] outlining how heterotrophic microbes and in particular their extracellular enzymes may be of key importance for deciphering the dilute state and chemical diversity of marine DOM, and provide novel insights on the persistence of DOM and the ocean's role in long-term storage of organic carbon.

Dissemination:

Scientific publications:

[1]Traving SJ, Thygesen UH, Riemann L and Stedmon CA (2015) A model of extracellular enzymes in free-living microbes: which strategy pays off? Applied and Environmental Microbiology 81:7385-7393.
Significance and relevance: the work takes a theoretical approach in the attempt to solve the best enzyme strategy for a single free-living microbe; something current technology is not able to measure quantitatively. Understanding the ecological role of bacterial enzymes is an important goal, as it plays a central role of bacterial driven carbon cycling in the oceans.

[2]Traving SJ, Bentzon-Tilia M, Mantikci M, Knudsen-Leerbeck H, Sørensen H, Hansen JLS, Markager S and Riemann L (2016) Coupling Bacterioplankton populations and environment to community function in coastal temperate waters. Frontiers in Microbiology 7:1-13.
Significance and relevance: Seasonal dynamics in primary productivity and DOC regulates bacterial abundance, activity, and composition, but a detailed understanding is lacking. Here we investigate the impact of seasonality on microbial enzymatic activity, bacterial growth efficiency and dynamics in the DOC pool, which will lead to an improved understanding of microbial carbon cycling in a fjord.

[3]Traving SJ, Rowe OF, Jacobsen NM, Sørensen H, Dinasquet J, Stedmon CA, Andersson A and Riemann L (submitted) Increased loads of dissolved organic matter shape estuarine bacterial communities and their function. Submitted to Frontiers in Microbiology.
Significance and relevance: Climate change is predicted to increase river inflow and thus elevate the nutrient and carbon loads to the Baltic Sea. This might have severe consequences for the microbial community, ultimately affecting the entire food-web of the system. In this experimental study we mimicked an increased future river outlet and examined effects on plankton organisms.

[4]Traving SJ, Wünsch UJ, Reader HE, Sjöstedt J, Hambly A and Stedmon CA (submitted) Can microbes "perceive" the complexity of dissolved organic matter? Submitted to L&O Letters.
Significance and relevance: Dissolved organic matter (DOM) in marine waters is a chemically complex and diverse mixture of compounds and is one of the largest and most reactive carbon

reservoirs in Earth. Current analytical methodologies used for characterization DOM reveal an extreme chemical diversity, yet these methods are unable to resolve the underlying mechanisms controlling the persistence and turnover rate of DOM, which is fundamental for understanding the ocean´s role in long-term storage of organic carbon. We propose that prokaryotic microbes and in particular their extracellular enzymes, hold the key to interpret the extreme complexity of DOM and yield new insights to the long term persistence of organic carbon in the oceans.

Andersen KH, Berge T, Goncalves R, Hartvig M, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer A, Olsson K, Payne M, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T. (2016) Characteristic sizes of life in the oceans - from bacteria to whales. Annual Review in Marine Science 8:3.1-3.25.
Significance and relevance: Provide a comprehensive explanation for the emergence of traits and general relationship as a function of size across the full marine, animal kingdom.

Mantikci M, Bentzon-Tilia M, Traving SJ, Knudsen-Leerbeck H, Riemann L, Hansen JLS and Markager S (in prep) Pelagic primary production, respiration and net community production in two temperate estuaries of contrasting nutrient richness.
Significance and relevance: Estuaries are among the most productive ecosystems on Earth, but most of them are under severe threat from anthropogenic activities. This study investigates how various environmental parameters influence net community production in two Danish estuaries over the seasons.

Knudsen-Leerbeck H, Mantikci M, Bentzon-Tilia M, Traving SJ, , Riemann L, Hansen JLS and Markager S (submitted) Seasonal dynamics and bioavailability of dissolved organic matter in two contrasting temperate estuaries. Submitted to Biogeochemistry.
Significance and relevance: Most estuaries are under severe pressure from anthropogenic activities, receiving large nutrient inputs which potentially affect their ecosystems. This study investigates the role of dissolved organic matter on nutrient cycling in Danish estuaries, revealing that a large flux of bioavailable nitrogen is cycled through the dissolved organic matter pool.

Presentations at conferences, scientific courses and meetings:

Traving S J, Rowe OF, Paczkowska J, Lefebure R, Brutemark R, Miranda F, Lindehoff E, Stedmon CA, Båmstadt U, Andersson A and Riemann L. *Enzymatic activities in the Baltic Sea bacterial communities*. Poster at BIO, PhD Day, Copenhagen, Denmark, 1 November-15 November 2012.

Traving SJ, Rowe OF, Paczkowska J, Lefebure R, Brutemark R, Miranda F, Lindehoff E, Stedmon CA, Båmstadt U, Andersson A and Riemann L. *The influence of increased river inflow on a coastal bacterial community in the Baltic Sea*. Poster at Dansk Havforskermøde, Roskilde, Denmark, 16 January 2013.

Traving SJ, Thygesen UH, Stedmon CA and Riemann L. *Bacterial diversity meets chemical complexity*. Talk at Nordic Environmental NUcleotide Network workshop and Microbial Ecology Theory PhD course, Swedish University of Agricultural Sciences and Uppsala University, Uppsala, Sweden, 6-10 May 2013.

Traving SJ, Thygesen UH, Riemann L and Stedmon CA. *Extracellular enzymes – foraging strategy for free-living marine bacteria*. Flash-talk and poster at International workshop on Trait-based approaches to Ocean Life, Royal Academy of Sciences and Letters, Copenhagen, Denmark, 26-28 August 2013.

Traving SJ, Stedmon CA and Riemann L. *My PhD research*. Invited talk at MSc course Marine Biology, University of Copenhagen, Helsingør, Denmark 10 October 2013.

Traving SJ, Thygesen UH, Riemann L and Stedmon CA. *Extracellular enzymes – Foraging strategy for free-living marine bacteria*. Flash-talk and poster at BIO, PhD Day 2013, University of Copenhagen, Copenhagen, Denmark, 14 November, 2013.

Stedmon CA, Jørgensen L and Traving SJ. *Why does dissolved organic matter persist in the deep ocean? Is part of the solution, dilution?* Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) Open Science Conference, Bergen, Norway, 23-27 June 2014.

Traving SJ, Bentzon-Tilia M, Knudsen-Leerbeck H, Mantikci M, Hansen JLS, Stedmon CA, Markager S and Riemann L. *Dynamics in microbial composition and functionality – a study of two contrasting estuarine systems over a year*. Poster at SAME Conference, Uppsala, Sweden, August 2015.
Traving SJ. *Marine Biology – heterotrophic bacteria*. Invited talk at MSc course Marine Biology, University of Copenhagen, Helsingør, Denmark 7 October 2015.

Traving SJ, Bentzon-Tilia M, Mantikci M, Knudsen-Leerbeck H, Hansen JLS, Markager S and Riemann L. *Dynamics in microbial composition and functionality*. Poster at BIO, PhD Day 2015, University of Copenhagen, Copenhagen, Denmark, November, 2015.

Traving SJ, Bentzon-Tilia M, Knudsen-Leerbeck H, Mantikci M, Hansen JLS, Stedmon CA, Markager S and Riemann L. *Microbial composition and function in two contrasting estuarine systems*. Poster at Danish Microbiology Society, Copenhagen, Denmark, October 2015

Traving, SJ. *Microbial marine ecology – the role of marine heterotrophic bacteria in the carbon cycle*. Invited talk at Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Neuglobsow, Germany, 25 September – 26 September 2016.

Outreach activities:

During my PhD I have been very active within the of the Ocean Life Centre, organizing and presenting talks at the weekly Ocean Life meetings (2012-2016), and I was an active member in the organizing committee of the Centre for Ocean Life Annual Retreat in 2013 and Summer Meeting 2013.

Traving SJ, Stedmon CA, Riemann L and Thygesen UH (2015) Kulstof i havet – en tynd kop te? Aktuel Naturvidenskab 5:14-17

Otto the copepod – an online, interactive story for all ages (contributed with the section on bacteria), www.heuschele.com/otto/

The wonderful world of microbes (in preparation) – a children’s book for ages 6-8 years, a collaboration with Katla Forlag, Sweden, www.katlaforlag.se

Traving SJ, interview for Discover Magazine – The extremophiles. “The promise and pitfalls of extracellular Biochemistry, October 9, 2015. http://blogs.discovermagazine.com/the-extremo-files/2015/10/09/the-promise-and-pitfalls-of-extracellular-biochemistry/#.V9auNjUprXg

6.2 Trait-based studies of mixotrophy in the marine plankton

Terje Berge, Post Doc.
Employment period: 1 February 2012 – 31 December 2014
Supervisors: Per Juel Hansen (MBL) and Ken H. Andersen (DTU Aqua).

Description of project:

Background

A new plankton paradigm describes the base of ocean food webs dominated by eukaryotic single cells that combine photosynthesis with food uptake, i.e., microscopic organisms that are both plants and animals at the same time. The traditional view of flows of resources through ocean ecosystems is founded on the distinction between phytoplankton producers (plants) and zooplankton consumers (animals). However, planktonic unicells cover the whole spectrum from nearly entirely plant-like phototrophs (e.g. diatoms and cyanobacteria) to entirely animal-like heterotrophs (e.g. ciliates and dinoflagellates) and display varying degrees of mixotrophy. The major aim of my project has been to arrive at a mechanistic understanding of planktonic mixotrophy that enables the nutritional trait distribution of populations and ecosystems to be modeled through time and space. To achieve this I have identified key-traits and trade-offs of mixotrophs by conducting laboratory experiments[1, 7-10,] , synthesized experimental data[6], reviewed the literature in collaboration with international experts in the field[2, 4, 5, 11] and engaged in modeling[3, 6].

Key traits and trade-offs

We have found that the traditional view of two equally contributing and substitutive nutritional pathways in mixotrophs for carbon and nutrients does not observations. Rather, mixotrophy appears synergistic and cooperative in its action: phagotrophy providing primarily essential nutrients, whereas carbon acquisition happens mainly through photosynthesis[1,3,7,8,11]. Experiments showed that investments in feeding was positively related to investments in photosynthesis[1,7,8]. This contrasts the traditionally view of substitutive mixotrophy, and discard the use of the often imposed trade-off between feeding and photosynthesis[3,6,11]. Considering only two resources harvesting traits, i.e., photosynthesis and feeding, is insufficient for a proper description of mixotrophy. The inclusion of at least one extra key resource harvesting trait is required, the ability of dissolved nutrient harvest[1-3,6-8,11]. In developing the trait-based model[6], we assumed that the effect of light on feeding rates was due to an obligate dependence on energy from photosynthesis to support feeding and nutrient uptake. Thus, carbon fixed by photosynthesis needs to be cover the respiratory costs of harvesting nutrients and taking up food. This potentially gives rise to a trade-off between these two harvesting traits. Investing in one trait increases the affinity and maximum uptake rates for the related substrate. However, investing the trait is also associated with both maintenances and metabolic respiratory costs. The potential trade-offs will emerge from the balance between the costs and benefits across environmental gradients.

From individuals to populations

Our experiments demonstrated large amounts of inter-and intraspecific trait variation in the resource harvesting traits[9]. Even within the same population of a single species, trait variation is very large and much larger than in metazoan populations[9]. This provides strong support for the use of trait-based approaches that will account for natural selection and adaptation in contrast to traditional functional-type models[6]. We parameterized the mechanistic mixotrophy model using available and obtained experimental data on photosynthesis, ingestion and nutrient uptake[1,6,9]. The trait-based model reproduced the general pattern observed in nature during the course of a typical seasonal succession in temperate waters[6]. This involves an initial phototrophic bloom period in the spring, following the input of new nutrients to the ecosystem during the winter/autumn and the increased light availability. During this period the plankton invest mostly in phototrophy and harvesting of dissolved nutrients. Subsequentially when dissolved nutrients are depleted, mixotrophs acquiring nutrients primarily through food uptake and carbon from photosynthesis become dominating.

Further developments:

Organismal size

Cell size affect resource harvesting and allometric scaling laws dictates that small cells are superior nutrient competitors, while larger cells gain relatively more nutrients by active feeding. Further employments of the developed model should generalize further, by focusing on organismal size as a master trait that affects the resource affinities and uptake rates. This study will benefit from a large dataset compiled during this project[1,5,6].

The developed trait based model is sufficiently simple to be adopted into larger food-web and ecosystem models.

Dissemination:

Scientific publications:

[1] Berge T, Chakraborty S, Hansen PJ, Andersen KH (2016). Modeling succession of key resource harvesting traits of mixotrophic plankton populations. The ISME Journal. doi: 10.1038/ismej.2016.92
Significance and relevance: This paper describes the developed mechanistic representation of a general mixotroph. It demonstrates the use of trait-based approaches in ecosystem models, by reproducing observed patterns of phototrophy, nutrient harvest and feeding in a seasonal cycle in temperate water.

[2] Berge T, Hansen PJ (2016)**.** Role of the chloroplasts in the predatory dinoflagellate *Karlodinium armiger*. Marine Ecology Progress Series 549: 41-54- doi: 10.3354/meps11682.
Significance and relevance: This paper reports experimental data that identify key traits and provides the basis for a mechanistic understanding of the flows of carbon and nutrients in a general mixotroph. Significant for the development of the trait based-model and parameterization.

[3] Hansen PJ, Ojamäe K, Berge T, Trampe E, Lips I, Nielsen L, Kühl M (2016). First evidence of photoregulation in a kleptoplastidic dinoflagellate, *Dinophysis acuta* Frontiers in Microbiology. Doi: 10.3389/fmicb.2016.00785
Significance and relevance: This paper reports lab data on photoregulation, photosynthesis, ingestion and growth of a second and much larger mixotrophic species. Significance for the development of the mechanistic model.

[4] Mitra A, Flynn KJ, Burkholder JM, Glibert PM, Granéli E, Hansen PJ, Raven JA, Stoecker DK, Berge T, Calbet A, Thingstad TF, Tillmann U, Våge S, Wilken S, Zubkov MV, Caron D, Hallegraeff G, Jeong HJ, Johnson M, Kana T, Lundgren V, McManus G, Not F, Pitta P, Sanders

RW, Schoener DM (2016). Defining planktonic protist functional groups on mechanisms for energy and nutrient acquisition: incorporation of diverse mixotrophic strategies. Protist 167.2: 106-120
Significance and relevance: Review on mixotrophic plankton organisms, providing a frame work for functional group categorization and types of mixotrophs. Significance for the inclusion of mixotrophy in ocean models, and thus the correct understanding of resource flows in the oceans. Significance for the choice of model organisms used throughout this project.

[5] Andersen KH, Aksnes DL, Berge T, Fiksen Ø and Visser A (2015). Modelling emergent trophic strategies in plankton. Journal of Plankton research 37.5: 862-868.
Significance and relevance: Horizon paper providing a framework toward the inclusion of trait-based simulations of global ocean models.

[6] Hansen PJ, Nielsen LT, Johnson M, Berge T, Flynn KJ (2013). Acquired phototrophy in *Mesodinium* and *Dinophysis* – A review of cellular organization, prey selectivity, nutrient uptake and bioenergetics. Harmful Algae 28:126-139.
Significance and relevance: Review on the currently most studied consortium of mixotrophs, due to their ecological importance and effects of humans through shellfish poisoning.

[7] Mitra A, Flynn KJ, Burkholder JM, Berge T, Calbet A, Raven JA, Granéli E, Glibert PM, Hansen PJ, Stoecker DK, Thingstad F, Tillmann U, Våge S, Wilken S, Zubkov MV (2014) The role of mixotrophic protists in the biological carbon pump. Biogeosciences 11: 995-1005.
Significance and relevance: This paper demonstrates the effects of including mixotorphs in addition to hetertrophs and phototrophs on carbon and nutrient flows through food webs in an oligotrophic plankton community. Significance for our understanding of the biological carbon pump and global biogeochemistry.

[8] Andersen KH, Berge T, Goncalves R, Hartvig M, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer A, Olsson K, Payne M, Prowe F, Saintmont J, Traving SJ, Visser A, Wadhwa N and Kiørboe T (2016). *Characteristic sizes of life in the oceans – from bacteria to whales.* Annual Review of Marine Science Vol 8 2016

Manuscript in preparation:

[9] Mogensen SB, Vismann B, Hansen PJ, Berge T. Adverse effects of *Karlodinium armiger* on juvenile and adult stages of the blue mussel ***Mytilus edilus.***
Significance and relevance: This paper reports lab data on the feeding behavior of our model mixotorph and shows that feeding by dinoflagellates can cause severe effects on mussel populations. Significance for development of the trait-based model.

Presentations at international science meetings:

Mitra A, Berge T, Calbet A, Flynn K, Glibert P, Granéli E, Hansen PJ, Raven J, Stoecker D, Thingstad F, Tillmann U, Vage S, Wilken S, Zubkov M (2013): The rise and dominance of mixotrophic protists in a changing world - Refining the functionality of the biological & microbial carbon pumps , The future of marine biogeochemistry, ecosystems and societies. IMBIZO III, Goa, India, 28 January 2013 - 31 January 2013.

Berge T, Hansen PJ. Mixotrophy. International workshop on Trait-based approaches to Ocean Life, 26-28 August 2013. Copenhagen, Denmark.

Mogensen SB, Vismann B, Hansen PJ, Berge T. *Adverse effects of* Karlodinium armiger *on juvenile and adult stages of the blue mussel* Mytilus edilus.16th International Conference on Harmful Algae. 27–31 October 2014. Wellington, New Zealand.

Berge T. Mixotrophy. Symposium of The Danish Microbiological Society Monday, November 5th, 2012. Copenhagen, Denmark.

Berge T, Daugbjerg N, Moldrup M, Moestrup Ø, Mogensen SB, Poulsen LK, Hansen PJ: Multiple roles of a mixotrophic dinoflagellate in the marine food web (2012). 17. danske havforskermøde. RUC, Roskilde, Denmark.

Berge T, Daugbjerg N, Jakobsen HH, Hansen PJH. Elevated pH, intraspecific variation and laboratory selection in two red-tide marine dinoflagellates. 15th International Conference on Harmful Algae. October 29 - November 2 2012. Changwon, Korea.

6.3 Mixotrophy in marine pelagic food webs

Starrlight Augustine, Post Doc.
Employment period: 1 July 2013- 28 February 2015
Supervisors: Thomas Kiørboe and Ken H. Andersen (DTU Aqua).

Description of project:

Interactions between species are instrumental in shaping food webs and those interactions drive ecosystem dynamics. There are many types of interactions between species ranging from different degrees of symbioses or partnership to predation. The large diversity of species in addition to the complex nature of interactions between them and their environment is a challenge. Mixotrophy is the capacity to take up both inorganic (e.g. fixation of CO2 via photosynthesis) and organic (prey items, organic molecules such ambient amino acids) substrates. Thus mixotrophy is a general case encompassing all types of interactions between organisms. This project focussed on understanding the role of mixotrophy in marine pelagic food webs. This is a complex scientific problem because first I need to find the simplest possible basis to compare between all of marine life. And then I need to compare across species on the basis of differences in their energetics which includes substrate uptake. I have chosen to use the framework of Dynamic Energy Budget (DEB) theory for this task. This is because the theory is based on first principles and specifies the metabolic organization of all living organisms from bacteria to whales using a same simple set of underlying rules. The standard DEB model is the simplest of DEB models because it applies to animals which have the simplest metabolisms: one type of food, one reserve and one structure. The idea is that all animals are represented by this same model and differences between animals can be seen as differences in parameter values. Each parameter quantifies a single metabolic process. Parameter estimation for these models is possible but generally requires having data on different aspects of the energy budget (growth, reproduction, development etc.).

Main results:

The first major result of this project was to collaborate with three other experts in DEB theory and develop a perfect map between nine simple life-history traits and 9 parameters of the DEB model (paper 1). This constitutes an important milestone not only for my project for DEB theory itself: it turns out that a very simple metric quantifies the position of organisms along the supply-demand spectra. this metric, the supply stress, turned out to be a very simple function of parameter values. In parallel I worked on completing a case study on an animal of high ecological relevance: the invasive comb jelly *Mnemiopsis leidyi*. This was a larger collaboration involving a local scientist as well as collaborators in France, Holland and Portugal. Through this study, we discovered mechanisms behind the metabolic flexibility of this species (paper 2). The standard DEB model is an individual based model specifying food intake and its use for different metabolic processes over the full life-cycle. But for my project I need to understand how this translates to dynamics of communities of species in a marine food web. Thus I need to work on ways to include properties of individuals into ecosystem models. Several routes allow for this and I explored via collaboration two possible routes of how the standard DEB model might be coupled to population models: papers 3 and 4. In paper 3 three different models were applied to study the reproduction, survival and dispersal of *Mnemiopsis leidyi* in the Scheldt estuaries and the southern North Sea: a high resolution particle tracking model with passive particles, a low resolution particle tracking model with a reproduction model coupled to a biogeochemical model, and the DEB model. In paper 4 a DEB

model was coupled with an individual-based model (IBM) specifying the population. What I conclude as the main drawbacks of these methods for my purpose is that they both do not specify a full ecosystem; indeed it would be far too complex. So what could be the solution?
At this time, I received a job offer at Akvaplan-niva (Tromsø Norway) to work as a full time researcher developing Dynamic Energy Budget theory as a framework for solving real word problems. I never saw a clear distinction between applied and fundamental research. The theory is only useful so long as it helps solve societal problems. And such problems often lead to extremely interesting and fundamental insight into energetics underlying organisms. I accepted the position meaning that I left my project at Ocean Life earlier than initially planned.
In the next paragraph I will describe the ongoing scientific developments as I left them in Feb. 2015 and which will resume if funding if obtained.

Ongoing scientific developments:

While I was still thinking of solutions to the problems of upscaling to ecosystems while still having a handle on properties of individuals, I was also working on extending the standard DEB model to deal with mixotrophic uni-cellulars. The reason is that these organisms are extremely important for primary production and nutrient cycling and are important players in food webs. It is more complex to model these species because they have several independent sources of substrate which are not all available in the environment in the same ratios. Thus these organisms must be modelled as several reserve systems. A large level of high quality data of mixtrophic eucaryotes has been published by the Ocean Life group. I decided to focus on a first species and parameterize an extended version of the DEB model for animals to this species: *Dinophysis acuminata* (in prep). But I hope to develop this extension such that it is the simplest general model possible so that in the future I can parameterize to other species of uni-cellulars and then compare across all species on the basis of differences in parameter values. It turns out that while experimental microbiologists often have an interest in understanding the physiology at the cell level, all of the data are in the form of population level statics. Namely, the most common type of data is cell density as function of time. Even carbon fixation rates are taken on groups of cells who might be anywhere in the cell cycle (= life cycle). Thus microbiologists are in fact population biologist with an interest in sub cellular processes. I surprisingly could not find anywhere studies which deal with this complex problem: how to infer properties of individuals based on population level statistics. Paper 5 *in prep* is a study which seeks to provide a solution to this problem. We are working on approximating the dynamics of a population of uni-cellulars with simple ordinary differential equations by working out a very special way in which properties of individual cells under changing food regimes maps to those of the population at each different food level.

Scientific outreach:

I participated in the weekly Ocean Life meetings by presenting the aims of my project to the whole group (4/12/2013), the standard DEB model for animals (26/02/14), extensions which are needed for uni-cellulars (18/06/14). This has stimulated much constructive discussion across disciplines. I also co-organised the annual retreat for the Centre (12-13 Dec 2014, Holbæk). I further co-develop software (DEBtool) which enables the estimation of parameters for the standard DEB model. I contributed code and results from paper to a free online library of DEB model parameters (Add my Pet). I joined the algae network with gives seminars several times a year and was invited to give a talk at one of the seminars. The network brings together algae specialist of different disciplines. Finally, I taught concepts and history of the DEB theory development at an 8 day course in

Roskilde as well as gave a short lecture for a master course focused on scientific aims of the Centre. I volunteered one day aboard the RV Dana during the science fair in (21-23 June 2014) to help disseminate the aims and results of the Centre. Thus I have in accordance with the aims of the center promoted exchange across many disciplines (modellers and experimentalists) within the Centre while developing collaborations with scientists in France, Greece, and Holland. I have been active in communicating my scientific results: I presented at the international algal seminar at DTU, Lyngby. I was also invited to give a seminar in Marseilles on my results concerning *Mnemiopsis*. In addition I provided a keynote lecture at the 4th international symposium on DEB theory in Marseilles, 2015. I am now organizing here in Tromsø the 5th international Symposium on DEB theory in 2017 as well as an 8-d practical course on parameter estimation preceded by a 5 week tele-course on DEB. "All applications of models, including testing of the model against data, start with knowledge of parameter values"

Dissemination:

Scientific publications:

Published:
[1] Lika K, Augustine S, Pecquerie L, Kooijman SALM (2014) The bijection from data to parameter space with the standard deb model quantifies the supply-demand spectrum. 354:35-47 J Theor Biol
Significance and relevance: The supply-demand spectrum for animals is quantified. There is a perfect map between parameters and life-history of species.

[2] Augustine S, Jaspers C, Kooijman SALM, Carlotti F, Poggiale J-C, Freitas V, van der Veer H, van Walraven L (2014) Mechanisms behind the metabolic flexibility of an invasive comb jelly. J. Sea Res. DOI:10.1016/j.seares.2014.09.005
Significance and relevance: (1)Application of the DEB model to an important group of organisms. (2)It was found that *Mnemiopsis* delays accelerating its metabolism sometime after birth and that this might explain how it waits out the bleak season.

[3] van der Molen J, van Beek J, Augustine S, Vansteenbrugge L, van Walraven L, Langenberg V, van der Veer H, Hostens K, Robbens J. (2015) Modelling survival and connectivity of Mnemiopsis leidyi in the southern North Sea and Scheldt estuaries. 11:405-424 Ocean Sci
Significance and relevance: Exploration of ways the DEB model could be used to understand processes at the ecosystem level.

[4] Beaudouin R, Goussen B, Piccini B, Augustine S, Brion F, Devillers J, Péry ARR. (2015) Zebrafish population dynamics DEB-IBM: an integrated framework for ecological risk assessment. PLoS ONE 10(5): e0125841. doi:10.1371/journal
Significance and relevance: Coupling the standard DEB model to an IBM.

Planned (with tentative title, authors, journal and submission date):

Augustine S, Kooijman SALM. Modelling the eco-physiology of uni-cellulars: translating properties of individuals to properties of ecosystems.
Target journal: J Ecol Model.
Target date for submission: 30 Jan. 2018

Significance and relevance: Find an approximation such that complex dynamics of individuals can be approximated by simple ODE’s such that properties of individuals which are quantified on the basis of laboratory data can be generalized and implemented into eco-system models.

Presentations:

Augustine S (Apr 2015) What is maturity? Discussing links between the concept and the underlying physiology of organisms. Invited keynote for the 4th international DEB symposium in 2015

Augustine S (October 2014) Comparing energy budgets of a comb jelly (Mnemiopsis leidyi) and a pelagic medusa (Pelagia noctiluca). Invited speaker at Seminar, Mediterranean Institute of Oceanography, Marseilles, France.

Augustine S, Nielsen LT, Riisgard K, Andersen KH, Mariani P (27-29 Aug 2014) Modelling the growth, division and starvation of D. acuminata in fed-batch cultures. 2nd International Conference on Algal Biorefinery, Tecnical University of Denmark, Lyngby, Denmark

Augustine S, Andersen KH, Berge T, Nielsen LT (6 Feb 2014) Quantifying cellular investment in autotrophic and heterotrophic machineries for Dinophysis and Karlodinium. Invited speaker at Algae Seminar, DTU Env, Lyngby, Denmark

Zimmer EI, Jager T, Kooijman SALM, Augustine S (26-29 Aug 2013) How to identify the metabolic mechanism of action (mMoA) from toxicity data? Comparing species and effects in a DEB framework. International Conference MPDE’13, Osnabrück University, Germany

Outreach: Teaching of DEB theory concepts

8th international DEB course (20 – 27 April 2015) Aix-Marseille University, France. Lectures and practical exercises.

Copenhagen University DEBtox course (5 – 13th august 2014) Roskilde, Denmark. Lectures and practical exercises.

MEMS summer school (29th August – 02 September 2016) Plouzané, Brest. Lectures and practical exercises.

Guest lecture (6 June 2014) Ocean Life Day Masters course, Charlottenlund, Denmark

Copenhagen University DEBtox course (9 – 16th august 2016) Holbæk, Denmark. Lectures and practical exercises.

6.4 Hydrodynamics of zooplankton

Navish Wadhwa, past PhD student
Employment period: 1 August 2012 - 31 July 2015
Supervisors: Anders Andersen (DTU Physics), Tomas Bohr (DTU Physics) and Thomas Kiørboe (DTU Aqua).
Graduation date: 22 October, 2015
Current position: Postdoctoral fellow, Harvard University

Description of project:
My PhD work aimed at a fluid dynamic investigation of the swimming and feeding behavior of zooplankton to assess the trade-offs associated with these processes. Since zooplanktons inhabit an aquatic environment, hydrodynamics plays a dominant role in all the life processes of the zooplankton, ranging from locomotion, feeding to mate finding and reproduction. This necessitates a physics based investigation of the traits and tradeoffs associated with these processes and calls for interdisciplinary research.

Main results:
As the first step into understanding the fluid dynamics of zooplankton, we studied copepods. Copepods are the dominant zooplankton group among the marine plankton and are one of the most evolutionary successful groups on the planet. They play an important role in the food-web by forming a link between the primary producers (autotrophs and mixotrophs) and the higher organisms such as fish, which largely feed on copepods. Within its life cycle, a copepod goes through drastic changes in size, shape and swimming mode. In particular, there is a stark difference between the early (nauplius) and later (copepodid) stages. We expected the life stage related changes experienced by a copepod to result in hydrodynamic and energetic differences.

To quantify these traits and to identify the tradeoffs, we measured the swimming kinematics and fluid flow around jumping *Acartia tonsa* at different stages of its life cycle, using flow velocimetry. We found that the flow structures formed around nauplii and copepodids are topologically different, with one and two vortex rings, respectively. Our measurements suggest that copepodids cover a larger distance compared to their body size in each jump and are also hydrodynamically quieter, as the flow disturbance they create attenuates faster with distance. Also, copepodids are energetically more efficient than nauplii, presumably due to the change in hydrodynamic regime accompanied with a well-adapted body form and swimming stroke. Thus, through this work, we have for the first time quantified the hydrodynamic traits associated with the coupling of ontogenetic development and swimming in copepods.

While it appears that the nauplii are consistently worse than copepodids and adults in swimming related traits, we found some evidence of the superiority of nauplii compared to other planktonic life forms. Through a cross-species investigation, we noticed that while many other planktonic swimmers produce hydrodynamic disturbances decaying with the inverse of the distance or the distance square, for nauplii it decayed as inverse of the distance cubed. Motivated by this finding, we demonstrated that a simple three force based model of a swimming organism which uses breast stroke type kinematics explains the observations. From analyzing the model, we found that the fluid disturbance in both the near field and the far field are significantly reduced by appropriately arranging the propulsion apparatus. These results suggest that breast stroke swimming, common in crustacean nauplii and many other planktonic organisms, may have evolved due to pressures of reducing the hydrodynamic disturbances to avoid predation.

As a part of the centre-wide “Size in the ocean” project, Erik Martens and I let the subgroup which worked on size and senses in the ocean. The broad idea was to understand the physical and physiological phenomena which enable the use of different senses (chemosensing, mechanosensing, vision etc.) by aquatic organisms, and how size of the organism affects these phenomena. The goal was to identify the limiting sizes for each of the senses investigated, based on the physical principles, and compare the predictions with the observations from nature. We identified the physical processes involved in all the major senses and evaluated the tradeoffs (e.g. resolution vs metabolic cost) associated with these, resulting in identification of upper and lower size limits for the usability of the senses.

Dissemination:
Scientific publications:

Wadhwa N, PhD thesis: Hydrodynamics of zooplankton (August 2015)

Martens EA, Wadhwa N, Jacobsen NS, Lindemann C, Andersen KH, Visser A, 2015, Size structures sensory hierarchy in ocean life, Proceedings of the Royal Society B (282), 20151346.
Significance and relevance: Provides a physical explanation of crossovers between dominant sensory modalities as a function of size.

Andersen KH, Berge T, Gonçalves RJ, Hartvig M, Heuschele J, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer AB, Olsson K, Palacz A, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T, 2016, Characteristic sizes of life in the oceans, from bacteria to whales, Annual Review of Marine Science (8), 217-241,
Significance and relevance: Provides a comprehensive explanation for the emergence of traits and crossovers as a function of size across the whole marine animal kingdom.

Andersen A, Wadhwa N, Kiørboe T, 2015, Quiet swimming at low Reynolds number, Physical Review E (91), 042712.
Significance and relevance: Provides a theoretical explanation of the observed flow fields around breast stroke swimmers and demonstrates the role of spatial organization of propulsive apparatus in determining the hydrodynamic characteristics of microbial swimming.

Kiørboe T, Jiang H, Gonçalves RJ, Nielsen LT, Wadhwa N, 2014. Flow disturbances generated by feeding and swimming zooplankton, PNAS (111), 11738-11743
Significance and relevance: Presents experimental evidence and quantification of hydrodynamic tradeoffs associated with feeding and swimming in marine zooplankton. It is shown that the modes of propulsion combined with feeding, though advantageous for food intake, have a high hydrodynamic disturbance, thus jeopardizing the survival.

Wadhwa N, Andersen A, Kiørboe T. 2014, Hydrodynamics and energetics of jumping copepod nauplii and adults, Journal of Experimental Biology (217), 3085-3094
Significance and relevance: Direct measurement of the hydrodynamic traits associated with swimming in copepods, evaluated from the perspective of ontogenetic development.

Articles in conference proceedings and newsletters

Wadhwa N, Kiørboe T, Andersen A, 2015, Hydrodynamics of stealthy propulsion by plankton, EUROMECH newsletter (46), 28-36.

Ergin FG, Watz BB, Wadhwa N, 2015, Pixel-accurate dynamic masking and flow measurements around small breaststroke-swimmers using long-distance MicroPIV, International Symposium on Particle Image Velocimetry - PIV15, Santa Barbara, CA.

Presentations at conferences, seminars etc.

Wadhwa N, Andersen A, Kiørboe T, 2014, How to be invisible as a microscopic swimmer (talk). 67th Annual Meeting of American Physical Society's Division of Fluid Dynamics, San Francisco, CA

Wadhwa N, Andersen A, Kiørboe T, 2014, Hydrodynamics and energetics of jumping copepod nauplii and adults (talk). 10th European Fluid Mechanics Conference, Kgs. Lyngby, Denmark.

Wadhwa N, Andersen A, Kiørboe T, 2014, How plankton hide: swimming quietly at low Reynolds numbers (talk). Active Fluids Workshop, Mariehamn, Aaland.

Wadhwa N, Andersen A, Kiørboe T, 2013, Swimming by jumping in marine zooplankton (poster). International workshop on Trait-based approaches to Ocean Life, Copenhagen, Denmark.

Wadhwa N, Andersen A, Kiørboe T, 2013, Size dependent flow structure changes in swimming copepods (poster), Microscale interactions in aquatic environments, Les Houches, France.

Outreach: Public talks and popular article:

Guest Lecturer, Introduction to Biophysics course, DTU, Kgs. Lyngby, October 2014.

Guest Lecturer, Physical Oceanography course, DTU, Charlottenlund, October 2014.

“Future academy press conference” with student journalists, EuroScience Open Forum 2014.

Guest Lecturer, Introduction to Biophysics course, DTU, Kgs. Lyngby, October 2013.

Guest Lecturer, Physical Oceanography course, DTU, Charlottenlund, October 2013.

Honors and Awards:

Young Scientist Award, European Fluid Mechanics Conference, Copenhagen, Denmark, 2014

Best poster award, DTU Physics Conference, Kgs. Lyngby, Denmark, 2013

6.5 Behaviour as key trait in zooplankton: trade-offs of different motile behaviours in copepods

Hans van Someren Gréve, PhD student
Employment period: 1 May 2014 – 30 April 2017
Supervisors: Thomas Kiørboe and Rodrigo Almeda (DTU Aqua).

Description of project:

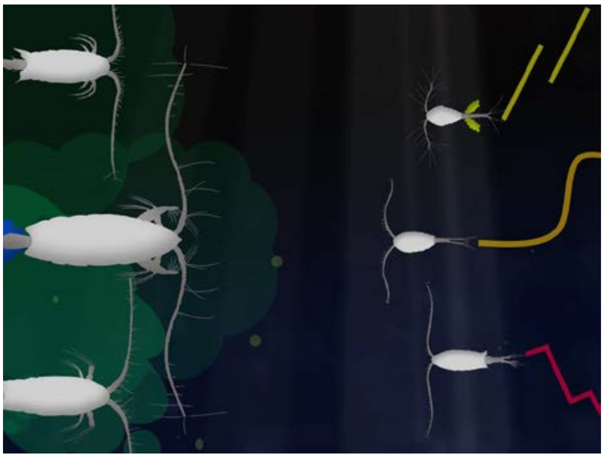


Figure 1 Copepods have to trade-off between feeding and survival. Behavioral differences between copepods (right) influence encounter probability with their prey and predators (left)

Feeding, reproduction and survival are the three main objectives in the life of any organism. However, every organism faces conflicts, or trade-offs between these objectives and all cannot be optimized simultaneously. Copepods exhibit three different ways of feeding which are inextricably linked to their motility behavior. They generate a feeding current, they cruise through the water searching for prey (or ´active` feeding strategies), or they wait motionless in the water and ambush passing prey (or ´passive´ feeding strategies). Each of these feeding modes has specific trade-offs between feeding efficiency, meeting mates and the risk of being predated and has certain metabolic expenses.

In general, passive feeders feed less efficient on immotile prey compared to active strategies; however the feeding dependent energetic investment and the theoretical predation risk are lowest. Active feeding strategies on the other hand feed more efficiently, but theoretically have higher predator encounter rates. Especially for male copepods these different feeding strategies imply a difference in conflict between time spend on feeding and mate searching. Mate-searching males have to sacrifice feeding in order to find females and simultaneously increase predator encounter rates.

Although predation is considered as a major contributor to copepod mortality in the field, empirical evidence on the influence of copepod feeding behavior and gender dependent behavior on predation risk is scarce. Further, feeding rates are thoroughly studied for female copepods, whereas studies on feeding of instar stages and males are rare. Therefore, the general goal of my research is generate empirical data on these important trade-offs in copepods and to contribute to the development of trait based models for marine ecosystems. This will be achieved by experimental quantification of the trade-offs between 1) feeding efficiency and 2) predation risk for copepods with different feeding behaviors and between genders.

Achieved results:

1) We experimentally quantified feeding rates associated with the main copepod feeding strategies using prey of different sizes and with different motility characteristics. In general feeding rates increased with increasing life stage. Size specific feeding rates on motile prey do not differ between feeding strategies, whereas ambush feeders have a significantly lower feeding rate on immotile prey (diatoms). Furthermore, males have lower feeding rates than females, which can be generally explained by the size difference between sexes for all feeding strategies. However, the feeding efficiency of mate searching

males (ambush feeders) is lower than for females as it sacrifices efficient feeding for ca. 30% of the time to actively search for mates.

2) We experimentally tested a behavior-dependent encounter model that considers fluid signal generation and perception as well as encounter velocities to predict predation risk in planktonic copepods. We used prey and predator motility characteristics obtained by low and high-speed video-observations as input to the model and conducted bottle incubation predation experiments to determine predation risk associated with i) differences in feeding strategy (active vs. passive feeders) and with ii) gender differences in mate searching behavior. Observed predation risk varied significantly with behavior and was well predicted by our model. Specifically, we found higher predation risk for copepods with active compared to passive feeding strategies, and higher predation risk in mate-searching males than in females.

Overall, our results demonstrate that behavior is a key factor which influences trophic interactions and inter- and intraspecific population structure in zooplankton communities.

Dissemination:

Scientific publications:

Kiørboe T, Gonçalves RJ, Couespel D, van Someren Gréve H, Saiz E, Tiselius P (2016). Prey perception in feeding-current feeding copepods. Limnol Oceanogr. 61 (4): 1169-1171
Significance and relevance: Explains what mechanism governs prey perception in copepods and why other mechanisms are less likely to be dominating.

Gonçalves RJ, van Someren Gréve H, Couespel D, Kiørboe T (2014). Mechanisms of prey size selection in a suspension feeding copepod, *Temora longicornis*. Mar Ecol Prog Ser. 517: 61-74
Significance and relevance: Provides the mechanistic underpinning of the prey size spectra of an important group of zooplankton; significant for development of size-based ecosystem models.

Almeda R, van Someren Gréve H, Kiørboe T (Accepted). Behavior is a major determinant of predation risk in zooplankton. Ecosphere
Significance and relevance: Provides proof on the relation between zooplankton motility behavior and predation risk and an explanation for the observed skewed sex-ratio in plankton communities; significant for the development of trait-based models.

van Someren Gréve H, Almeda R, Kiørboe T (Submitted). Motile behavior and predation risk in planktonic copepods. Limnol Oceanogr
Significance and relevance: Provides proof on the relation between zooplankton motility behavior and predation risk and an explanation for the observed skewed sex-ratio in plankton communities; significant for the development of trait-based models.

Manuscripts in preparation:

van Someren Gréve H, Almeda R, Kiørboe T. Gender dependent feeding behavior in planktonic copepods
Significance and relevance: Provides empirical data on gender dependent feeding rates of an important group of zooplankton; significant for the development of size and trait-based ecosystem models.

van Someren Gréve H, Almeda R, Kiørboe T. The risk of feeding: feeding activity dependent predation risk in zooplankton
Significance and relevance: Provides insight on how prey abundance affects copepod behavior and consequently their susceptibility to predation by higher trophic levels. Significant for the development of trait-based ecosystem models.

Almeda R, van Someren Gréve H, Kiørboe T. Behavior dependent feeding efficiency and saturation food levels in marine planktonic copepods.
Significance and relevance: Provides empirical evidence on feeding rates of an important group of zooplankton; significant for the development of size and trait-based ecosystem models.

Presentations at conferences, seminars etc.:

van Someren Gréve H, Almeda R, Kiørboe T. *Gender differences in copepod feeding behavior.* Scientific Seminar, part of the PhD course: Aquatic science and living resources-research communication (25801), Hirsthals, Denmark, September 2014.

van Someren Gréve H, Almeda R, Kiørboe T. *Gender dependent differences in feeding and predation risk in copepods*. Poster presentation, Ocean Life annual Retreat, Holbæk, Denmark, December 2014

van Someren Gréve H, Almeda R, Kiørboe T. *Behaviour-dependent predation risk in marine planktonic copepods*. ASLO Aquatic Sciences Meeting, Granada, Spain, February 2015

van Someren Gréve H, Almeda R, Kiørboe T. *Behavior-dependent predation risk in marine planktonic copepods.* Scientific Seminar, part of the PhD course: Aquatic science and living resources-research communication (25801), Charlottenlund, Denmark, September 2015

van Someren Gréve H, Almeda R, Kiørboe T. *Behavior-dependent predation risk in marine planktonic copepods.* Ocean Life annual Retreat, Holbæk, Denmark, December 2014

van Someren Gréve H, Almeda R, Kiørboe T. *Behavior as key trait in zooplankton predation risk.* Poster presentation, NAEM Netherlands Annual Ecology Meeting, Lunteren, The Netherlands, February 2016

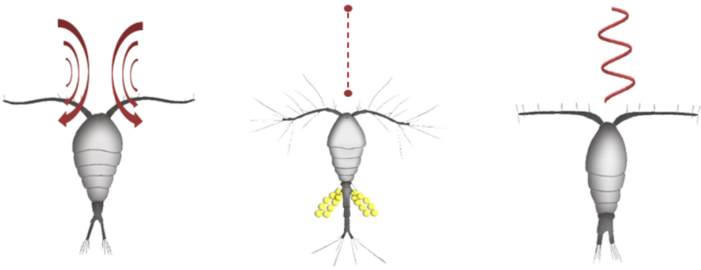
van Someren Gréve H, Almeda R, Kiørboe T. *Behavior-dependent predation risk in marine planktonic copepods - an experimental and modelling approach.* ICES/PICES 6th Zooplankton Production Symposium, Bergen, Norway, May 2016

Scientific outreach:

EUSO 2017, Copenhagen, Denmark . EUSO is the European Union Science Olympiad for second level school science students and will be hosted by DTU in 2017. I developed a mathematical task, which will be part of the ´science-based challenges´ the students will be confronted with. Recent work on ´copepod escape responses´ is used and put it in perspective of the suitability of copepods as food source in the sustainable cultivation of fish.

6.6 Behavior as a key trait in zooplankton: tradeoffs of different motile behaviors in copepods

Rodrigo Almeda, Post Doc.
Employment period: 1 May 2014 – 30 September 2017
Supervisors: Thomas Kiørboe (DTU Aqua).



This project will be conducted from May 2014 to Sept 2017 and is funded by 2 grants:

1) DFF-FNU postdoctoral grant from The Danish Council for Independent Research.
2) MARIE CURIE IIF fellowship from the “7th European Community Framework Programme”, EU.

Description of project:

The present project aims to experimentally quantify the tradeoffs (i.e., feeding efficiency vs. metabolic cost and mortality risk) of motile behaviors associated with (i) mating and (ii) feeding strategy (i.e. ambush feeders vs feeding-current vs cruising feeders) in zooplankton. The trait of relevance in this project is motile behavior of zooplankton. The copepods *Temora longicornis* (feeding-current feeder), *Oithona nana* (ambush feeder) and *Centropages hamatus* (cruising feeder) were used as model organisms. Our general goal is to increase our understanding on predator-prey interactions in the ocean and the factors that govern the structure and function of plankton food webs. The results will help further development of trait-based models for marine zooplankton.
The specific objectives of the project are to:

1. Estimate the feeding efficiency of different feeding strategies in copepods depending on prey type.
2. Determine the predation risk associated with each feeding mode or gender-dependent behaviour.
3. Quantify the metabolic cost of the different motile behaviours in zooplankton.
4. Generalization of experimental results using simple models and implement the behaviour trade-offs in models of zooplankton trait distributions.

Progress of the project towards objectives:
Most of the experimental research proposed in the project has been successfully completed. We conducted 127 laboratory experiments and analysed 2500 samples. I summarize here the main tasks conducted for each specific objective and some main results:
Objective 1: We conducted 54 functional feeding response experiments with nauplii, copepodites, males and females of copepods with different feeding behaviour using four prey types. Clearance and ingestion rates of the studied copepods in relation to food concentration followed functional responses type II or III, depending on species, stage and prey type. We found similar feeding efficiency (in terms of maximum clearance rates, F_{max}) among the studied feeding behaviours when prey are motile (Fig 1 B, C, D). On contrast, ambush feeding was significantly less efficiency than feeding-current feeding and cruising feeing for non-motile prey (diatom *T. weissflogii*. Fig. 1, A). Additionally, even though this was part of the initial specific objectives, we are analysing samples to estimate growth rates and gross growth efficiencies of nauplii with different behaviours feeding on different prey.

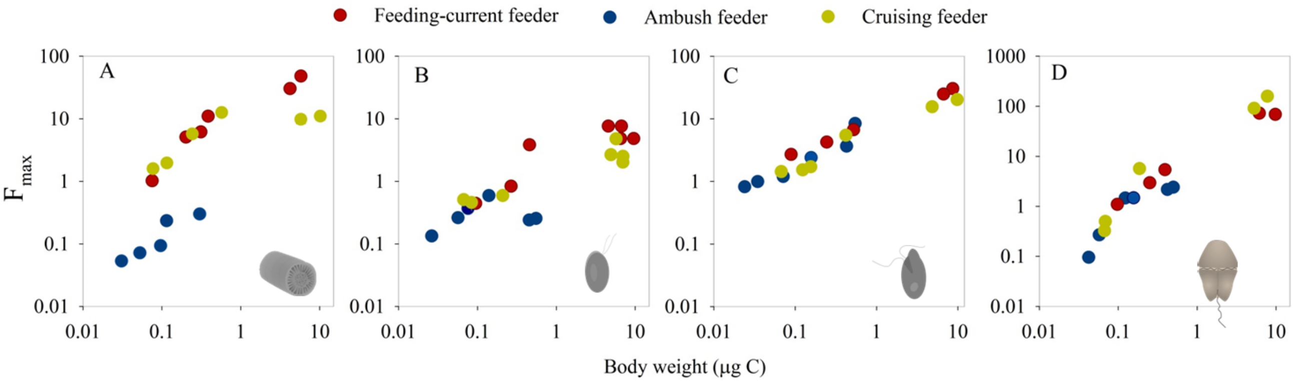


Fig. 1. Feeding efficiency (estimated as maximum clearance rates, $\mathbf{F_{max}}$,) of copepods with different feeding behaviour in relation to body weight feeding on 4 different prey: non-motile diatom *T. weissflogii*, 14 µm (**A**), flagellate *R. salina*, 7 µm (**B**); and dinoflagellates *O. marina*, 16 µm (**C**) and *A. sanguinea*, 42 µm (**D**).

Objective 2: We conducted 34 video filming experiments and 29 predation experiments to determine predation mortality associated with (i) feeding activity (ambush feeders vs feeding-current vs. cruising feeders) and (ii) mate finding behaviour (males vs females). The copepods *Oithona nana*, *O. davisae* (ambush feeders), *Temora longicornis* (feeding-current feeder), and *Centropages hamatus* (cruising feeder) were used as prey for different predatory copepods. We quantified motility behavior of copepods with the three main zooplankton feeding strategies and four reothactic predators using video observations. Copepods with “active” feeding behaviours (feeding-current and cruising feeders) showed significantly higher mortality from predation (~2-8 times) than similarly sized copepods with low motility feeding behaviour (ambush feeders) (Fig. 2A). Copepod males, which have a more active motile behaviour than females (mate-seeking behaviour), suffered a higher predation mortality than females in most of the experiments (Fig. 2 B). However, the predation risk for mate-searching behaviour in copepods varied depending on feeding behaviour with ambush feeders consistently having the greatest difference in predation mortality between genders (~4 times higher for males than for females) (Fig. 2 B). This gender-specific predation pressure may partially explain field observation of female biased sex ratios in ambush feeding copepods (e.g. Oithonae). Overall, our results demonstrate that small-scale motile behaviour significantly affects decisively predation risk and therefore is a main determinant of distribution and composition of zooplankton communities in the ocean.

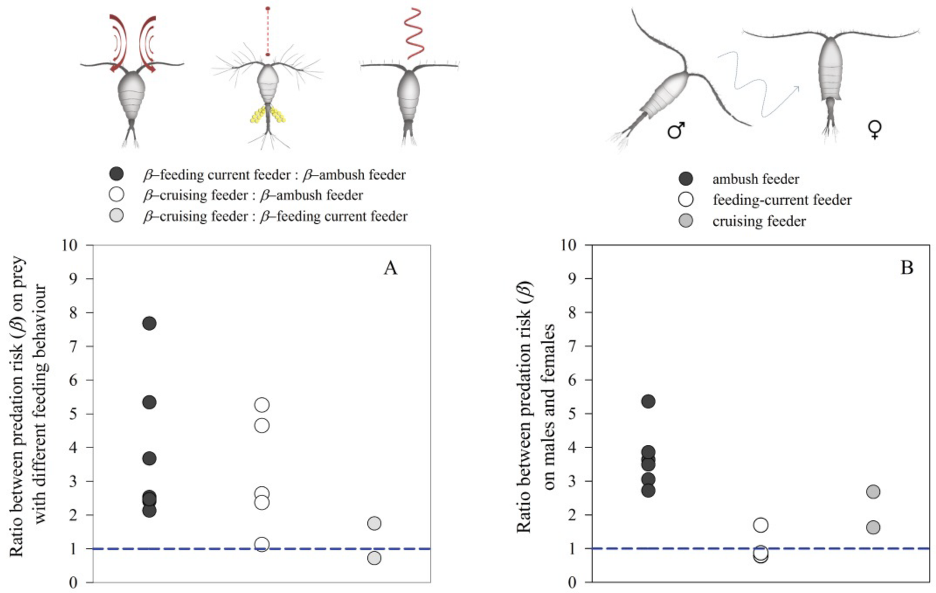


Fig. 2. Ratios between predation risk, estimated as predator maximum clearance rates (β, L predator-1 d-1), on prey with different feeding behaviours (**A**) and between maximum clearance rates (β) on males and females of copepods with different behaviour (**B**). The discontinuous line indicates ratio=1, i.e., no difference on predation risk between prey.

Objective 3: We have conducted 10 respiration experiments with nauplii, copepodites and adults of the copepods with three different behaviours to evaluate the metabolic cost associated to each feeding mode. We still need to conduct more experiment to complete this objective and have consistent results. We plan to complete these experiments by the trimester of 2017. Preliminary results showed than carbon- specific respiration rates of cruising feeders and feeding-current feeders were higher than ambush feeders.

Objective 4*:* In relation with the experimental results from objective 2, we have proposed the following *prey behaviour-dependent encounter model* to predict predation risk in zooplankton:

$B = p\pi (R_1 + R_2)^2 (u^2 + v^2)^{0.5} + (1-p) \pi (R_2 + R_3)^2 u$

where B is clearance rate of a predator (assuming that all encountered prey are captured and eaten), p is the fraction of the time that prey is swimming (p is 0 for an ambusher prey, >0 and <1 for prey that swim intermittently, and 1 for a cruising prey), u is predator cruise-velocity (assuming that the predator is a rheotactic cruiser), v *is* prey swimming velocity, R_1 is predator encounter-radius (‘body size’), R_2 is the extension of the prey fluid signal that it generates when it swims and R_3 is the equivalent radius of the prey when it does not swim. We use prey and predator motility characteristics obtained by low and high-speed video observations as input to the model. Observed predation risk varied significantly with behaviour and was well predicted by our model. The implement the behaviour tradeoffs in models of zooplankton trait distributions is expected by the last trimester of project when all data will be available.

Dissemination:

Peer reviewed publications:

Almeda R., van Someren Gréve H., Kiørboe T (2016). Behavior is a major determinant of predation risk in zooplankton. *Ecosphere* (accepted).

Almeda R., Harvey T. E., Connelly T.L., Baca S., Buskey E (2016). Influence of UVB radiation on the lethal and sublethal toxicity of dispersed crude oil to planktonic copepod nauplii. *Chemosphere* 152, 446–458.

Almeda R., Connelly T.L., Buskey E. (2016). How much crude oil can zooplankton ingest? Estimating the quantity of dispersed crude oil defecated by planktonic copepods. *Environmental Pollution* 208, 645–654.

Almeda R., Connelly T.L., Buskey E. (2014). Novel insight into the role of heterotrophic dinoflagellates in the fate of crude oil in the sea. *Nature: Scientific Reports* 4, 7560

Alcaraz M., **Almeda R.**, Duarte C., Hortskotte B, Lasternas S. Agustí S. (2014). Changes in the C, N, and P cycles by the predicted salps-krill shift in the southern ocean *Frontiers in Marine Science*.

Almeda R., Bona S., Foster C., Buskey E.J. (2014). Dispersant Corexit 9500A and chemically dispersed crude oil decreases the growth rates of meroplanktonic barnacle nauplii (Amphibalanus improvisus) and tornaria larvae (Schizocardium sp.). *Marine Environmental Research* 99, 212-217.

Submitted manuscripts

van Someren Gréve H., **Almeda R.**, Kiørboe T. Motile behavior and predation risk in planktonic copepods. L&0 (2016).

Manuscripts in prep.

Almeda R. and Buskey E. Oil spills and dispersants can cause the initiation of rides tides. To be submitted to Nature Communications.

van Someren Gréve H., **Almeda R.**, Kiørboe T. Gender-specific feeding rates in planktonic copepods. To be submitted to Journal of Plankton Research.

Almeda R., van Someren Gréve H., Kiørboe T. Efficiency of different feeding behaviours in planktonic copepods. To be submitted to L&0.

Almeda R., Alcaraz M., Calbet A., Saiz E. Seasonality and vertical distribution of zooplankton in NW Mediterranean coastal waters: importance of small planktonic metazoans. To be submitted to Progress in Oceanography.

Rodriguez-Torres, R., **Almeda R**., van Someren Gréve H., Kiørboe T. Growth rates and gross growth efficiencies of copepod nauplii with different feeding behaviour. To be submitted to L&0.

Horne C., **Almeda R.**, Hirst A., Kiørboe T. Temperature-Size response in copepods with different feeding strategy.

Other expected publications at the end of the project

Almeda R., van Someren Gréve H., and Kiørboe T. Metabolic costs of different motile behaviours in zooplankton.

van Someren Gréve H., **Almeda R.**, and Kiørboe T. Predation risk associated to feeding activity in zooplankton.

van Someren Gréve H., **Almeda R.**, and Kiørboe T. Behavior as a key trait in zooplankton: tradeoffs of different motile behaviors in copepods. "Student Review" to be submitted to Marine Biology.

Holm M.W., Kiørboe T., **Almeda R.**, Hansen B.W. Behavior-dependent starvation tolerance in planktonic copepods with different overwintering and feeding strategies.

Holm M.W., **Almeda R**, Rodriguez-Torres, R., Kiørboe T., Hansen B.W. Influence of mating behaviour on starvation tolerance of planktonic copepods.

Presentations at conferences, seminars, symposiums, etc:

Almeda, R., van Someren Gréve H., Kiørboe T. Trade-offs in zooplankton feeding behaviour. ICES/PICES 6th Zooplankton Production Symposium. Bergen, Norway. May 2016.

van Someren Gréve H., **Almeda, R.**, Kiørboe T. Behaviour-dependent predation risk in marine planktonic copepods. ICES/PICES 6th Zooplankton Production Symposium. Norway. May 2016.

van Someren Gréve H., **Almeda, R.**, Kiørboe T. Behavior as key trait in zooplankton predation risk. Netherlands Annual Ecology Meeting 2016(NAEM), Lunteren, Netherlands. Feb. 2016.

van Someren Gréve H., **Almeda, R**., Kiørboe T. Behavior-dependent predation risk in marine zooplankton. DTU PhD course: 'Aquatic Science and living resources', Feb 2016, Charlottenlund, Denmark

Almeda, R., van Someren Gréve H., Kiørboe T. Behaviour-dependent predation risk in marine zooplankton: an experimental and modelling approach. ASLO-Ocean Sciences Meeting. New Orleans, USA. Feb., 2016

Almeda R., Connelly T.L., Buskey E.J. Role of crude oil ingestion by zooplankton in the fate of crude oil spills in the sea. SETAC North America 36th Annual Meeting. Salt Lake City, USA, Nov., 2015.

van Someren Gréve H., **Almeda, R.**, Kiørboe T. Gender-dependent predation risk in copepods with different motile behaviour. DTU scientific seminar: "Aquatic science and living resources-research communication". Søminestationen, Holbæk, Denmark. Sept., 2015.

Almeda R., Connelly T.L., Buskey E.J. Novel insight into the role of heterotrophic dinoflagellates in the fate of crude oil spills in the sea. 2015 Gulf of Mexico Oil Spill & Ecosystem Conference. Houston, USA, 2015

Buskey E.J., **Almeda R.**, Gemmell B.J., Katz J. Physical and chemical dispersion of marine crude oil spills and effects of dispersed oil on zooplankton. 2015 ASLO Aquatic Sciences Meeting, Granada, Spain, 2015.

van Someren Gréve H., **Almeda R.**, Kiørboe T. Behaviour-dependent predation risk in marine planktonic copepods. 2015 ASLO Aquatic Sciences Meeting. Granada, Spain, 2015.

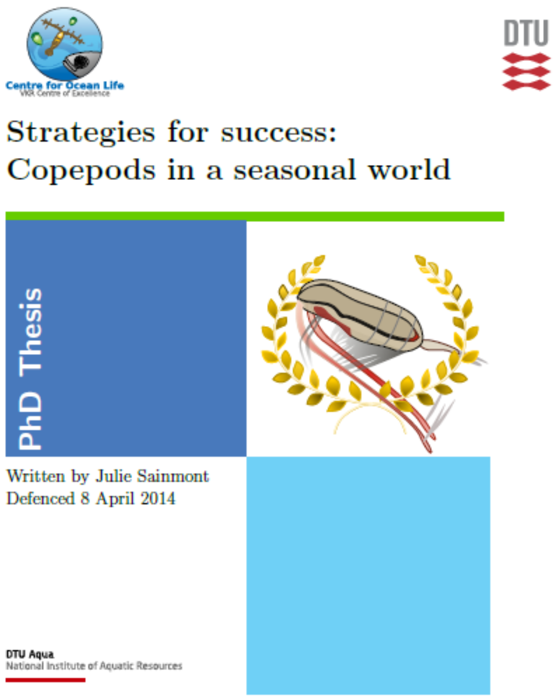
Almeda R., Connelly T.L., Hyatt C., Villarreal T., Buskey E.J. Ingestion of dispersed crude oil by zooplankton. 2015 ASLO Aquatic Sciences Meeting. Granada, Spain, 2015.

Almeda R. Ingestion, bioaccumulation and toxic effects of chemically dispersed crude oil on marine zooplankton. 2014 DTU-Seminar series Kaffeklubben. Invited speaker. Denmark, Oct. 2014.

6.7 Copepods in a seasonal world

Julie Sainmont, PhD student
Employment period: 1 December 2010 – 15 February 2014
Supervisors: André Visser (DTU Aqua) and Ken H. Andersen (DTU Aqua).

Description of project:


Centre for Ocean Life
VKR Centre of Excellence

Strategies for success:
Copepods in a seasonal world

PhD Thesis

Written by Julie Sainmont
Defenced 8 April 2014

DTU Aqua
National Institute of Aquatic Resources

Amongst the zooplankton community, copepods display complex and diverse life history strategies, which could explain their wide success in the world ocean. Specifically, in temperate and high latitude ecosystems, copepods are subject to “boom and bust" conditions where annual cycles are punctuated by a short, productive spring blooms, but with relatively little food and harsh conditions for the rest of the year. Due to their world-wide dominance in biomass, and their importance in the food webs, copepods are fairly well studied. However, the success of their complex life-history strategies remain open scientific questions, in particular, how these are attuned to environmental conditions, and how these may be compromised by climate change. Due to their ability to concentrate lipids in their small bodies, copepods are indeed of great ecological significance as they are an important link between phytoplankton production and higher trophic levels such as, seas-birds and marine mammals. Their most striking life-history trait includes multiple moulting from egg to adult stages (energetically costly but allowing them to have the most efficient shape to swim relative to their size in water), overwintering at great depth and plastic behaviors such as switching between feeding modes and daily vertical migration allowing them to quickly adapt to local conditions. Some of their life history traits also vary widely amongst species, including how resources are allocated to reproduction and size at maturity. My thesis covered two of these life-history traits: diel vertical migration and the allocation of resource to reproduction.

Diel vertical migration (DVM) strategies arise from a trade-off between feeding and predation risk - both of which tend to be maximized in the surface ocean. The latter is modulated on a day-night cycle as the efficiency of visual predators varies with ambient light. An efficient strategy is thus to migrate vertically, feeding at the surface at night, and taking refuge at depth during the day. The first part of my thesis treated DVM with some observations and models. A first study, made from a video plankton recorder in the West coast of Greenland, shows the wide range of migration patterns adopted in the zooplankton community but also within the *Calanus* copepods taxa as a function of size. A second study shows the emergence of the DVM strategy in a game theory approach, not only of the organism, but also their predator. In addition to controlling trophic transfer in marine ecosystems, DVM also plays a potential role biogeochemistry of the world´s oceans. A simple modeling method taking behavior into account in large models is therefore needed, as ocean system model are already computationally intensive. The third study investigates how well a simple (myopic) optimization of DVM compares with life-history optimization using dynamic programming. The myopic optimization shows surprisingly accurate predictive power over a large range of parameter space.

Inspired by the copepods *Calanus finmarchicus* and *C. hyperboreus,* an individual based model is used to study the success of their reproduction strategy as a function of the feeding season duration. The first of these two species is close to an income breeder, relying only on the incoming food supply, while the latter is a capital breeder, storing reserves to spawn at a time not directly dictated by food availability. Although from the same genus, their size at maturity and their distributions differ dramatically. Including behavior and energetic allocation, we thus investigate the effect of the resource allocation trait to reproduction coupled with the most suited maturity size as a function of the feeding season duration. Capital breeding favors large maturity size and is successful in short blooms, while the income breeders are favored in long blooms and benefit from small size. As the output fitness curve functions seem fairly standard, the model is simplified to an analytical approach that is used to investigate the same problem and gives similar results. The closed solutions are then used to explore the parameter space and the resulting pattern is shown to be robust.

My thesis therefore focused on two main aspects of the life-history trait of copepods: diel vertical migration and reproduction strategy. The results may be generalized and applied to other species living in a seasonal environment.

Dissemination:

Scientific publications:

Sainmont J, Thygesen UH, Visser AW. 2013. Diel vertical migration arising in a habitat selection game. Theoretical Ecology 6:241–251.
Significance and relevance: Show that diel vertical migration behaviour emerges as soon as the gain of feeding counterbalance the risk of predation for zooplankton but also for their predator. Some mixed strategies can also emerge within a population where some part of the population will perform this daily vertical migration, while the other will adopt a“sit and wait strategy”and have the same pay off.

Sainmont J, Webster C, Heuschele J, Gislason A, Sylvander P, Wang M, Varpe Ø. 2014. Inter- and intra-specific diurnal habitat selection of zooplankton during the spring bloom. *Marine Biology*
Significance and relevance: Provide the presence and absence of diel vertical migration of zooplankton community during a spring bloom in the Arctic, and the specific diurnal behviour of *Calanus* copepods as a function of their size, which is put in relation of their life history strategy.

Sainmont J, Andersen KH, Varpe Ø, Visser AW. 2014 Capital versus Income breeder in a seasonal environment. *American Naturalist.* 184: 466–476

Significance and relevance: Provide a proof of the benefit of capital versus income breeding and maturity size as a function of the feeding season duration alone. As feeding season duration can be link to latitudinal gratient, it can give an insight into the dominance of small income breeders at moderate latitude and of large capital at high latitude.

Sainmont J, Andersen KH, Thygesen UH, Fiksen Ø, Visser AW. (2015) An effective algorithm for approximating adaptive behavior in seasonal environments. Ecological Modelling. 311: 20-30.
Significance and relevance: Provides an efficient method to take an approximation of behaviour, such as diel vertical migration, into account in large computation model where techniques which gives the optimal solution are too computational demanding to be taken into account.

Andersen KH, Berge T, Goncalves R, Hartvig M, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer A, Olsson K, Payne M, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T. (2016) Characteristic sizes of life in the oceans - from bacteria to whales. Annual Review in Marine Science.
Significance and relevance: Provide a comprehensive explanation for the emergence of traits and general relationationship as a function of size across the full marine animals kingdom.

Neuheimer AB.; Hartvig M; Heuschele J; Hylander S; Kiørboe T; Olsson KH; Sainmont J, Andersen KH. (2016) Adult and offspring size in the ocean: a database of size metrics and conversion factors. Ecology 97, (4) 1083.
Significance and relevance: Provides the relationship between adult and progeny size across the marine animal kingdom.

Webster CN, Silva T, Ferreria AS, Wiedmann I, Juul-Pedersen T, Varpe Ø, Gislason A, Saiz E, Calbet A, Sainmont J, Agersted MD, Helenius L, Tammilehto A, Torstensson A, Brierley AS, Arendt KE, Nielsen TG. (submitted) Fate of an Arctic spring bloom *Marine Ecology* Progress Series. Submitted
Significance and relevance: Provide a comprehensive explanation for the emergence of traits and general relationship as a function of size across the full marine animals kingdom.

Presentations at conferences, seminars etc.:

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, T. Kiørboe. International workshop on Trait-based approaches to Ocean Life, 2013, Copenhagen. Conference abstract for conference

Feeding season duration and the relative success of capital and income spawning copepods. J. Sainmont, K. H. Andersen, Ø. Varpe, A. W. Visser. Aquatic Sciences Meeting (ASLO), 2013, New Orleans. Conference abstract for conference

Relative success of Income and Capital breeder in a seasonal environment. J. Sainmont, K. H. Andersen, Ø Varpe, A. W. Visser. International workshop on Trait-based approaches to Ocean Life, 2013, Copenhagen. Poster

Optimal foraging and diel vertical migration in a life history model. J. Sainmont, K. H. Andersen, A. W. Visser . Aquatic Sciences Meeting (ASLO), 2013, New Orleans. Poster

Outreach: Public talks and popular article:

Strategies for success: Copepods in a seasonal world. *Popular abstract linked to the PhD thesis.*

A simple analytical model explains latitudinal patterns in breeding strategies. *American Naturalist. Press Release*

Thesis:
Strategies for success: Copepods in a seasonal world (2014)

Awards:
DTU´s Young Researcher Award 2014

6.8 Zooplankton feeding traits in a global biogeochemical ocean model

Friederike Prowe, Post Doc.
Employment period: 1 February 2012 - 31 July 2014 (maternity leave 22 December 2013 - 31 July 2014)
Supervisors: Thomas Kiørboe, Ken Andersen, Andy Visser (DTU Aqua).

Description of project:

Aim
This project aims to improve the representation of plankton communities in global ocean biogeochemical models used i.a. for predicting oceanic global change. These models typically employ a reasonable variety of different phytoplankton traits in terms of different plankton functional types (PFTs), but use oversimplified descriptions of zooplankton ecology oblivious of all but the most basic traits and any trade-offs. We want to refine the zooplankton formulations by implementing feeding strategies observed in the lab and their associated trade-offs between foraging success and predation risk. We thereby upscale trade-off based individual behaviour to the global ocean and aim to assess its relevance for large-scale ecosystem functions and biogeochemical cycles.

Model design
Our main constraints for the development of the plankton model are to create a model that is 1) structurally similar to, and 2) only one step more complex than models currently employed on the global scale. Thereby we ensure that our model is readily implemented and can be easily compared to existing simplistic models and assessed in a meaningful way. The model describes the encounter between motile and non-motile predator and prey types divided in two size classes by taking into account the trade-off between foraging activity and predation risk. Active cruise feeding zooplankton feed most efficiently, but are also highly visible to predators. In contrast, passive ambush feeders are protected from predation, but also encounter less prey. Our model thus comprises four PFTs each for zooplankton and phytoplankton distinguished by the two main traits motility and size.

Seasonal dynamics
This encounter model has been developed in an idealized 0-dimensional seasonal cycle for testing parameter combinations and getting a feel for its dynamics. In a next step the model has been set up in a realistic 1-dimensional context at the time series station L4 in the western English Channel, where comprehensive datasets of phytoplankton and zooplankton with taxonomic resolution and a biweekly sampling frequency are available for several years (cooperation with A. Atkinson and C. Widdicombe, PML, UK). We have classified the taxonomic groups with respect to our traits motility and size and have thereby obtained a trait-based description of seasonal succession (Fig. 1). The model is forced by physical data from a local shelf model provided by our cooperation partners A. Hickman (Univ. Southhampton, UK) and J. Sharples (Univ. Liverpool, UK).

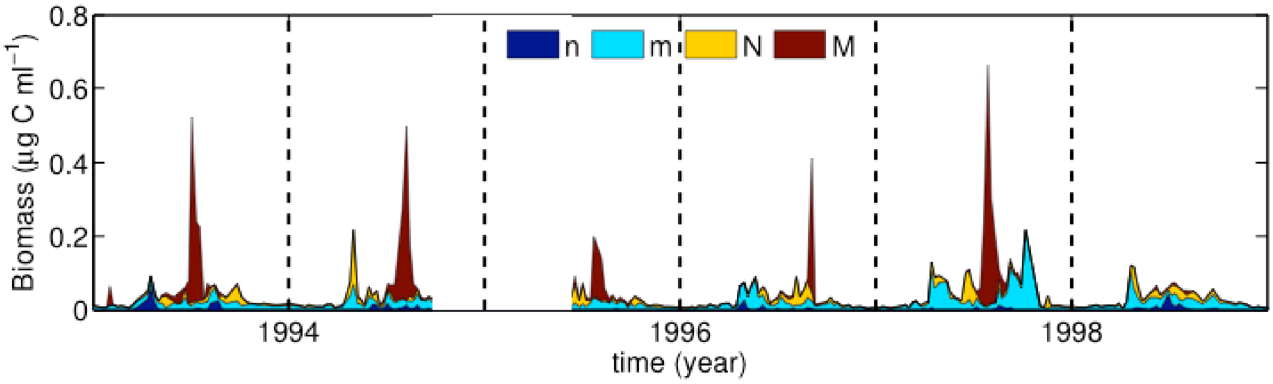


Fig. 1: Phytoplankton biomass at station L4 classified into the model PFTs small non-motile (n), small motile (m), large non-motile (N) and large motile (M). Data: Western Channel Observatory <http://www.westernchannelobservatory.org.uk>, obtained through the British Oceanographic Data Centre.

For this part of the project, we now want to proceed with model simulations of the seasonal cycle for parameter calibration in comparison to the field data. An important question is whether we can explain complex seasonal succession in a coastal environment with a simple model featuring the two traits size and motility, and top-down mechanisms like feeding strategies. The succession may in addition be controlled by bottom-up traits like nutrient affinity or light harvesting, and may be influenced by seeding from the sediment at this coastal location. Phytoplantkon bloom dynamics are being investigated by the PML partners, which will help us to understand bottom-up controls of the trait succession. Even though this potentially complex interplay of controls may complicate the analysis, the L4 data are one of the very few marine datasets that allows a characterization of traits for feeding interactions on a seasonal time scale. The trait characterization of the different plankton groups and model-based analysis of their seasonal succession is envisioned to be published together with the cooperation partners.

Biogeographical trait distributions

The encounter model has also been implemented in the global model framework of the MITgcm (in cooperation with S. Dutkiewicz and M. Follows at MIT, USA) and is being evaluated under realistic environmental conditions. The global model simulates distinct biogeographies of both phytoplankton and zooplankton traits, distinguishing oligotrophic and more productive oceanic regions. Predicted patterns of zooplankton feeding strategies agree well with patterns estimated from observed copepod abundances (Fig. 2). The resulting phytoplankton size structure is overall realistic in contrast to simulations with a simplistic standard zooplankton model typically employed in global ocean ecosystem models. Sensitivity experiments have shown that the model is sensitive to particular zooplankton feeding traits (e.g. the threshold food concentration) as well as to the trade-offs implemented for nutrient uptake and predation risk. Since appropriate observational data are scarce on this scale, an extended analysis of the model dynamics under different environmental conditions is at this point essential to obtain meaningful predictions.

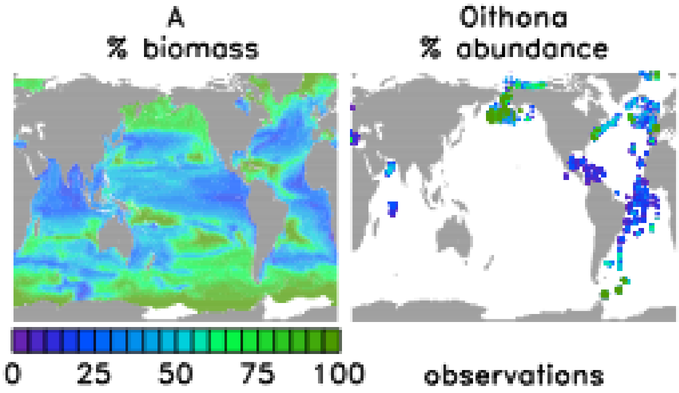


Fig. 2: Percentage of large ambushers to total zooplankton biomass in the model (left) and derived from abundance observations of the ambush-feeding genus Oithona sp. Data: NMFS-COPEPOD global plankton database <http://www.st.nfms.noaa.gov/plankton> (May 2013).

We are currently assessing the global encounter model by comparing biogeographical patterns of the PFTs in comparison to a standard model in a range of different sensitivity experiments. Observations of biomass, primary production and phytoplankton size constrain the parameter choice. In a next step, we aim to complement the global and biogeographical view by an analysis of seasonal dynamics at characteristic locations, to further understand the model's strengths and limitations. Once the model is established in this way, we aim to look at the length of the trophic chain and the export production to describe the effects of feeding traits and a trade-off base description on ecosystem functions and biogeochemical cycles. The global model results will be published in a first paper focussing on model establishment and assessment, with effects on the ecosystem and biogeochemical cycles combined or or in a separate publication.

Dissemination:

Scientific publications:

Prowe AEF, Pahlow M, Dutkiewicz S, Oschlies A (2014). How important is diversity for capturing environmental-change responses in ecosystem models? Biogeosciences 11(12), 3397-3407, doi: 10.5194/bg-11-3397-2014.
Significance and relevance: demonstrates using phytoplankton as example group that traits and trade-offs between model groups determine the ability of a global model to capture ecological effects, i.e. plankton diversity effects on ecosystem functions.

Prowe AEF, Andersen KH, Visser AW, Kiørboe T (planned). Global biogeography of zooplankton feeding traits.
Significance and relevance: upscale from individual trait-based interactions to global patterns and relevance for ecosystem functions and biogeochemical cycles.

Prowe AEF, Andersen KH, Visser AW, Atkinson A, Hickman A, Sharples J, Widdicombe C, Kiørboe T (planned). Trait-based plankton seasonal succession and its control by feeding strategies at station L4.
Significance and relevance: establishes a trait characterization relevant to feeding interactions and describes their influence on seasonal succession and community composition.

Presentations at conferences, seminars etc.

Prowe AEF, Andersen KH, Kiørboe T, Visser AW. Better (?) zooplankton in a global biogeochemical ocean model. Presentation, Danish Marine Modelling Centre (DMC) joint meeting, 29/11 2012, Aarhus University in Roskilde, Risø, Denmark

Prowe AEF, Andersen KH, Kiørboe T, Visser AW. Zooplankton feeding traits and community composition in a global ecosystem model. Presentation, 45th International Liège Colloquium, 16/5 2013, Liège, Belgium.

Prowe AEF, Pahlow M, Oschlies A. Phytoplankton community effects on productivity changes in a global reduced mixing scenario. Poster, 45th International Liège Colloquium, 16/5 2013, Liège, Belgium.

Prowe AEF, Andersen KH, Kiørboe T, Visser AW. Zooplankton feeding traits and community composition in a global ecosystem model. Poster, International Workshop on Trait-based approaches to Ocean Life, Copenhagen

Lindemann C, Palacz A, Prowe F. Towards an adaptive evolutionary and ecological trait-based model. Poster, International Workshop on Trait-based approaches to Ocean Life, Copenhagen

Prowe AEF, Andersen KH, Kiørboe T, Visser AW, Dutkiewicz S, Follows M. Trait-based trophic interactions in a global ecosystem model. Presentation, 29th Annual Meeting of the German Limnological Society & 43rd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, 9/11 2013, Potsdam, Germany.

6.9 Traits and trade-offs in microzooplankton grazing

Lasse Tor Nielsen, Post Doc.
Employment period: 1 March 2013 – 31 December 2017
Supervisors: Thomas Kiørboe (DTU Aqua) and Anders Andersen (DTU Physics).

Description of project:

My project aims to describe and understand various microzooplankton grazing techniques, and to quantify the traits and trade-offs associated with each of them. Microzooplankton deploy various prey capture techniques, ranging from single cell predation using some form of ambush feeding, to filtering of water masses followed by collection and ingestion of the prey particles retained. With the former, prey cells are often almost as large as or even larger than the predator, whereas prey cells are typically one order of magnitude smaller than the predator in the latter. While filter feeding is often considered the most effective in a high food environment, it also comes with several trade-offs, including the larger energy expenditure and the elevated risk of predation due to the strong hydromechanical signals produced. The trade-offs will favor different feeding strategies under various environmental conditions. I work with several microzooplankton grazers, with various prey capture techniques, to describe and understand the mechanisms involved, as well as to quantify and parameterize the associated trade-offs. High-speed videomicroscopy, micro particle image velocimetry, hydrodynamically scaled models, particle tracking and modeling of flow fields are some of the methods that we apply in order to achieve this. The ultimate aim is to improve our understanding of spatial and temporal distributions of various feeding mechanisms found in the world's oceans - today and in the future.

Results

We have shown that there is a clear trade-off between swimming and the hydrodynamic disturbances that it creates. This has sparked zooplankton organisms of all sizes to develop hydrodynamically quiet modes of propulsion – especially those which do not combine their propulsion and feeding [6].

The small grazers of the oceans are faced with the challenges of their viscous environment; the high viscosity of water makes it difficult to approach other particles, including prey items. We have demonstrated how dinoflagellates, the most important group of aquatic, unicellular grazers, manage to overcome this issue by producing near-cell feeding currents that pulls prey cells in rather than push them away [5]. Many of these dinoflagellates are mixotrophic, and thus also take up inorganic nutrients. We have also demonstrated that swimming increases this nutrient uptake rate significantly compared to a non-motile cell. There are differences, however, among dinoflagellate morphology and the flow fields that they produce, and this seems to be related to the trade-off between swimming, feeding and nutrient acquisition on one hand and the flow signals that it produces on the other.

We are currently publishing an improved mechanistic understanding of a filter-feeding microorganism, another of the few major feeding modes found among planktonic grazers [8]. Filter-feeding for bacteria-sized particles presents major challenges, since the resistance produced by a filter with adequately small-sized pores is supposedly very large. Nonetheless, several groups of filter-feeding microbes exist. We have improved our understanding of how this is possible, and thereby identified key features of filter-feeding organisms.

Our unique ability to visualize and quantify the flow fields around free-swimming flagellates using micro particle image velocimetry has also allowed us to demonstrate the hydromechanical constraints imposed on swimming and feeding of the biflagellated, mixotrophic haptophytes [1]. This has revealed strong trade-offs between efficient and quiet swimming vs. prey encounter.
I also recently contributed to a modelling study that presented the first comprehensive prediction of the structure of the auto- to heterotrophic continuum of aquatic unicellular plankton [2]. This is one of the first fully fledged attempts to predict marine plankton biodiversity in time and space using a trait based approach.
We have also helped shed light on the workings of so-called kleptochloroplasts, or stolen chloroplasts [3 & 7]. A few aquatic unicellular organisms are able to perform the remarkable feat of stealing the chloroplasts of their prey, and utilize them for photosynthesis rather than digest them. This is important to the understanding of the evolution that led from bacteria to all other, more complex, life forms.

Ongoing scientific work

We have several manuscripts in preparation: Our work on dinoflagellate feeding [3], has revealed a significant gap in the knowledge about how dinoflagellates swim. What is the morphology, and what forces propel them forward? Mophological details were revealed in the 1980s by biologists with scanning electro microscopes, but these details have never been deployed to obtain a mechanistic understanding of dinoflagellate swimming. It is not even known which of their two flagella contributes the primary propulsive force. A few different, rather distinct, morphological types exist, and this could be coupled to the way they swim. The centre, with its pronounced interdiciplinarity, provides an excellent opportunity for biologists and physicists to collaborate to solve this issue, and most of the data have already been collected [10 & 13]. I'm also currently visualizing and quantifying the flow fields around many different free-swimming flagellates in order to identify and quantify traits and trade-offs broadly within this group [11 & 12]. I speculate that the various (highly different) flagellar arrangements will affect the near-cell flow fields, and hence the ability to encounter prey, remain hydromechanically silent and take up inorganic nutrients. It seems obvious that there should be trade-offs between the different arrangements.

Dissemination:

Scientific publications:

Published:

[1] Dölger J, Nielsen LT, Kiørboe T & Andersen A. (In press) Swimming and feeding of mixotrophic biflagellates. Scientific Reports.
Significance and relevance: Identifies and quantifies traits and trade-offs in swimming and feeding of one of the most abundant groups of marine plankton. Quantifies swimming velocity, hydrodynamic strealth and prey capture as a function of flagellar arrangements.

[2] Chakraborty S, Nielsen LT & Andersen KH. (In press) Trophic strategies of unicellular plankton. American Naturalist.
Significance and relevance: The first comprehensive prediction of the structure of the auto- to heterotrophic continuum of aquatic unicellular plankton.

[3] Hansen PJ, Ojamae K, Berge T, Trampe E, Nielsen LT, Lips I & Kühl M (2016) Photoregulation in a kleptochloroplastidic dinoflagellate, *Dinophysis acuta*. Frontiers in Microbiology 7, 785.
Significance and relevance: Show how a dinoflagellate which steals its chloroplasts, is able to regulate and maintain them for extended periods of time. Sheds light on the evolution of cell organelles. Important for the understanding of the workings of mixotrophic organisms.

[4] Nielsen LT, Hansen PJ, Krock B & Vismann B. (2016) Accumulation, transformation and breakdown of DSP toxins from the toxic dinoflagellate *Dinophysis acuta* in blue mussels, *Mytilus edulis*. Toxicon 117, 84–93.
Significance and relevance: First laboratory study to demonstrate how mussels are intoxicated with DSP-toxins from Dinophysis spp. and the following depuration. Relevant to biotoxins, bioaccumulation, harmful algal blooms, and the transfer of biotoxins to human consumers of seafood.

[5] Nielsen LT & Kiørboe T (2015) Feeding currents facilitate a mixotrophic way of life. ISME Journal. 9, 2117–27.
Significance and relevance: Provides mechanistic understanding of the feeding modes in the most important group of single-celled marine grazers; significant for development of feeding mode based ecosystem models.

[6] Kiorboe T, Jiang H, Goncalves RJ, Nielsen LT & Wadhwa N (2014) Flow disturbances generated by feeding and swimming zooplankton. Proc Natl Acad Sci 111.
Significance and relevance: Demonstrates that there is a trade-off between swimming and the fluid disturbances that it creates. Underpins that this has shaped the evolution of aquatic life. Relevant to development of feeding-mode ecosystem models.

[7] Hansen PJ, Nielsen LT, Johnson M, Berge T & Flynn KJ (2013). Acquired phototrophy in Mesodinium and Dinophysis – A review of cellular organization, prey selectivity, nutrient uptake and bioenergetics. *Harmful Algae*, *28*, 126–139.
Significance and relevance: Provides a review of the rare phenomenon of stolen chloroplasts in two ubiquotous, harmful algal species. Important for the understanding of the workings of mixotrophic organisms and the evolution of all eukaryotic life.

Submitted:

[8] Nielsen LT, Dölger J, Kiørboe T & Andersen A. (Submitted) Hydrodynamics of microbial filter-feeding. PNAS.
Significance and relevance: Choanoflagellates perform filter-feeding where it should not (seen from a physicist’s viewpoint) be possible. We show how choanoflagellates circumvent the laws of physics, and what enables them to perform such small-scale filter feeding. Important to the understanding of the spatial and temporal distribution of filter-feeders.

[9] Xu J, Hansen PJ, Nielsen LT, Krock B, Tillmann U & Kiørboe T. (Submitted) Distinctly different behavioral responses of a copepod, *Temora longicornis*, to different strains of toxic dinoflagellates, *Alexandrium* spp. Harmful Algae.
Significance and relevance: We demonstrate several different copepod behaviours in response to algae with diffent PSP toxin profiles. Results elucidate some of the ecological and evolutionary roles of phytoplankton defence mechanisms.

In progress:

[10] Nielsen LT, Scheuch R, Humpries S, Smith D & Kiørboe T. How dinoflagellates swim. Elife. Target date: 31 Dec 2016.
Significance and relevance: Elucidate how dinoflagellates, propel themselves forward. By gaining a mechanistic insight, we will also be able to identify crucial elements of dinoflagellate morphology and function, and show how these interplay to secure optimum swimming and feeding.

[11] Nielsen LT, Dölger J, Andersen A & Kiørboe T. Direct measurements of flow fields reveal trade-offs in flagella arrangement. PNAS. Target date: 31 Dec 2016.
Significance and relevance: Identifies and quantifies traits and trade-offs in swimming and feeding among all marine planktonic flagellates. Quantifies swimming velocity, hydrodynamic strealth and prey capture as a function of flagellar arrangements, and thus elucidates what each of these arrangements are optimized for.

[12] Nielsen LT, Almeda R & Kiørboe T. Quatifying trade-offs in microzooplankton swimming and feeding. Target date: 30 June 2017
Significance and relevance: Quantifies the increased risk of predation to marine protists in response to swimming and feeding activities.

[13] Scheuch R, Nielsen LT, Humpries S, Smith D & Kiørboe T. Optimizing the dinoflagellate design. . Target date: 31 July 2017.
Significance and relevance: Thousands of dinoflagellate species share a very distinct flagellar arrangement. We explore this arrangement with regards to optimal feeding and swimming. The study reveals the competietive advantages of this design, and explains how dinoflagellates has managed to atain some of the largest cell sizes among motile unicellular plankton.

Presentations at conferences, seminars etc.

Nielsen LT, Dölger J, Andersen A & Kiørboe T. (Oct-Nov 2016) Prey Capture at Low Reynolds Number. Oral presentation at Microscale Ocean Biophysics. Eilat, Israel.

Nielsen LT, Andersen A & Kiørboe T. (Feb 2015) Dinoflagellates create flows that mediate feeding and nutrient uptake. Oral presentation at Association for the Sciences of Limnology and Oceanography. Granada, Spain

Nielsen LT, Andersen A, Bohr T & Kiørboe T (26-28 Aug 2013) Traits and trade-offs in microzooplankton feeding modes: from filter feeding choanoflagellates to ambush feeding dinoflagellates. Poster at Workshop on Trait-based approaches to Ocean Life, Copenhagen.

Nielsen LT, Couespel D, Haaning K, Aagaard J, Thomsen HA, Andersen A & Kiørboe T (May 22-25 2013) Hydrodynamics of choanoflagellate feeding. Oral presentation at the 2013 International Choanoflagellate Workshop, Cologne, Germany.

Outreach: Public talks and popular article

Dansk Naturvidenskabsfestival, 2014-2016: Ten 2-hour presentations at high schools in and around Copenhagen. Title: “Tales from the plankton”. Collectively more than 400 high school students.

Kiørboe T & Nielsen LT. (2015) Forskere afslører flagellaternes hemmelighed. Populærvidenskabelig artikel på http://videnskab.dk/miljo-naturvidenskab/forskere-afslorer-flagellaternes-hemmelighed

ESOF Copenhagen June 21–26, 2014: Presentation of Centre for Ocean Life and my work to the general public at R/V DANA open ship.

Nielsen LT & Kiørboe T. (2013) Plankton med Helgardering. Populærvidenskabelig artikel i Weekendavisen 2. august 2013.

6.10 Hydrodynamics of small marine organisms

Julia Dölger, PhD student
Employment period: 15 December 2014 – 14 December 2017
Supervisors: Anders Andersen (DTU Physics), Thomas Kiørboe (DTU Aqua), Tomas Bohr (DTU Physics)

Description of project:

In the course of my PhD studies at the Centre for Ocean Life I am investigating the traits and trade-offs of small marine organisms such as flagellates and gelatinous filter feeders by analysing their interactions with the fluid environment around them using theoretical models in comparison to experimental measurements.

Flagellates are unicellular organisms with actuated whip-like appendages, so-called flagella, that are used for propulsion and to produce feeding currents. There exists a large variety regarding numbers, lengths and beat patterns in different flagellate species. Many flagellates are mixotrophic and have common goals which are efficient prey capture, swimming, and predator avoidance. Those functions are all related to the flow created by the flagellar beat, and in general there are trade-offs so that not all functions can be optimized at once. By using measured near-cell flows around freely swimming flagellates and an analytical model that reproduces those flows for different flagellar force arrangements we can investigate how swimming velocity, the extension of flow disturbance zones attracting predators, and feeding rates depend on the flagellar force arrangement. The flow measurements were performed by Lasse Tor Nielsen using micro-particle image velocimetry. The analytical model is based on point forces representing each flagellum and a no-slip sphere representing the cell body. For biflagellates with left-right symmetrically arranged forces we found that puller force arrangements favour feeding while equatorially arranged forces are optimal for fast as well as quiet swimming.
We developed the analytical model framework further to model time-dependent dynamics of ciliary beat strokes and to determine the shape of helical trajectories for different asymmetric force arrangements which also has implications on swimming and feeding flows.

As another main part of my PhD I am investigating aquatic filter feeders such as gelatinous salps which use large and watery bodies with low carbon densities to produce large filter areas that efficiently collect and up-concentrate sufficient numbers of small prey. Centimetre-sized salps compete with micron-sized, carbon-dense flagellates for submicron-sized prey and using a fitness model including filter and swimming hydrodynamics we are investigating the trade-offs related to the body carbon-density to analyse under which conditions the gelatinous body plan is optimized. For the fitness model we analysed filter hydrodynamics of gelatinous (salps) and carbon-dense (choanoflagellates) filter feeders. From the trade-off between filter resistance and prey size range we calculated optimal mesh sizes utilizing filtration theory and for example found that choanoflagellates have optimal filters in this sense. We will explore if the fitness model can explain and predict the two distinct optima for carbon densities matching gelatinous and dense organisms in accordance with observations suggesting that intermediate densities are rare.

The ocean is a very dilute environment and typically aquatic organisms living purely on prey capture need to scan one million times their own body volume of sea water per day to fulfil their energy needs. With the above-mentioned analytical hydrodynamics model we can calculate advective clearance rates for different capture zones and force arrangements in flagellates. We furthermore are investigating how encounter rates for different aquatic organisms, especially by ballistic motion, depend on and are optimized by shapes and velocities of encounter zones. For this we use an analytical model to calculate the flux into the encounter zones.

With this PhD project I hope to contribute to the trait-based approach to ocean life by identifying key traits such as the flagellar arrangement in flagellates, the carbon density for dense and gelatinous plankton, or the shape of encounter zones. With a thorough investigation of those traits we analysed related trade-offs and optima for essential functions. This will be useful to design population dynamics models and to interpret field data in order to predict the behaviour of ecosystems, for example in environments where gelatinous and unicellular plankton compete.

Dissemination:

Scientific publications:

Dölger J, Nielsen LT, Kiørboe T, and Andersen A (2016) Swimming and Feeding of mixotrophic biflagellates (in review)
Significance and relevance:
Investigates the flagellar force arrangement in biflagellates with symmetrically arranged flagella as key trait to determine the trade-offs between swimming, feeding and predator avoidance. We used experiment and an analytical model to analyze the flow around freely swimming organisms.

Nielsen LT, Dölger J, Kiørboe T, and Andersen A (2016) Hydrodynamics of microbial filter feeding (under revision)
Significance and relevance:
Explores and provides significant understanding of the pumping mechanism and filter morphology in filter feeding microbes (choanoflagellates).

Dölger J, Bohr T, and Andersen A (2016) An analytical model of flagellate hydrodynamics (submitted)
Significance and relevance:
Develops and describes a broadly applicable analytical model framework that can be used to explore the hydrodynamics and kinematics of various kinds of flagellates with different flagellar numbers, lengths, and beat patterns.

Andersen A and Dölger J (2016) Planktonic encounter rates: simple formulas for encounter zones of any shape (in preparation)
Significance and relevance:
Provides analytical formulas to calculate ballistic encounter rates for encounter zones of different shapes and velocities, and calculates optima. This has important implications for the survival in a dilute oceanic environment.

Dölger J, Andersen A, Bohr T, and Kiørboe T (2017) Optimal design and body composition of gelatinous filter feeders (planned)
Significance and relevance:
Employs a fitness model based on energetics of active filter feeders to explore optimal carbon densities matching with large gelatinous and small dense organisms.

Presentations at conferences etc.:

Dölger J, Andersen A, Kiørboe T, and Bohr T. Salps versus flagellates. (talk) Ocean Life Annual Retreat, Holbæk (Denmark), December 2014

Dölger J, Andersen A, Kiørboe T, and Bohr T. Optimal design of salps as gelatinous filter feeders. (talk) DANSIS research seminar, Kgs. Lyngby (Denmark), May 2015

Dölger J, Nielsen LT, Kiørboe T, Bohr T, and Andersen A. Feeding and swimming of flagellates. (talk) Complex Motion in Fluids Summer School, Krogerup (Denmark), August 2015

Dölger J, Nielsen LT, Kiørboe T, Bohr T, and Andersen A. Feeding and swimming of flagellates. (talk) 68th Annual APS DFD Meeting, Boston (USA), November 2015

Dölger J, Nielsen LT, Kiørboe T, Bohr T, and Andersen A. Feeding and swimming of haptophytes. (talk) Ocean Life Annual Retreat, Holbæk (Denmark), December 2015

Dölger J, Nielsen LT, Kiørboe T, Bohr T, and Andersen A. Swimming and feeding of mixotrophic biflagellates. (poster + talk) Microscale Ocean Biophysics Meeting, Eilat (Israel), November 2016

Dölger J, Nielsen LT, Kiørboe T, Bohr T, and Andersen A. Hydrodynamics of freely swimming flagellates. (abstract for talk accepted) 69th Annual APS DFD Meeting, Portland (USA), November 2016

Dölger J, Nielsen LT, Kiørboe T, Bohr T, and Andersen A. Hydrodynamics of freely swimming flagellates. (title for talk submitted) Ocean Life Annual Retreat, Holbæk (Denmark), December 2016

6.11 Prey selection and behavior of copepods fed on toxic and nontoxic algae

Jiayi Xu, PhD student
Employment period: 1 December 2014 – 30 November 2017
Supervisors: Thomas Kiørboe (DTU Aqua), Per Juel Hansen (KU)

Description of project:

Harmful algae (HA) cause a variety of impacts in marine ecosystems through the synthesis of toxic compounds altering the cellular process of organisms from plankton to humans. Copepods as an important link between ocean primary production and higher trophic levels concentrate and transport HA, serving as an important entry point of phytoplankton toxins to pelagic food webs. Some types of algal toxin cause adverse effects on the copepods, including reduced feeding rate, reduced egg production, reduced egg hatching success, reduced survival, delayed development, and many other behavioral changes, when ingested.

The total number of marine toxin-producing algae is over 150 species, accounting for about 4% of all known phytoplankton taxa. Some harmful algae leak toxic compounds to the ambient water as feeding deterrents and can possibly be remotely detected by the grazer. In such a case, algae deter the feeding behavior prior to ingestion without reducing the algal population. The evolution of such a strategy is difficult to understand since it allows cheaters that let other individual to carry the cost. Other algae contain toxins that are only toxic to the copepods upon being ingested. Only when the cell is ingested by copepods it will be recognized as toxic. At that time the copepod has consumed the cell, and it is hard to understand how this kind of toxicity evolved as a predation defense because natural selection acts on the individual (now dead) cell.

Two main feeding strategies of copepod have evolved: passive ambush feeding, or active cruising or generation of a feeding current by the beating of appendages. Many copepods generate a feeding current by the rapid beating (~50 Hz) of 5 pairs of feeding appendages and harvest prey that arrive in the feeding current. The animal will change the movements of the appendages when it perceives an alga and use viscous forces to catch the alga by an appendage. The mechanism of prey detection, whether by mechanical or chemical cues, remains controversial, but pre-capture chemical characterization of potential prey particles has been suggested as a means of prey selection. Upon capture, the copepod may handle the cell during some time and decide to ingest or reject it. Prey selection at this stage may be through physical or chemical characteristics of the prey particle. The feeding appendages are equipped with both mechano- and chemo-sensors. Thus, potential particle selection may be by mechanical, olfactory (sniffing), or gustatory (tasting) means, but essentially remains unknown. Potential prey selection mechanisms may also depend on the type of prey being encountered, prey cell density, and on the prior experience of the copepod with a particular prey type.

The main objective of the project is to investigate the behavior and prey selection of copepods fed on different toxic or nontoxic algae, and to describe the mechanisms of prey selection. The project implements a high-speed video microscopy to observe the activity of feeding copepods. Tethered or free swimming individual copepods are fed with different types of toxin producers (different kinds of toxins) and strains of the same algal species with different levels of toxicity.

Dissemination:

Scientific publications:

At least 3 publications directly related to the project are planned.

Xu JY, Hansen PJ, Nielsen LT, Krock B, Tillmann U, Kiørboe T. Distinctly different behavioral responses of a copepod, *Temora longicornis*, to different strains of toxic dinoflagellates, *Alexandrium* spp. (submitted).
Significance and relevance:
Provides different feeding behaviors of copepod and various evolutional strategies of toxic algae.

Presentations at conferences, seminars etc.

Xu JY, Hansen PJ, Nielsen LT, Kiørboe T. 2016, Feeding behavior and prey selection of *Temora longicornis* fed on toxic dinoflagellates, *Alexandrium* spp (poster). ICES/PICES 6th Zooplankton Production Symposium, Bergen, Norway.

6.12 Chemical ecology of copepods

Jan Heuschele, Post Doc.
Employment period: 1 February 2012 – 31 August 2014
Supervisors and Collaborators: Thomas Kiørboe (DTU Aqua) and Erik Selander (University of Gothenborg).

Description of project:

This project aimed at exploring how chemosensation, a trait common in most zooplanktonic organisms, works and whether it could be applied in aquaculture of copepods. In particular we wanted to determine the sex pheromone of copepods. Therefore we looked at the differences in the exudates of males and females a metabolomic approach. This was done for the Calanoid copepod *T. longicornis* and the Cyclopoid *Oithona davisae*. In both species females are well known to produce pheromone trails. The limiting factor in these kinds of experiments is to pick a large enough sample of same sexed individuals of one species. We incubated large number of males and females separately in small amounts of water, and extracted the copepod exudates using a solid phase extraction column. The concentrated exudates were analyzed by high resolving LC-MS. To identify compounds that are more common in female or male exudates the analysis of the data was done using OPLS-DA, as well as conventional statistical methods. We discovered sex-specific copepod chemical signatures, but also common copepod compounds. While behavioral bioassays did so far not yield any positive results, our research is an essential first step to identify copepod pheromones. We also experimentally assessed the sex specific reactions of copepods to potential feeding attractants. Detailed knowledge about chemosensation and the involved infochemicals (pheromones) is needed to understand the structuring of the marine food web and population dynamics as processes like mate finding and food evaluation rely on it in many species. I further made substantial contributions to the “Size in the Ocean” project of the Centre for Ocean Life and conducted a collaborative experiment with Lars-Anders Hansson’s group at Lund University on “Personality in plankton”.

Dissemination:

Scientific publications:
Heuschele J, Nemming L, Tolstrup L, Kiørboe T, Nylund GM, Selander E. (2016) The sex specific metabolic footprint of *Oithona davisae*. Journal of Sea Research. 117:1-6.
Significance and relevance: We find sexual differences in exudate composition, reflecting the sexual dimorphism, with female specific exudates being possible sex-pheromones. We are able to remove the female sex pheromone from seawater using solid phase extraction columns, but were unable to re-gain the molecules and their activity as revealed in behavioural assays.

Bondoc KG, Heuschele J, Gillard J, Vyverman W, Pohnert G. (2016) Selective silicate-directed motility in diatoms. Nature communications 7: 10540.
Significance and relevance: This study for the first time demonstrates that diatoms are able to trace silicate minerals, the building material of their cell wall, in water. Moreover, they can even move actively to areas where the concentration of silicates is especially high.

Selander E, Heuschele J, Nylund GM, Pohnert G, Pavia H, Bjærke O, Pender-Healy LA, Tiselius P, Kiørboe T. (2016) Solid phase extraction and metabolic profiling of exudates from living copepods. PeerJ. Jan 12;4:e1529.
Significance and relevance: We describe a metabolomics approach to identify the signal molecules and provide a list of pheromone candidate molecules for a common coastal copepod. This technique can be used to potentially identify sex pheromones and other infochemcials of marine copepods.

Neuheimer AB, Hartvig M, Heuschele J, Hylander S, Kiørboe T, Olsson KH, Sainmont J, Andersen KH. (2015) Adult and offspring size in the ocean over 17 orders of magnitude follows two life history strategies. Ecology. 96:3303-11.
Significance and relevance: Life shows two distinct reproduction strategies with parents choosing to invest in either many small or a few large offspring. Our paper describes these strategy “choices” (and the reasons behind them) for ocean life ranging from the very small (zooplankton) to the very, very large (whales).

Andersen KH, Berge T, Gonçalves RJ, Hartvig M, Heuschele J, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer AB, Olsson K, Palacz A, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T, 2016. Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. Ann. Rev. Mar. Sci. 8, 150710224004001. doi:10.1146/annurev-marine-122414-034144
Significance and relevance: Provide a comprehensive explanation for the emergence of traits and general relationship as a function of size across the full marine animals kingdom.

Sainmont J, Webster C, Heuschele J, Gislason A, Sylvander P, Wang M, Varpe Ø (2014) Inter- and intra-specific diurnal habitat selection of zooplankton during the spring bloom. *Marine Biology*
Significance and relevance: Provides data about the presence and absence of diel vertical migration of zooplankton community during a spring bloom in the Arctic, and the specific diurnal behavior of *Calanus* copepods as a function of their size, which is put in relation of their life history strategy.

Heuschele J, Ceballos S, Andersen Borg CM, Bjærke O, Isari S, Lasley-Rasher R, Souissi A, Souissi S, Titelman J (2014) Non-consumptive effects of predator presence on copepod reproduction: insights from a mesocosm experiment. Marine Biology. doi:10.1007/s00227-014-2449-z
Significance and relevance: Shows experimental evidence for that the presence of predators alone can influence the reproductive dynamics of zooplankton populations.

Heuschele J, Selander E (2014). The chemical ecology of copepods. Journal of Plankton Research, 0, 1–19. doi:10.1093/plankt/fbu025
Significance and relevance: Summarizes and synthesizes 100 years of studies about the chemical ecology of copepods and highlight the importance of the chemosensory trait in copepods.

Ceballos S, Sichlau MH, Heuschele J, Kiørboe T (2014) Low fertilization rates in a pelagic copepod caused by sexual selection? Journal of Plankton Research, doi: 10.1093/plankt/fbu021
Significance and relevance: We find empirical evidence that mating in copepods is far from being solely an encounter problem in copepods. This suggests that behavioural traits, like the presence of sexual selection have a relevant role in population dynamics of copepods.

Heuschele J, Eliassen S, Kiørboe T (2012) Optimal mate choice patterns in pelagic copepods. Oecologia. http://dx.doi.org/10.1007/s00442-012-2516-4
Significance and relevance: Calculates the circumstances when sexual selection is relevant in the reproductive biology of copepods.

Heuschele J, Kiørboe T (2012) The smell of virgins: mating status of females affects male swimming behaviour in Oithona davisae. J. Plankton Res. 34:929–935
Significance and relevance: Shows the changes in behavioral traits in the presence and absence of pheromones.

Presentations:

Heuschele J, Kiørboe T. 2013. The smell of virgins. ESEB conference Lund Sweden, Poster

Female choice in eutrophied waters. J. Heuschele, S. Eliassen,Ø. Fiksen.International workshop on Trait-based approaches to Ocean Life, 2013, Copenhagen. Poster

Outreach: Public talks and popular article

Kiørboe T, Heuschele J, Selander E (2013). Havets dufte. Aktuel Naturvidenskab 3: 30-33

The world of Hopfs - a small bedtime story about evolution. 2015 Jan Heuschele. Createspace and Beijing Science and Technology Press

Otto the copepod. 2015 Jan Heuschele. Ebook and webpage. https://itunes.apple.com/us/book/otto-the-copepod/id970438108

6.13 Trait-based modeling as an ecosystem approach to fisheries management

Nis Sand Jacobsen, PhD student
Employment period: 1 November 2012 – 1 November 2015
Supervisors: Ken H. Andersen (DTU Aqua) and Henrik Gislason (DTU Aqua).

Description of project:

The main aim of the project is to investigate consequences of direct and indirect effects of fishing on marine communities. Fishing often targets certain species and sizes, and their interactions with the remaining community causes indirect effects, for instance a release of predation mortality. As these effects are not currently implemented in impact assessments of fisheries, there is a need to explore and develop models that can predict long-term community impacts of fishing, so-called strategic fisheries management. One candidate for such models is size and trait-based fish community models. These models describe fish communities using fish life history, where they grow from eggs to large adults. The description is performed using a trait-based representation instead of actual species identity. The models currently stand as a theoretical approach to community ecology, but are developing towards implementation in marine ecosystems.

Results:

The first result of the trait based approach to strategic fisheries management was to explore the consequences of “balanced harvesting” on fish communities. We showed that targeting all sizes and groups according to productivity can provide marginally larger yields, but also lesser impact on the size structure of the community. The downside of this fishing pattern is that the yield is mainly comprised of small (and often immature) fish, which may possibly provide lower economic revenue. The paper is the first attempt to investigate impacts of a balanced fishing pattern imposed on the community level, rather than on individual species. The second result relates to how different ecosystem models respond to fishing. For this study, we calibrated a size and trait based model to an Ecopath w. Ecosim model of the Northern California Current ecosystem. The analysis aimed at quantifying differences between using a size based model and a model where species are described in compartments. The results show that indirect effects around the asymptotic size of a fished species are quite similar in the two models. When size differences are larger, there is a differentiated response, for instance the indirect effect on very large fish when catching small ones. We find that this effect can be attributed to size structure in the models, where fish compete throughout their lives, rather than just through a predetermined food web that relates to the adult biomass. This work was done in collaboration with Professor Tim Essington at University of Washington, Seattle. The third project is an application of a size and trait based model to Lake Kariba, situated between Zambia and Zimbabwe. The lake holds a time series of fish distributions from both an unfished area and a highly fished area. By using a size- and trait-based model we mimic the size distribution of species in the lake fished and unfished, and show that by using smaller mesh sizes it is possible to get higher yields, without changing the size distribution in the community. The work is the first attempt to combine model and data efforts in an analysis of “balanced harvesting” mentioned in the first project. This work was done in collaboration with Assoc. Professor Jeppe Kolding from University of Bergen and Paul van Zwieten from University of Wageningen.

The final project quantified ‘Efficiency frontiers’ in five large marine ecosystems using novel multispecies model calibrations. The efficiency frontier is the optimal trade-off space between yield (biomass or economic) and ecological state (measured as deviation from an unfished system). We found that three out of five systems were close to efficiency on the biomass yield frontier (North Sea, Barents Sea and the Benguela Current) and two systems had scope for efficiency gains (Northeast US Continental Shelf and the Baltic Sea). Furthermore, we investigated the economic efficiency and showed that even though the efficiency had increased, there was still room for improvement. The work was done in collaboration with Matthew Burgess from University of California, Santa Barbara.
The results from the projects listed above have all been synthesized in a PhD thesis that was defended in November 2015.

Dissemination:

Scientific publications:

Jacobsen NS, Gislason H, Andersen KH (2014) The Consequences of Balanced Harvesting of Fish Communities. Proceedings of the Royal Society B: Biological Sciences 281 (1775): 2013 2701.
Significance and relevance: Explores the balanced harvesting fishing strategy in a size- and trait-based fish community model. The paper has led to invitations to talks in the Danish Society for Marine Biology, ICES working group for ecosystem impacts of fisheries and a working group on “balanced harvesting” at FAO, Rome.

Jacobsen NS, Andersen KH, Essington TE (2015) Comparing model predictions for ecosystem based management. Canadian Journal of Aquatic and Fisheries Science.
Significance and relevance: We describe differences and commonalties in two multispecies models (a trait based model and a species based model), where fishing is imposed. In particular we look at direct and indirect community effects of fishing. It is found that a detailed species description and a trait based description provides many similar results (MSY and biomass changes close to the fished species), but also that competition effects at earlier stages in the trait based model yields differentiated effects when fishing lower trophic levels.

Kolding, J., Jacobsen, N.S., Andersen, K.H. and van Zwieten, P.A.M. 2015. Maximizing fisheries yields while maintaining community structure. Canadian Journal of Fisheries and Aquatic Sciences 73, 644–655.
Significance and relevance: The paper uses a time-series from Lake Kariba to look at fish size distributions in an unfished and a fished area. A size- and trait-based model then describes the differences between management regimes in the Zambian and the Zimbabwean side of the lake, using the time series for calibration. We provide the first empirical data set related to balanced harvesting, and show a good fit for the community size spectrum in the trait-based model to the observed data.

Jacobsen N.S., M. G. Burgess, K.H. Andersen (2016) Efficiency of fisheries is increasing at the ecosystem level. Fish and Fisheries.
Significance and relevance: The paper uses biomass distributions to calibrate novel multispecies ecosystem models to give large marine ecosystems. The results show how efficient fisheries are when accounting for indirect effects, such as changes in predation due to fishing. The results are

applicable to management that can use the presented models and results as guidelines to incorporate the ecosystem approach to fisheries management.

Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N.S., Lindemann, C., Martens, E.A., Neuheimer, A.B., Olsson, K., Palacz, A., Prowe, F., Sainmont, J., Traving, S.J., Visser, A.W., Wadhwa, N., and Kiørboe, T. 2016. Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. Ann. Rev. Mar. Sci. Annual Reviews. doi: 10.1146/annurev-marine-122414-034144.
Significance and relevance: The paper is a synthesis of how size determines feeding, sensing, offspring size and mobility of individual organisms. We provide a trait-based description of life in the ocean and physical arguments to explain observed patterns.

Andersen KH, Jacobsen NS (Submitted) A reappraisal of fisheries selectivity in light of density-dependent regulation. Fish and Fisheries, December 1st 2014.
Significance and relevance: The paper describes how reference points and population structure arises from different density dependence regimes. Using a trait-based model we show that if density dependence occurs late in life, size selective fishing will not generate the highest yields. Conversely, if density dependence happens early in life, the highest yields are achieved by fishing around size at maturation.

K.H Andersen, N.S Jacobsen and Keith D Farnsworth. 2015. The theoretical foundations for size spectrum models of fish communities. Canadian Journal Fisheries Aquatic Sciences.
Significance and relevance: The paper is a synthesis and review of the current state of size spectrum models. Size spectrum models are increasingly being used in the literature to investigate questions regarding ecology and fisheries.

K.H Andersen, J L Blanchard, E A Fulton, H Gislason, N. S Jacobsen and Tobias van Kooten, (2015) Assumptions behind size-based ecosystem models are realistic. ICES J Mar Sci Rev.
Significance and relevance: The paper is a response to Froese, et al. (2015). ‘A critique of the balanced harvesting approach to fishing’, that clarifies misunderstandings about models and approaches to the concept of ‘balanced harvesting’.

Martens EA, Wadhwa N, Jacobsen NS, Lindemann C, Andersen KH, Visser AW (2015) Size structures sensory hierarchy in ocean life. Proceedings of the Royal Society: B.
Significance and relevance: The paper uses size as a main trait in describing senses of an individual, i.e. chemosensing, mechanosensing, vision and echolocation. We find the transition sizes where one sense becomes superior in terms of foraging.

Burgess, M.G., Diekert, F.K., Jacobsen, N.S., Andersen, K.H., and Gaines, S.D. 2015. Remaining questions in the case for balanced harvesting. Fish Fish.: n/a–n/a. doi: 10.1111/faf.12123.
Significance and relevance: The paper is an opinion piece that identifies issues and unresolved questions regarding the concept of balanced harvesting.

K.H Andersen, N.S Jacobsen, T.E Jansen, J.E Beyer, Spatial cohort dynamics determines density dependent regulation in fish populations. In press, Fish and Fisheries, 2016.
Significance and relevance: This project shows how and when in life density dependence can emerge. The main result is that increasing spatial cohort spreading means that density dependence will happen early in life, while little spreading causes density dependence to occur late in life. These

results have significant impact on how fish stocks are assessed, and how the maximum sustainable yield can be obtained.

Popular scientific articles:

Jacobsen NS (2014) Fiskeyngel er fremtidens nytårstorsk. Aktuel Naturvidenskab 3 July 2014.

Reports
Garcia Serge M., Bianchi Gabriella, Charles Anthony, Kolding Jeppe, Rice Jake, Rochet Marie-Joelle, Zhou Shijie, Delius Gustav, Reid David, Van Zwieten Paul A. M., Atcheson Megan, Bartley Devin, Borges Lisa, Bundy Alida, Dagorn Laurent, Dunn Daniel C., Hall Martin, Heino Mikko, Jacobsen Birgitte, Jacobsen Nis S., Law Richard, Makino Mitsutaku, Martin Felix, Skern-Mauritzen Mette, Suuronen Petri, Symons Despina (2015). Balanced harvest in the real world. Scientific, policy and operational issues in an ecosystem approach to fisheries. 29th of September 2014, FAO Headquarters, Rome, Italy.

WGSAM, Interim Report of the Working Group on Multispecies Assessment Methods (WGSAM), 21-25 October 2013, Stockholm, Sweden.

WGECO, Report of the Working Group on the Ecosystem Effects of Fishing Activities (WGECO), 8-15 April 2014, ICES Copenhagen.
Popular scientific articles

Nis S Jacobsen, 2014, "Fiskeyngel er fremtidens nytårstorsk", Aktuel Naturvidenskab 3 July 2014.

Conference oral presentations

Nis S Jacobsen, Henrik Gislason and Ken H Andersen, "Balanced fishing as an ecosystem management strategy", FACTS symposium November 2012, Nantes.

Nis S Jacobsen, Henrik Gislason and Ken H Andersen, "The consequences of balanced harvesting on fish communities", ICES Annual Science Conference, September 2013, Reykjavik.

Nis S Jacobsen, Tim E Essington and Ken H Andersen, "Comparing ecosystem models as fisheries management tools: a case study in the California current", April 2014, KBBE workshop, feature talk for the multispecies session, Wellington.

Nis S Jacobsen, Tim E Essington and Ken H Andersen, "Comparing ecosystem models as fisheries management tools – a case study in the California Current", Symposium on size based approaches to fish and fisheries, June 2014, Copenhagen.

Nis S Jacobsen, Tim E Essington and Ken H Andersen, "Comparing ecosystem models as fisheries management tools – a case study in the California Current", American Fisheries Society, August 2014, Quebec.

Nis S Jacobsen, "The consequences of balanced harvesting on fish communities", American Fisheries Society, August 2014, Quebec.

Nis S Jacobsen and Ken H Andersen, “A reappraisal of fisheries selectivity in light of density-dependent regulation”, Balanced harvesting meeting, September 2014, FAO, Rome.
Nis S Jacobsen, Jeppe Kolding, Ken H Andersen, Paul van Zwieten, “Maximizing fisheries yield, while maintaining community structure”, Balanced harvesting meeting, September 2014, FAO, Rome.

Nis S Jacobsen and Ken H Andersen, “Size based models predict efficiency frontiers in large marine ecosystems”, American Fisheries Society, August 2015, Portland.
Other presentations

Nis S Jacobsen et al, April 2014, “Identify and adapt models necessary for data-poor situations”, MYFISH yearly meeting, Nantes.

Nis S Jacobsen, Tim E Essington and Ken H Andersen, August 2013, “Comparing compartment and trait-based models in fisheries management”, (Poster), Trait based workshop in Copenhagen.

Nis S Jacobsen, April 2013, “Balanced Harvesting and size spectrum models – a multispecies approach to fisheries management”, School of Aquatic and Fisheries Science quantitative seminar, University of Washington, Seattle.

Nis S Jacobsen, December 2014, “Can we use traits to determine fisheries reference points?”, Ocean Life Annual Meeting, Søminestationen, Roskilde.

Nis S Jacobsen March 2016, “Size based models as tools for an ecosystem approach to fisheries management”, Quantitative Seminar, University of Washington, Seattle.
Invited presentations:

Nis S Jacobsen, March 2014, “Små fisk på spisebordet – et balanceret fiskeri”, Dansk selskab for marinbiologi (Popular science presentation).

Nis S Jacobsen, Henrik Gislason and Ken H Andersen, May 2014, “The consequences of balanced harvesting on fish communities”, WGECO, Copenhagen.

Nis S Jacobsen, September, 2014, “Babyfisk på middagsbordet – et balanceret fiskeri”, Naturvidenskabsfestival, Copenhagen (Popular science presentation).

Nis S Jacobsen, April 2015, ”Can you catch a fish before it is mature?”, Naturskyttsforeningen, Stockholm, Sweden.

Nis S Jacobsen, June 2016, Size structured multispecies models to evaluate indirect effects of fishing. ISEC, Seattle, USA.

Other activities:

Representing “Centre for Ocean Life” in the two ICES working groups ”WGSAM” and “WGECO”

Arranging a mini-symposium on size-based approaches to fish and fisheries (www.size-based-symposium.dk) with 25 participants.

Teaching assistant in courses “Mathematical biology” and “Mathematical models in ecology”, at DTU.

Visiting the Tim E Essington lab, School of Aquatic and Fisheries science, University of Washington, Seattle, from March to June 2013.

Invited and attended discussion panel on balanced harvesting in “AFS Symposium on Fishing Gear Selectivity”, Quebec, August 2014.

Invited participant for “Balanced harvesting” meeting at FAO, Rome, September, 2014.

Reviewer for
ICES Journal of Marine Science, Philosophical Transactions B, Canadian Journal of Aquatic and Fisheries Science, Fish and Fisheries, PLOS One.

6.14 A trait-based approach of the composition of marine communities

Laurène Pécuchet, PhD student
Employment period: February 2014 – February 2017
Supervisors: Martin Lindegren and Mark Payne (DTU Aqua)

Description of project:
There is an increasing awareness in ecology that ecosystem functioning do not directly depend of the species composition but instead of the species functional trait distribution. The trait-based approach permits to describe a community by its composition in key traits. The occurrence of these traits and their distribution in communities permits to link between organisms and ecosystem functioning. Furthermore, the trait-based approach permits to give general and predictable statements, whereas the taxonomic approach is based on special cases. Their use can enable to point out directly to candidate mechanisms to explain ecological phenomena and permits comparison between different ecosystems and regions.
The aim of my thesis is to develop and use a trait-based approach to characterize marine fish communities from an ecosystem scale (e.g. Baltic Sea, North Sea) to a large scale (e.g. North-eastern Atlantic), to investigate how functional diversity patterns and key traits are distributed along environmental gradients and how the latest impact community composition. The thesis is separated in 3 projects: (1) Implementing the trait-based approach in the Baltic Sea, a species poor ecosystem with high environmental heterogeneity, (2) going form traits to life history strategies and investigating the influence of the environment on the distribution of these strategies, and finally (3) studying the spatial pattern in traits composition of different trophic levels' communities (benthos, plankton, fish) in the North Sea and relate them to environmental gradients.

For the first project, we studied the fish communities in the Baltic Sea by using international trawl survey. The Baltic Sea is one of the most studied marine areas and is characterized by a strong gradient in salinity from euhaline water in the Kattegat to freshwater in the Bothnian Bay. A consequence of this environmental pressure is reflected in the decreasing trend in species richness along the gradient. However, there is still a knowledge gap on the traits distribution and on the mechanism that shape the communities diversity. Therefore, in this first project we characterized and described the spatial pattern of functional diversity, i.e. the range and value of species key traits, of Baltic fish communities and its relation to taxonomic richness. We also investigate the mechanism (assembly rules) influencing the community diversity. We found that while species richness was sharply decreasing from the saline Kattegat to the brackish Gdansk Bay, functional richness tended to decrease at a lower rate. We also found that the fish composition of the Baltic Sea followed an environmental filtering pattern, with the species co-occurring in the communities having a significantly higher functional similarity than by expected by random chance alone. In a second project we studied the prevalence of fish life history strategies in the European seas and explained their spatial patterns in function of the environment. The life history strategies were obtained by analyzing a six-trait matrix of more than 300 species inhabiting the European seas. We found that based on their traits values the species could be decomposed into three primary life history strategies: Equilibrium species producing few but big offspring, Periodic producing many small offspring and high lifespan, and Opportunistic species which had a small lifespan and produced many small eggs. The prevalence of the strategies in the fish communities exhibited strong spatial patterns (Fig.1) which could be explained by spatial variability in annual sea surface temperature, temperature seasonality and depth.

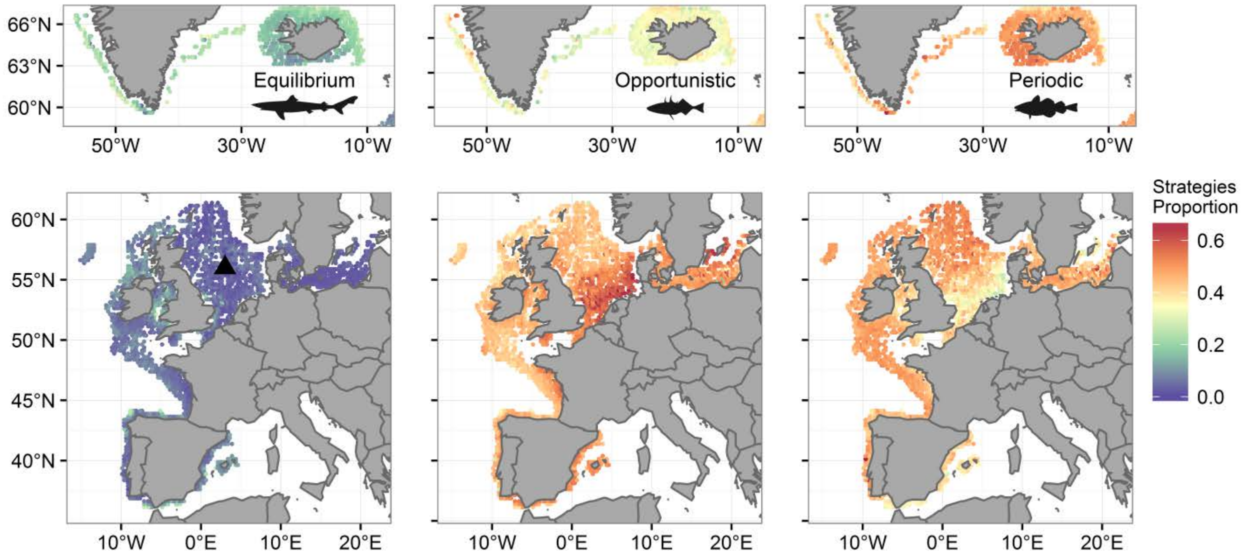


Figure 1: Proportions of each life history strategy in the fish assemblages of the European Seas calculated from species abundance data.

For my third ongoing project, we extended the taxonomic scope by analysing the spatial pattern of the communities' traits of copepod, benthos, and fish in the North Sea. We studied the spatial traits' composition of the communities by calculating community weighted mean (CWM) traits of three taxon-transcendent traits, i.e. adult size, offspring size and fecundity, on a regular grid. We found no consistent spatial patterns for these three traits across the three taxa. However, when studying the first axis of multi-traits spatial variability (PC1 of a PCA) we found a very strong spatial relation between fish and copepod, a lower one for fish and benthos, and very weak one between copepod and benthos. Several CWM traits from different taxon where co-varying. In general, the spatial difference between each taxon CWM could be explained by their different habitats, e.g. bedstress for benthos and mixed layer depth for copepod, while depth and the seasonality in chlorophyll and temperature appeared to impact the three taxon.

Dissemination:

Published papers:

Pecuchet L, Nielsen JR, Christensen A (2015) Impacts of the local environment on recruitment: a comparative study of North Sea and Baltic Sea fish stocks. *ICES Journal of Marine Science* 72:1323–1335
Significance and relevance: Environmental variables influencing the recruitment of 18 fish stocks in the North Sea and Baltic Sea was investigated and co-variability in recruitment strength between the different stocks was assessed. Recruits' survival of some species with similar life history traits where co-varying, notably small pelagic in the Baltic Sea and gadoids in the North Sea.

Pecuchet L, Törnroos A, Lindegren M (2016) Patterns and drivers of fish community assembly in a large marine ecosystem. *Marine Ecology Progress Series* 546:239–248
Significance and relevance: Using a trait-based approach, the diversity and the mechanism influencing community composition of Baltic Sea fish assemblages was studied. We found that the species co-occurring in the Baltic where in general more ecologically similar that by random and

found a strong influence of the environment on the distribution and traits composition of the communities.

Submitted papers:

Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzon A, Solmundsson J, Payne MR. From traits to life history strategies: deconstructing fish community composition across European Seas. *Global ecology and biogeography* (under review)
Significance and relevance: Based on their traits, fish species could be categorized into three strategies that reflect the evolutionary and environmental constraint of the species. Due to their tight coupling to the environment, notably temperature and fishing, life history strategies could be a suitable tool to monitor and understand community changes in response to natural and anthropogenic stressors, including climate change.

Planned papers:

Pecuchet L, Reygondeau G, Beauchard O, Beukhof E, Brun P, Cheung W, Dencker T, Van Dendere D, Licandro P, Törnroos A, Payne MR, Lindegren M. Spatial structuration of life history traits: congruence between multiple taxa and environmental drivers in the North Sea. *Submitted.*

Presentations:

Pécuchet L., Nielsen, J. R., & Christensen, A. (2015). Impacts of the local environment on recruitment – a comparative study of North Sea and Baltic Sea fish stocks. Abstract from 18. Danske Havforskermøde, Copenhagen, Denmark.

Pécuchet L, Törnroos & Lindegren: Environmental filtering drives functional diversity of fish assemblages in a temperate system. Third international Symposium on the Effects of climate change on the world's Oceans, Santos city, Brazil, March 2015.

Pécuchet L, Törnroos & Lindegren: Environmental filtering drives functional diversity of fish assemblages in a temperate system. ICES Annual Science Conference, Copenhagen, Denmark, September 2015.

Pécuchet L, Hidalgo & Lindegren: Taxonomic and functional diversity patterns of fish assemblages in the European Seas (poster). ICES Annual Science Conference, Copenhagen, Denmark, September 2015.

Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzon A, Solmundsson J, Payne MR. From traits to life history strategies: deconstructing fish community composition across European Seas. ICES Annual Science Conference, Riga, Latvia, September 2016

Pecuchet L, Reygondeau G, Beauchard O, Beukhof E, Brun P, Cheung W, Dencker T, Van Dendere D, Licandro P, Törnroos A, Payne MR, Lindegren M. Spatial structuration of life history traits: congruence between multiple taxa and environmental drivers in the North Sea. (poster) ICES Annual Science Conference, Riga, Latvia, September 2016

6.15 Functional trait diversity and the resilience and stability of marine ecosystems

Martin Lindegren, researcher
Employment period: February 2014-December 2016

Description of project:

Anthropogenic impacts, notably biodiversity loss, climate change and overexploitation, threaten the provision of ecosystem functioning and services worldwide. Therefore, maximizing resilience has emerged as a central tenet in ecosystem management. Although theory provides a conceptual basis for understanding the stabilizing role of biodiversity, its applicability to real ecosystems, especially marine areas encompassing complex biotic interactions, variable environmental conditions and vast spatio-temporal scales, requires empirical insight regarding the underlying mechanisms promoting resilience and stability.

In this project, I aim to investigate the effect of marine biodiversity on ecosystem stability by focusing on functional (trait related) aspects of diversity, involving functional complementarity and redundancy within communities and trophic levels. The project will utilize the great wealth of observational data on marine fish traits and distribution to investigate large-scale biogeographic patterns of functional diversity and investigate and compare regional dynamics across ecosystems of various complexity and diversity; where long-term, high resolution data is available (e.g., the Baltic Sea and California Current). The approach may be extended to include other marine organisms for which similar data is available, e.g., plankton and benthos.

The project will consist of the following basic sections: (i) compile available information on observed key ecological traits of marine fish; (ii) correct and estimate trait values (including uncertainties) for missing taxa (or model derived values) using a phylogenetic approach; (iii) map the spatial distribution of functional traits and relate these to key environmental indices using statistical models; (iv) derive a number of functional diversity (FD) indices and assess the degree of spatio-temporal mismatch between FD and species richness; (v) investigate the degree of functional redundancy and dispersion within marine fish communities as a proxy for resilience; (vii) assess the relationship between patterns of resilience and stability, defined as the degree of variability in long-term time-series of fish abundance.

Dissemination:

Scientific publications:
Lindegren, M., Checkley, D.M., Jr., Ohman, M.D., Koslow, A., Goericke, R (2016) Resilience and Stability of a Pelagic Marine Ecosystem. Proceedings of the Royal Society B-Biological Sciences, 283: 20151931.
Significance and relevance: This study investigates the relative importance of statistical averaging and functional complementarity and provide insights into the underlying mechanisms promoting community stability and resilience in a large marine ecosystem.

Pécuchet L Törnroos A, Lindegren M (2016) Patterns and drivers of fish community assembly in a large marine ecosystem. Marine Ecology-Progress Series, 546: 239–248.
Significance and relevance: Using a trait-based approach, the diversity and the mechanism influencing community composition of Baltic Sea fish assemblages was studied. We found that the species co-occurring

in the Baltic where in general more ecologically similar that by random and found a strong influence of the environment on the distribution and traits composition of the communities.

van Deurs, M., Persson, A., Lindegren, M., Jacobsen, C., Jorgensen, C., Neuenfeldt, S., Nilsson, A. 2016. Marine ecosystem connectivity mediated by migrant-resident interactions and the concomitant cross-system flux of lipids. Ecology and Evolution doi:10.1002/ece3.2167
Significance and relevance: This study shows how lipid storage (a trait used for storing energy required to survive winter and/or produce offspring) in a mobile marine prey species may benefit the reproductive success of resident predator channeled through cross-ecosystems migrations.

Submitted papers:
Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzon A, Solmundsson J, Payne MR. From traits to life history strategies: deconstructing fish community composition across European Seas. Global ecology and biogeography: in review.
Significance and relevance: Based on their traits, fish species could be categorized into three strategies that reflect the evolutionary and environmental constraint of the species. Due to their tight coupling to the environment, notably temperature and fishing, life history strategies could be a suitable tool to monitor and understand community changes in response to natural and anthropogenic stressors, including climate change.

Lindegren M, Holt B, MacKenzie BR, Rahbeck C. A global mismatch in the protection of biodiversity and ecosystem services. Submitted
Significance and relevance: Using global data on fish taxonomy, phylogeny and functional traits we find pronounced spatial differences in the response of marine ecosystems to biodiversity loss and a noticeable global mismatch between marine protected areas, biodiversity and ecosystem services worldwide.

Griffiths J., et al. (including Lindegren M, Törnroos A). The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. Global Change Biology: In review.
Significance and relevance: This paper reviews and explains the various abiotic and biotic pathways and processes by which the pelagic and benthic zone interacts and exchanges nutrients and energy using the Baltic Sea as a case study.

Lindegren M, Checkley DM, Ohman MD, Koslow AJ, Goericke R (Submitted) Climate variability and Interacting Trophic Control in the Southern California Current.
Significance and relevance: This study investigates the underlying modes of ecosystem regulation, i.e., bottom-up and top-down control and the extent to which climate affects the relative importance of these forces in marine ecosystems.

Lindegren M, Holt B, MacKenzie BR (in prep.) Resilience and vulnerability of marine ecosystems to biodiversity loss.
Significance and relevance: This study investigates the degree of spatial mismatch between biodiversity, resilience and ecosystem services across large marine ecosystems worldwide and show how the current designation of marine protected areas is insufficient to protect key components of biodiversity, including phylogenetic and functional aspects, or ecosystem services.

Presentations:

Lindegren M. A trait-based assessment towards understanding long-term changes in ecosystem functioning: the Central Baltic Sea as a case. ICES Annual Science Conference, Riga, 19-23 September 2016.

Tim Spaanheden Dencker T, Payne M, Lindegren M. Three decades of spatio-temporal patterns of taxonomic and functional diversity in the North Sea fish community. ICES Annual Science Conference, Riga, 19-23 September 2016.

Beukhof E, Spaanheden Dencker T, Pécuchet L, Lindegren M. Spatio-temporal changes in life-history traits of the North Sea fish community under climate change and fishing. ICES Annual Science Conference, Riga, 19-23 September 2016.

Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzon A, Solmundsson J, Payne MR. From traits to life history strategies: deconstructing fish community composition in European Seas. ICES Annual Science Conference, Riga, 19-23 September 2016.

Lindegren M. Understanding long-term changes in ecosystem functioning: the Central Baltic Sea as a case. ICES/HELCOM Working Group of Integrated Assessment in the Baltic Sea (WGIAB) Annual meeting, Helsinki, 18-22 April 2016.

6.16 Species or traits? Exploring plankton biogeography with different approaches

Philipp Brun, PhD student
Employment period: 1 December 2013 – 30 November 2016
Supervisors: Dr. Mark Payne (DTU Aqua) and Prof. Dr. Thomas Kiørboe (DTU Aqua)

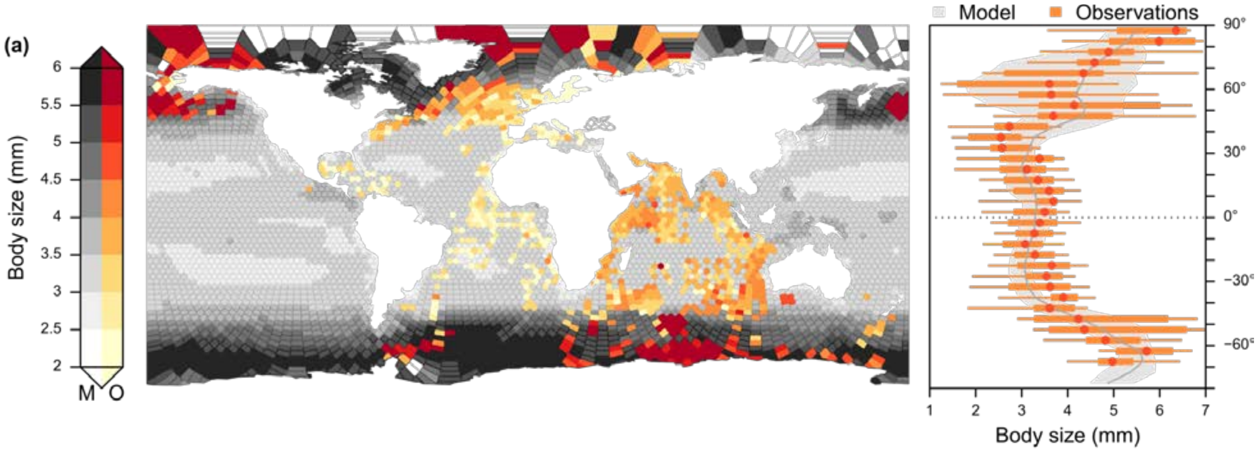
Description of project:

Plankton are ubiquitous in the world's oceans and build the fundament of marine ecosystems. Through their high abundance and metabolic activity they also strongly affect global biogeochemical cycles and ultimately the climate system. Conversely, the rate at which climate change modifies the distributions of plankton species is among the fastest across all forms of life. How planktonic communities differ across the global oceans, and what the consequences of continued relocations of species distributions are, are therefore questions of high relevance - but not a trivial ones: planktonic communities are complex and describing them in a meaningful way is challenging.

In my PhD I pursue these questions on large spatial scales, focusing on various plankton groups. All my studies are built on extensive sets of observational data, but for the analyses a variety of approaches are employed. In my first two projects, we worked with the ecological niche theory. Firstly, we investigated the ecological niches of 133 phytoplankton taxa in the global open ocean. Mixed layer depth turned out to be the environmental factor with the strongest predictive power for phytoplankton occurrence followed by light and temperature, suggesting that variables related to climatic conditions govern large-scale patterns in phytoplankton biogeography over nutrient availability. However, my second project showed that the skill of ecological niche-based predictions of the future distributions of 20 plankton species in the North Atlantic is relatively low. We found predictions to be imprecise, in particular for phytoplankton, and identified great spatial variations in predictive skill. Furthermore, we found prevalence errors to increase the further away in time a prediction was made. Finally, when comparing species distribution model predictions to the assumption that distributions remain stable over time (although significant spatial relocations have been observed for the species investigated) we found that only for copepods (zooplankton) the predictions showed higher skill for time lags of 10-30 years, while for phytoplankton no useful model predictions were possible.

In my third and fourth projects we switched from studying ecological niches to investigating the distributions of plankton with the trait-based approach. Whether or not organisms can thrive in a certain environment is determined by their traits rather than by their taxonomic identity. The trait-based approach seeks to identify and study the key features of organisms which govern the success and failure. For copepods we studied the distributions of four such key features including body size, feeding mode, relative offspring size and myelination (a defense trait). The analysis was performed on the global scale and in the North Atlantic, requiring trait information on hundreds of copepod taxa. Before we could investigate trait biogeography, we therefore had to produce an extensive collection of data on copepod traits, which we published in a separate data paper (project 3). The subsequent biogeographical analysis revealed strong patterns with latitude and season (Figure 1). As expected by theory, we found copepods to be larger in environments with cold temperatures than in the tropics To our surprise, however, we also observed large, unexplained differences in trait distributions between ocean basins, for example between the South Atlantic and the Indian Ocean, which may be interesting to further investigate in the future.

Figure 2: Global distributions of community-weighted mean body size from observations (color) and model predictions (grey-scales). The panels on the right shows aggregated patterns per latitude.



For my ongoing fifth project, we moved on from using the trait-based approach in a purely empirical sense, to using it as a way to inform mechanistic models aiming to quantify important ecosystem functions. Specifically, we investigate the contribution of copepods to the export of carbon from the surface ocean to the deeper, stable water layers. Copepods migrate vertically over relatively large distances, over which they also transport significant amounts of carbon. In this context two behaviors are particularly important, daily vertical migration to avoid predation in the sunlit surface layer, and seasonal dormancy – a state of diapause over several months that is conducted at several hundred meters depth. In this project we combine empirical information on copepod communities, trait data, and environmental factors in a mechanistic frame work to estimate to which extent these migration behaviors export carbon from the surface, how carbon fluxes are distributed in space and season, and how they changed throughout the past decades.

Dissemination:

Published papers:

Brun, P., M. Vogt, M. R. Payne, N. Gruber, C. J. O'Brien, E. T. Buitenhuis, C. Le Quéré, K. Leblanc, and Y.-W. Luo (2015). Ecological niches of open ocean phytoplankton taxa. Limnol. Oceanogr., 60(3), 1020-1038, doi:10.1002/lno.10074
Significance and relevance: Estimates phytoplankton ecological niches for the first time from global observational data, and tests traditional concepts of phytoplankton classification for similarity in ecological niches.

Brun, P., T. Kiørboe, and M. R. Payne (2015). Measuring evolutionary adaptation of phytoplankton with local field observations. Proc. Natl. Acad. Sci. 201513353, doi:10.1073/pnas.1513353112
Significance and relevance: Criticizes a recently published paper for its methodology to measure evolutionary adaptation to climate change in phytoplankton with local field observations.

Brun, P., T. Kiørboe, P. Licandro, and M. R. Payne (2016). The predictive skill of species distribution models for plankton in a changing climate. Glob. Chang. Biol. 22(9), 3170-3181, doi:10.1111/gcb.13274
Significance and relevance: Provides a thorough analysis of the strength of popular ecological niche models to foresee how species distributions are affected by climate change and highlights the limitation of currently used model performance metrics.

Brun, P., M. R. Payne, and T. Kiørboe (2016). Trait biogeography of marine copepods - an analysis across scales. Ecol. Lett., doi:10.1111/ele.12688
Significance and relevance: Provides the first ever global trait biogeographies of marine copepods based on observational data and compiled trait measurements and evaluates hypotheses about the role of the environment in shaping copepod communities.

Submitted papers:

Brun, P., M. R. Payne, and T. Kiørboe. A trait database for marine copepods. Earth Syst. Sci. Data Discuss., doi:10.5194/essd-2016-30
Significance and relevance: Describes an extensive database on key traits of marine copepods, compiled from the literature information and from expert judgements.

Planned papers:

Brun, P., M. R. Payne, A. W. Visser, P. Licandro, and T. Kiørboe. Carbon fluxes through North Atlantic copepods estimated from observations.

Presentations:

Brun, Kiørboe & Payne: *The predictive potential of ecological niche models for plankton in the North Atlantic*. International symposium on “Effects of Climate Change on the World’s Oceans”, Santos, March 2015

Brun, Kiørboe & Payne: *A trait biogeography of marine pelagic copepods*. International workshop “PlankDiv” on “Impact of climate change on the distribution of plankton phylogenetic and functional diversity”, Villefranche sur mer, March 2016

Outreach:

Persson, C. P., Danske forskere gør op med darwinistisk tradition. www.videnskab.dk
Persson, C.P., Scientists do away with Darwinian tradition. www.sciencenordic.com
Kappel, U. S., Dansk forskning udfordrer Darwin-tradition. Kristeligt Dagblad, 5.11.2016

6.17 Patterns of reproduction and offspring size in fish

Karin Olsson, PhD student
Employment period: 1 March 2012 – 31 March 2015
Thesis defence: June 18, 2015
Supervisors: Henrik Gislason (DTU Aqua) and Ken Haste Andersen (OceanLife, DTU Aqua).

Description of project:

I studied reproduction in fish with particular emphasis on the selection pressures shaping offspring size. Broadly speaking, one can imagine a female fish choosing between producing few, large offspring with good survival prospects or many small offspring, few of which are likely to reach adulthood. Evolutions is expected to select for the strategy which yields the greatest number of surviving offspring and the evolutionary trade-off for which the majority of fish species have opted is to produce large numbers of small eggs, regardless of the adult size. This is sometimes referred to as the "many-small" egg strategy (Andersen et al, 2008). However, a number of species deviate from this pattern, notably elasmobranchs (sharks, skates, rays) and also a number of small, live-bearing teleost (bony fish) species. According to the body of work based on the theory of the community size spectrum, which relies on the observation that abundance and body mass of organisms in the sea are negatively correlated, mortality and growth can be expected to scale in such a fashion as to make it most advantageous to the female, in terms of number of surviving offspring, to produce small offspring. This does not, however, offer an explanation for the alternative, "large-few" strategy. The purpose of my PhD project was to explore the extent of the alternative offspring size strategy and also what processes that might give rise to it.

I approached this problem in two ways. First, I have explored the situation empirically by assembling a dataset on offspring size with available life history information on size, growth, mortality and reproduction in a range of species. From this I have examined the apparent pattern of realized offspring size strategies and analyzed it for correlations with traits such as growth, mortality and phylogeny. Second, I have addressed it theoretically by constructing life-history optimization models which explores the effect of ecological processes not addressed in the community size-spectrum theory. Where possible, I have utilized my database to parameterize these models.

Major results
From my database it has emerged that fish typically employ one of the two main offspring size strategies: either small larvae (about 2 mm in length) regardless of the adult size or roughly proportional to adult size (about 1/5 of the adult length). Elasmobranch species all have large offspring as do some small live-bearing teleosts. Mode of reproduction is not a causal agent, however, as live-bearing rockfish give birth to small larvae while egg-laying elasmobranchs hatch at a larger size.

We developed a model on competition-induced density-dependent growth and mortality, which suggests divergent evolution towards either small offspring or offspring of a fixed size ratio relative to the adult, depending on when in early life density-dependence is important . Assuming that density dependence is absent in the early pelagic phase characterizing the small larvae strategy, but operates throughout life in the proportional strategy, the model is able to reproduce the observed dual pattern in offspring size. Using life history parameter estimates from the literature, we found that model predictions corresponded well with observations.

In another project we examined some of the simple models that have been proposed to predict reproductive output and effort from growth parameters. Testing the predictions of three such models on fecundity data from a range of species, we showed how the simplifications required in a generalized energy allocation scheme are reflected in deviations between model predictions and empirical data, and this led us to question the validity of the assumptions underlying these models.

Collaborations
I collaborated with Stavroula Tsoukali (DTU Aqua) on a project on lifetime fecundity. In a non-growing population the number of surviving offspring the average individual produces should be one, however, lifetime fecundity differs widely between different species, which implies that offspring survival also differs. Using this as an indirect route towards empirically understanding offspring survival, we have characterised reproduction in a range of species with respect to spawning habitat, temperature, spawning physiology as well as size and age to evaluate
I have also contributed to the joint OceanLife project Size in the Ocean (see Dissemination) and shared my database on offspring size, putting the offspring size strategies observed in fish in a larger context of marine life.

Dissemination:

Publications:

Popular outreach:

Olsson KH. Hvorfor lægger fisk små æg? 2014:5. Aktuel Naturvidenskab

Scientific journals (peer-reviewed):

Olsson, K. H., Gislason, H., & Andersen, K. H. (2016). Differences in density-dependence drive dual offspring size strategies in fish. Journal of Theoretical Biology, 407, 118-127.
Significance and relevance: Proposes a model which combines theories of competition with general fitness modelling to predict divergent offspring strategies in fish. The model is parameterized using empirical data on fecundity and mortality to predict optimal offspring size for sharks and bony fish.

Olsson, K. H., & Gislason, H. (2016). Testing reproductive allometry in fish. ICES Journal of Marine Science: Journal du Conseil, fsw017.
Significance and relevance: Examines the empirical support for reproductive allometry and considers the validity of some of the assumptions underlying the models used for predicting reproductive output.

Andersen KH, Berge T, Goncalves R, Hartvig M, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer A, Olsson K, Payne M, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T. 2016. Characteristic Sizes of Life in the Oceans, from Bacteria to Whales
Annual Review of Marine Science. Vol. 8: 217-241

Significance and relevance: Offers a comprehensive explanation for the emergence of traits and general relationships as a function of size across the marine zoological size spectrum.

Neuheimer, A. B., Hartvig, M., Heuschele, J., Hylander, S., Kiørboe, T., Olsson, K. H.,Sainmont, J.,Andersen, K. H. 2015. Adult and offspring size in the ocean over 17 orders of magnitude follows two life history strategies. Ecology, 96(12), 3303-3311.
Significance and relevance: Charts the relationship between adult and progeny size across several orders of magnitude in marine animals.

Tsoukali, S., Olsson, K. H., Visser, A. W., & MacKenzie, B. R. (2016). Adult lifetime reproductive value in fish depends on size and fecundity type. Canadian Journal of Fisheries and Aquatic Sciences, 73(999), 1-8.
Significance and relevance: Explores how differences in lifetime fecundity vary with habitat and reproductive mode.

Presentations at conferences, seminars etc:

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, T. Kiørboe. International workshop on Trait-based approaches to Ocean Life, 2013, Copenhagen. Conference abstract

Optimal offspring size under variable mortality. K. Olsson, H. Gislason. Life History Theory workshop, 2013, Schiermonnikoog. Abstract + talk

Dual offspring size strategies in fish - theoretical and realised offspring size strategies K.H. Olsson, H. Gislason, K.H. Andersen. International workshop on Trait-based approaches to Ocean Life, 2013, Copenhagen. Poster

6.18 Ecological and evolutionary consequences of fisheries-induced selection on boldness

Lise Marty, Post Doc.
Employment period: 1 May 2013 – 17 July 2015
Supervisors: Ken H Andersen (DTU Aqua)

Description of project:

In several exploited fish populations, rapid evolution in response to size-selective fishing has been cited as the most plausible hypothesis to explain temporal trends in life-history traits. However, vulnerability to capture may not only be size-dependent but also behaviour-dependent, targeting personality traits such as boldness/shyness. Experimental evidence on personality traits show that bold individuals feed more than shy individuals, but to be smaller, most probably because of their higher metabolism, and to have weaker anti-predatory responses and therefore suffer higher natural mortality in the presence of predators. I extend a current life-history model of fish to account for a boldness personality trait. Trade-offs related to boldness involve feeding, metabolism and vulnerability to natural mortality. Individuals experience size-dependent fishing mortality from a fishery composed of either trawls or gillnets. On top of their size-selectivity, fishing gears are selective upon behaviour, bold and active individuals being more vulnerable than shy, less active ones. I am using quantitative genetics based on the breeder's equation to calculate expected evolutionary rates on personality trait, maturation size and investment in reproduction. I also empirically estimated selection strength upon behavioural traits related to boldness using experimental data on pike in collaboration with Robert Arlinghaus from IGB (Berlin) to calibrate the model.

Empirical estimation of fishing selection strength on pike behavioural and life-history traits showed that recreational angling selected for size and behaviour, and that selection on size was roughly 8 times stronger than selection for behaviour. In accordance with previous finding, theoretical results show that fishing induces a selection response in life-history traits, selecting for individuals with higher reproductive investment and lower size at maturation, but also in behavioural traits, selecting for shyer individuals. Different ecological (individual asymptotic size) and economic consequences (yield) will further be investigated, along with management strategies (minimum size limit, maximum size limit, harvestable slot) susceptible to reduce predicted negative impacts.

Dissemination:

Scientific publications:

Published articles:

Marty L, Rochet MJ, Ernande B (2014). Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. *Marine Ecology Progress Series, 497*, 179-197.
Significance and relevance: This paper assesses the contributions of alternative, but not mutually exclusive, processes also able to drive temporal changes in age and size maturation of four North sea gadoid species, namely evolution, demographic effects, and phenotypic plasticity in age and size at maturation that can arise from growth variations but also from environmental factors

influencing maturation independently from growth. It shows that the hypothesis of fisheries-induced evolution is plausible for cod, haddock, and whiting, but not for Norway pout.

Marty, L., Dieckmann, U., & Ernande, B. (2015). Fisheries-induced neutral and adaptive evolution in exploited fish populations and consequences for their adaptive potential. *Evolutionary applications*, *8*(1), 47-63.
Significance and relevance: Theoretical study on the interplay on the interplay between neutral and adaptive evolution caused by fishing. We find that evolutionary recovery is hampered by an association of weak selection differentials with reduced additive genetic variances. Third, the contribution of fisheries-induced selection to the erosion of functional genetic diversity clearly dominates that of genetic drift only for the traits related to maturation. Together, our results highlight the importance of taking into account population genetic variability in predictions of eco-evolutionary dynamics.

Book Chapter:
Jakobsen, T., Fogarty, M. J., Megrey, B. A., & Moksness, E. (Eds.). (2016). *Fish reproductive biology: implications for assessment and management*. John Wiley & Sons.

Submitted articles:

Jaspers C, Marty L, Kiørboe T. Selection for life-history traits to maximize population growth in an invasive marine species. Submitted to Nature Ecology and evolution
Significance and relevance: Invasive species may cause irreversible changes to local food webs and biodiversity with huge socioeconomic costs. However, it is unclear what life history traits promote invasiveness, although this may be essential for mitigation strategies. Here, we investigate life-history characteristics in native and invasive populations of a comb jelly. We found an astonishing two orders of magnitude smaller maturation size in invasive compared to native populations, consistent with a simple fitness-optimization model. We also observed a much larger variability in reproductive tactics in the native range. Such large variation in reproductive tactics in native populations may be a substrate upon which selection can act during the invasion phase and may explain the success of the examined species in invading new areas.

Andersen KHA, Marty L, Arlinghaus R. Evolution of fish personality in response to selective harvesting. Submitted to Canadian Journal of Fisheries an Aquatic Science. Under revision
Significance and relevance: see project description.

Presentations:

Marty L, Dieckmann U, Ernande B. Fisheries-induced neutral and adaptive evolution in exploited fish at the phenotypic and genotypic level. Poster. International Workshop on Trait-Based Approaches to Ocean Life, Copenhagen, 26-28 August 2013

Marty L, Dieckmann U, Ernande B. Fisheries-induced neutral and adaptive evolution in exploited fish populations and consequences for their adaptive potential. ICES Annual Science Conference, A Coruna, Spain, 15-19 September 2014.

6.19 Overwintering of copepods

Mark Wejlemann Holm, PhD student
Employment period: April 2013 – November 2016 (prolonged due to paternity leave)
Supervisors: Benni Winding Hansen (Roskilde University), André Visser (DTU Aqua), and Thomas Kiørboe (DTU-Aqua)

Description of project:

Copepods are the most numerous multi-cellular organism in the marine environment. They constitute a primary link between phytoplankton and higher trophic levels. During periods with adverse environmental conditions, *i.e.* during winter in temperate regions, copepods disappear partly or completely from the plankton. Copepods have developed different strategies to cope with the cold winter conditions, these traits can be divided into three categories; dormancy of adults and larvae, production of resting eggs, and winter activity. There is generally lack of understanding of which ecosystems that support these traits worldwide. Therefore, the aim of my research is to determine how copepod species with similar overwintering traits are distributed worldwide. The hypothesis is that the environment, in this case temperature, shapes the distribution of the trait. Furthermore, I focus more specifically on species that are active during the winter, where the phytoplankton abundance in very low, and hence food availability at a minimum. Species that are adapted to low food availability, must have a larger starvation tolerance, than species utilizing other strategies (e.g. resting eggs). To cope with starvation there are overall two pathways to conserve energy. One is to reduce metabolic costs (enzymatic activity etc.), and the second is to reduce motility. The latter is overall determined by two things how the species obtain food and how the find the opposite sex to reproduce. I therefore study how species with different feeding modes cope with starvation and which importance different mating behaviors have on starvation tolerance. By gaining an understanding of what governs population dynamics of copepods, it is possible to develop models that can predict how food webs will be influenced by climatic changes.

From reviewing the literature, I have found that 19 of 49 species, belonging to the families Acartiidae, Centropagidae, Pontellidae, Temoridae, and Tortanidae, produce exclusively cold-adaptive resting eggs, *i.e.* resting eggs that insure the persistence of populations after cold periods. However, it is an adaption that seems flexible, as five additional copepod species use resting eggs to cope with both cold and warm conditions. Based on the published literature on resting eggs of marine copepods, and presence data on these species obtained from the OBIS database, it has been possible to examine the occurrence of resting eggs in relation to the presence of the species. Combined with data from NOAA on SST it shows that resting eggs are produced to cope with both high and low temperatures, presumable related to the thermal tolerance of the adults, as findings of resting eggs (RE) are on the boards of the species geographical distribution (figure).

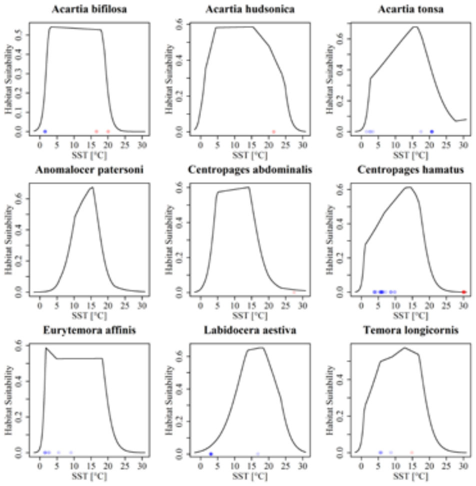


Figure 3. Temperature suitability curves based on presence of the species, combined with the average annual environmental maximum sea surface temperature (SST) for resting eggs produced to cope with warm periods (red) and minimum SST for resting eggs to cope with cold periods

Experiments testing whether species displaying winter activity is adapted to low food availability and thus has a higher starvation tolerance than species producing resting eggs is conducted on three species; *Acartia tonsa*, *Temora longicornis* and *Oithona nana*. The starvation tolerance of these three species that differs in size, feeding mode and presence in the plankton during the year differs quite a lot. The most active of the three *T. longicornis* and which is found in the plankton all year lived for five days in the absence of food. *O. nana* which is the smallest (half the size) and also present during winter lived for 11 days, whereas *A. tonsa* the only species that produce resting eggs to cope with winter conditions lived for 15 days. Changes in motility have not been analyzed yet, but specific respiration, measured as changes in O_2 consumption, seems unable to explain the difference in starvation tolerance between these species.

Dissemination:

Scientific publications:

Holm et al. (in prep.) – Resting eggs of marine free living copepods – distribution and adaptions
Significance and relevance: Comprises a review of the current observations of resting eggs and relates it to environmental conditions. Thus providing a fundamental knowledge of which type of ecosystems that support production of resting eggs.

Holm et al. (in prep.) Starvation tolerance of copepods displaying different overwintering strategies.
Significance and relevance: Will provide insight into the adaptions of copepods displaying different overwintering traits.

Holm et al. (in prep.) – The importance of mating behavior on starvation tolerance.
Significance and relevance: Will provide insight into one of the parameters that shape the gender ratio in copepods.

Presentations:
Holm MW. Kiørboe T, Almeda R, Hansen BW. Starvation tolerance of neritic copepods with different overwintering and feeding strategies. Dansk Havforskermøde, Jan 2017 (planned)

Holm MW. Seasonality of Zooplankton. Centre for Ocean Life, Charlottenlund 22 May 2013

Holm MW. Seasonality of zooplankton. Plankton Group Meeting, Roskilde University, 12 June 2013

Holm MW. Overwintering of Copepods. Improvement of Aquaculture High Quality Fish Fry Production (IMPAQ) meeting, Roskilde University, 23 October 2013

Holm MW. Cold-Adaptive Life-history Strategies in Marine Free-Living Copepods. Annual Meeting Centre for Ocean Life, Holbæk, 12 December 2013

Teaching activities (Selected lectures from bachelor and masters courses):
Lecturer in “Estuarine and coastal ecology and human impacts”

- Shelfs Planktonic Systems

- Estuarine Planktonic Systems
- Coastal Fish Production

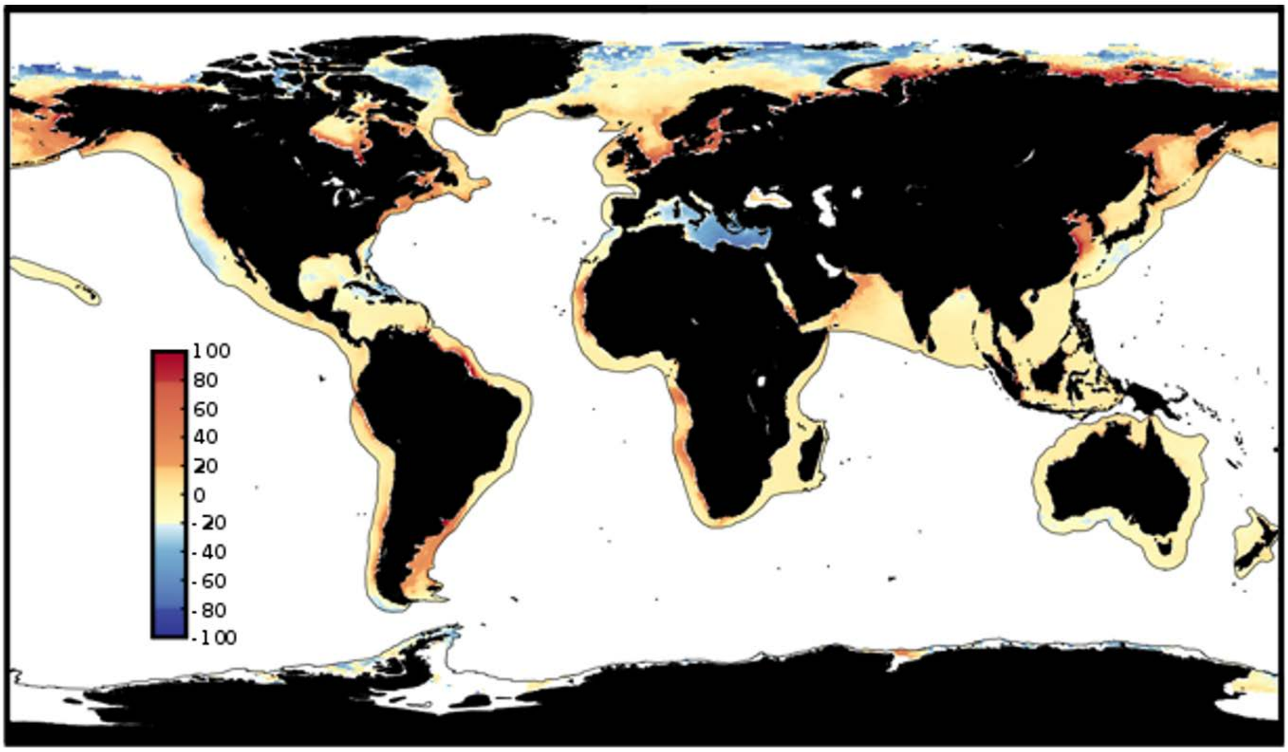
Lecturer in “Zoology” - physiology of:
- Acoelomata/Pseudocoelomata
- Mollusca og annelida

Lecturer in “An introduction to ecosystems”
- The abiotic environment
- Energy input and primary producers
- Stream fauna and community structure

Lecturer in “Biological Production”
- Shellfish; natural stocks, reefs, artificial reefs, relay of bycatch, physiology, interspecific competition, aquaculture’

6.20 Modelling the role of competition between fish and jellyfish in marine pelagic ecosystems

Nicolas Azaña Schnedler-Meyer, PhD student
Employment period: 1 August 2014 – 31 July 2017
Supervisors: Patrizio Mariani (DTU Aqua) and Thomas Kiørboe (DTU Aqua).



Ecosystem Susceptibility Index (ESI) for the Large Marine Ecosystems, as generated by our model. Positive values indicate that jellyfish are more likely to be present than forage fish, negative numbers the opposite.

Description of project:

In recent decades, reports of a supposed anthropogenic global increase in jellyfish abundances, and in the frequency and magnitude of blooms has been a subject of strong debate, reflecting a general lack of knowledge about jellyfish population dynamics and their role and significance in marine food webs. Jellyfish blooms can have many adverse effects, such as interference with fisheries, blocking of water intake pipes, impacts on important commercial fish stocks, and on tourism. The high ‘bloom potential’ of many jellyfish is hypothesized to be due to their high growth rates, linear functional responses and relatively low predation mortality. These general properties are linked to several key traits, which are shared among jellyfish, and differ fundamentally from those observed in other important marine groups, such as fish. Jellyfish are a common term for pelagic cnidarians and ctenophores. Though these two groups are evolutionarily distinct and differ in life cycles and body plans, they share a number of traits, including a tactile feeding mode depending on direct interception with prey, life cycles with large reproductive potentials, fast growth rates, and high water content. This high water content increases body size without increasing the carbon content, providing the benefit of increased capture surface area, higher Reynolds number and lower predation, without increasing metabolic demands. The aim of my PhD project is to: 1. investigate the interaction between traits and environment for the competition between jellyfish and fish. 2. Investigate the interplay between environment and the life history traits for the success of different types of jellyfish. This is achieved through the development of trait-based general food web models.

Dissemination:

Scientific publications:

Published papers:

Schnedler-Meyer NA, Mariani, P and Kiørboe, T., 2016, The global susceptibility of coastal forage fish to competition by large jellyfish. Proceedings of the Royal Society, B 283: 20161931
Significance and relevance: This paper demonstrates how the interaction between environmental factors such as water clarity and primary production can be combined with trait-based descriptions of the feeding processes of fish and jellyfish to model their competition and predict global occurrences of jellyfish blooms.

Planned papers:

The role of hydrography, jellyfish life history and environmental noise in structuring coastal ecosystems.
Significance and relevance: This paper will model the role interplay between advection and life history and their effects on jellyfish population dynamics and ecosystem structure in coastal waters. We examine the effect of autocorrelated environmental noise for the relative strengths of the metagenic (cnidarian) versus holoplanktonic (ctenophores) life cycles.

Optimal propagation strategies for scyphozoan polyps.
Significance and relevance: This paper will investigate how the benthic polyps of scyphozoan jellyfish should prioritize between four basic asexual reproductive modes, in the face of environmental conditions and variability.

Presentations at conferences, seminars etc.

Schnedler-Meyer N.A., Mariani P., Kiørboe T., 2016, Modelling global ecosystem susceptibility to jellyfish blooms (talk). Fifth International Jellyfish Symposium, Barcelona, Spain.

Schnedler-Meyer N.A., Mariani P., Kiørboe T., 2015, A model of fish and jellyfish competition (poster). 2nd International workshop on Trait-Based Approaches to Ocean Life, Waterville Valley, NH.

Outreach: Public talks and popular science articles:

Ecology of the Oceans. Guest lecturer, Tagensbo school, Copenhagen, April 2015.

Jellyfish in models. Guest lecture, Mathematical Biology course, DTU, April 2015.

Jellyfish! Lecture, at DTU Aqua for visiting German high school students. Oktober 2016.

Ida Eriksen. Hvad skal jeg gøre, når jeg bliver brændt af en brandmand? Interview for popular science article on videnskab.dk. http://videnskab.dk/krop-sundhed/hvad-skal-jeg-goere-naar-jeg-bliver-braendt-af-en-brandmand.

6.21 Trait-based modeling of trophic chains and seasonal forcing

Erik A. Martens, former Post Doc.
Employment period: 1 August 2013 – 31 September 2014
Supervisors: Ken H. Andersen (DTU Aqua) and Thomas Kiørboe (DTU Aqua).

Description of project:

My main research project aims at understanding how seasonality and its varying strength along different latitudes affects marine ecosystem structure: how does seasons affect predator-prey interactions in the ecosystem? How do seasonal variations influence overwintering and reproductive strategies of marine species? To answer these questions, I have studied mathematical models of the trophic chain in marine systems. Rather than employing the concept of species or functional groups, I used a trait-based approach, considering individuals with mechanistically based traits that are described by few parameters. 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 modeling approaches. Further, my research advances trait-based methods by extending current models to include seasonal forcing and multiple trophic levels, and in particular to consider all the links ranging from plankton to fish. To obtain an integral understanding of the dynamics of marine ecosystems, it is crucial to include all trophic levels. In this work, I used methods based on a combination of ordinary differential equations, perturbation analysis and simulation. This work is rather technical and in progress, and is expected to be finished early next year; this work is delayed due to my recent change of position, as I recently took on the position of Assistant Professor at the University of Copenhagen. During my stay at the Centre, I have led a group of students for the Size and Sense in the Oceans project. The purpose of this project is to uncover how size as a trait structures different sensing modalities. In the present work we have shown that certain sensing modalities (e.g. chemosensing, mechanosensing, vision, echolocation), serving as strategies for food acquisition, predator avoidance and mating, are only feasible above or below certain body sizes due to physical limitations in physiology or environment. This work is completed and submitted to the Journal of Royal Society Interface.Size and Sense in the Ocean forms an essential part of the Size in the Ocean project led by Prof. K.H. Andersen, leading to a further publication, see below.

Dissemination:

Scientific publications:

Martens EA**,** Wadhwa N, Jacobsen NS, Lindemann C, Andersen KH, Visser A. (2015) Size structures sensory hierarchy in ocean life. Proc. Royal Society B. 282: 20151346.
Significance and relevance: provides the physical reasoning behind size as a trait and modulator of senses in marine ecosystems.

Andersen KH, Berge T, Gonçalves RJ, Hartvig M, Heuschele J, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer AB, Olsson K, Palacz A, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T. (2016) Characteristic sizes of life in the oceans, from bacteria to whales. Annu. Rev. Mar. Sci., 8: 217-241.
Significance and relevance: provides the mechanistic underpinning of the size as a major trait in oceanic ecosystems.

Martens EA, Kiørboe T, Andersen KH. Effects of Seasonal Forcing on the Marine Trophic Chain (in preparation).
Significance and relevance: Provides an analytical understanding of the effect of seasonal forcing, depending on latitude, on population sizes along the trophic chain, depending on size as a key trait. This can be thought of as an extension to Sheldon's spectrum by introducing forcing on the trophic chain.

Martens EA, Thutupalli S, Fourrière A, Hallatschek O. (2013). Chimera States in Mechanical Oscillator Networks. Proc. Natl. Acad. Sci., 110(26), 10563–10567. doi:10.1073/pnas.1302880110
Part of previous employment work at the Max Planck Institute for Dynamics and Self-organization, Germany, has been finished during – and is thus affiliated with – my stay the Center for Ocean Life, which has resulted in a publication in the *Proc. National. Acad. Sciences.*

Presentations at conferences, seminars etc.:

Trait-based approaches to Ocean Life (International Workshop), Copenhagen, Aug 2013.
Poster: Trait-based modeling of trophic chains and seasonal forcing.

Trait-based approaches to Ocean Life (International Workshop), Copenhagen, Aug 2013.
Organization of speed talks.

6.22 Models for population dynamics in zooplankton

Sofia Piltz, Post Doc.
Employment period: 1 September 2014 – 31 August 2016
Working with: Ken Haste Andersen, Nicolas Azaña Schnedler-Meyer, Kasia Kenitz, Thomas Kiørboe, Patrizio Mariani, André Visser (DTU Aqua), and Jens Starke, Christopher Marschler (DTU Compute).

Background:

Phytoplankton are organisms that produce organic compounds from inorganic compounds and constitute the basis of the aquatic food web. They are responsible for roughly half of the Earth's net production of organic compounds and half of the Earth's carbon fixation. As phytoplankton and the zooplankton that graze upon them are the initial source of food for fish larvae, they play a crucial role in the population dynamics – that is, changes in the population size and composition, observed at higher levels of the food chain. According to the Food and Agriculture Organisation of the United Nations (FAO), world's fish production, of which 80 % is consumed by humans, is a globally important factor for ensuring food security and provides livelihood for more than 600 million people (The state of world fisheries and aquaculture, FAO, 2012). Despite the crucial importance of understanding the impact of climate change on aquatic ecosystems, there unfortunately remains much that is poorly understood. For example, recent scientific studies of large data sets have found contrasting trends in phytoplankton production in warmer seas. A recent study (Boyce et al., Nature 466 (2010)) documented a decline in phytoplankton production during the past century. Subsequent scientific communications (Mackas, Rykaczewski and Dunne, McQuatters-Gollop et al., Nature 472 (2011)) found contradictorily that primary production in the oceans had increased. As several components for bias in the data processing and analysing methods were identified, the disagreement was reported widely in the media (e.g. BBC, the New York Times) and reflects not only the importance of reliable long-term data collection but also the scientific insufficiency of relying only on descriptive studies without modelling of underlying mechanisms. As illustrated by the contradictory conclusions, merely finding a trend in a data set can lead to confusion rather than deep understanding of biological mechanisms and does not enable making predictions on how the situation would change under different future scenarios. Solving interdisciplinary challenges such as plankton population dynamics and climate change is important, especially when year 2013 was dedicated to the Mathematics of Planet Earth (http://mpe2013.org/), as a testament to the significance of mathematical models of biological processes. While looking at the data alone can give a description of the plankton dynamics, developing and analysing a mathematical model makes it possible to achieve a deep understanding of the mechanism behind the dynamics, which in turn can be used for estimating the consequences that changing environmental conditions have on plankton dynamics, and thereby on fish production, harmful algal blooms, biodiversity, and the Earth's carbon cycle, to mention only few.

Description of the project:

In this project, we use the mathematical framework of dynamical systems to study the mechanisms underlying plankton dynamics by constructing systems of differential equations. These equations describe the predator-prey interaction between both zooplankton predators feeding on phytoplankton prey and phytoplankton prey feeding on nutrients. By carrying out mathematical and computational analyses of the resulting systems of equations, we aim to gain insight into the underlying mechanisms of plankton observations in the presence of adaptivity, growth in body size, ecological trade-offs, and seasonality. Traditionally, differential-equation models for population dynamics have considered organisms as “fixed" entities in terms of their behaviour and characteristics, and ignored the physiological changes (e.g., growth in size) during their lifetime. However, there have been many observations of adaptivity in organisms, both at the level of behaviour and as an evolutionary change of *traits* (i.e., properties of an organism that can be measured from individuals and compared against measurements from individuals from other species), in response to environmental conditions. In addition, while many organisms (e.g., ciliates) undergo small physiological changes during their lifetime, some organisms (e.g., copepods) grow through a succession of developmental stages (e.g., egg -> nauplius -> copepodite -> adult) that span over several orders of magnitude in size. Taking adaptiveness and individual growth into account alters the qualitative dynamics of traditional models and is an important factor to be included, for example, when developing reliable model predictions under changing environmental conditions. In our first model, we consider the amount or population density of nutrients, phytoplankton, small zooplankton, and a large zooplankton. We take both juvenile and adult forms of the large zooplankton into account. We aim to provide an explanation for the observed coexistence of small zooplankton (e.g., ciliates) and large zooplankton (e.g., copepods) in the presence of seasonally varying light conditions that influence the phytoplankton growth and nutrient availability. Ultimately, our goal is to use this mechanistic understanding in constructing models with predictive power.

Dissemination of results:

Research visits:
University Centre in Svalbard (hosted by Øystein Varpe), Spitsbergen, Norway, Oct–Dec. 2014. Yggdrasil mobility programme (3 months individual grant) funded by the Research Council of Norway to work on modelling seasonality in predator-prey interaction and life strategies of zooplankton.

Planned scientific publications:
Coexistence of protists, small zooplankton, and stage-structured copepods in a seasonally varying environment. Expected date of submission: June 2015. Significance and relevance: Environmental conditions represented in terms of nutrient, light, and food availability that lead to the existence of copepods. This model can be later implemented in large ecosystem models.

Future presentations at conferences:
Invited talk: *Models for adaptive feeding and population dynamics in plankton*, Barcelona Mathematical Days, Congrés de la Societat Catalana de Matemàtiques, November 7-8 2014, Barcelona, Spain.

Invited minisymposium talk: *Are plankton discontinuous, smooth, or slow-fast (& furious)?* Society for Industrial and Applied Mathematics (SIAM) Conference on Applications of Dynamical Systems, May 17-21 2014, Snowbird, Utah, USA.

Planned outreach activity:
A popular dissemination on the activities of the research visit to University Centre in Svalbard in October-December 2014 through a similar program to Mathematics of Planet Earth (http://mpe2013.org/calendar/). We anticipate to encourage to establish new connections and strengthen the existing networks between biologists and applied mathematicians.

6.23 Trait-based approach to food-web interactions across environmental gradients

Kasia Kenitz, Post Doc.
Employment period: 1 October 2014 – 31 December 2016
Supervisors: Ken H. Andersen (DTU Aqua), Andre W. Visser (DTU Aqua)

Description of project:

A fundamental aim in plankton ecology is to understand the mechanisms that govern community structure and the effect of changing environments on interactions across trophic levels. Plankton communities are extremely diverse and a way to simplify this complexity is to summarize individual organisms by their key functional traits. The novelty of trait-based ecology lies in the assumption that an organism's fitness depends on its success in three fundamental life missions: feeding, survival and reproduction. Optimal traits that govern the relative success of these missions are determined by the environmental conditions experienced by the organism, and therefore they are expected to vary temporally and spatially.

At the initial stage of the project, we examined the role of seasonality of the physical environment in shaping plankton interactions and trait distribution. We characterized the seasonal succession of the plankton traits and their interactions using observations and model simulations of the plankton community in the western English Channel. We focused on activity traits that characterize the defensive and feeding ability of zooplankton and distinguish between low risk, low return ambush feeders and high risk, high return feeding-current feeders. While the phytoplankton succession depends on traits related to nutrient acquisition and photosynthesis, it also depends on grazing which couples feeding and motility traits across trophic guilds. Despite interannual variations in the species dominating the protist plankton community, the seasonal trait distribution revealed robust and repeatable seasonal patterns, changing between non-motile cells flourishing in spring and motile community dominating during summer. The zooplankton community was dominated by active feeding-current feeders with peak biomass in the late spring declining during summer. The model revealed how zooplankton grazing reinforces protist plankton seasonal succession and showed how the physical environment controls the vertical structure of plankton communities, where ambush feeders exhibited a preference for greater depths during summer. We characterized the seasonal succession as trophic trait coupling and conjecture that this coupling leads to a trophic trait cascade where successive trophic levels alternate in their expression of activity traits further up in the food chain (Fig. 1).

The analysis of trait distribution is currently being expanded by the spatial component. California Current system is a region characterized by steep environmental gradients and provides an ideal test case for the investigation of the impacts of environmental variability on the ecosystem functioning. We examine how the environment shapes ecosystem interactions by comparing contrasting provinces of the region: from nutrient-limited open ocean to the upwelling-dominated coast. Available plankton data include the size structured biomass of microzooplankton and macrozooplankton, with samples collected along two transects across the southern California Current system. Plankton taxa are characterized by their activity traits that are realized differently across trophic levels: for unicellular organisms we consider resource acquisition strategy and motility, for more complex organisms we characterize foraging mode, and for all we use size as a

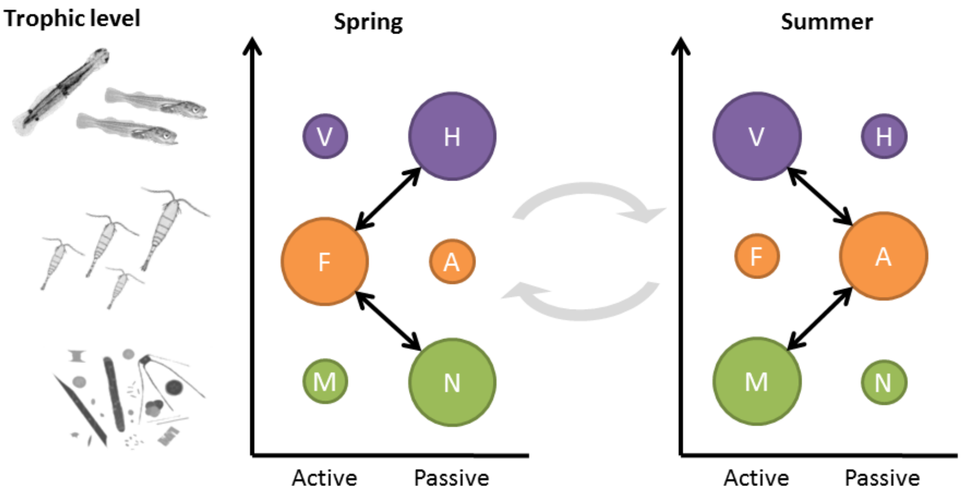


Fig. 1. Conceptual diagram illustrating seasonal selection for optimal traits and the trophic trait cascade. Traits are classified depending on the level of foraging activity, and are realized differently across distinct trophic levels: motile (M) and non-motile (N) protists, feeding-current feeding (F) and ambush feeding (A) zooplankton, and classification based on sensory traits for visual (V) and hydromechanical (H) predators from a higher trophic level. The dominant community axis (black arrows) indicates the dominant energy pathway and alternates between spring and summer with changing light, nutrient and turbulence conditions.

master trait. These traits affect interactions across the trophic levels by balancing feeding success and predatory risk, and their expression is closely linked to the physical environment.

Application of a theoretical model to compliment the data analysis is a key part allowing detailed testing of proposed mechanisms, and will be implemented during the next stage of the project.

Collaborations

The analysis of the plankton data from the California Current ecosystem (CCE) is conducted with collaborations with Prof. Mark Ohman and Prof. Mike Landry, managing the CCE Long Term Ecological Research (CCE-LTER) program at Scripps Institute of Oceanography (SIO), San Diego. The collaboration was established during a month-long visit to SIO as a Visiting Scholar in June 2016.

Research implications

The project advances the fundamental understanding of the processes controlling plankton community structure and functions. The study aims to provide a clear illustration of how environmental variability influences the optimal resource acquisition of protist plankton and feeding strategy of zooplankton, and how those traits interact across trophic levels. The analysis will provide a mechanistic underpinning for the shifts in plankton community composition observed in nature, with the main focus on food acquisition strategies, community size spectrum and interactions across multiple trophic levels.

Dissemination:

Scientific publications:

Kenitz, K., A.W. Visser, P. Mariani, K.H. Andersen (2016) Seasonal succession in zooplankton feeding traits reveals trophic trait cascade. Limnol Oceanogr *(accepted)*
Significance and relevance: proposes a view that the seasonal succession of species can be viewed in terms of seasonal succession of activity traits that acts to optimize species survival; further advances the understanding of mechanisms driving the seasonality of zooplankton feeding traits; introduces the concept of 'the trophic trait cascade', where activity traits are interrelated across trophic levels.

Kenitz, K., K.H. Andersen, T. Kiørboe, M.D. Ohman, M.R. Landry, A.W. Visser. Trait-based approach to food-web interactions across environmental gradients. *(in preparation)*
Significance and relevance: develops a novel trait-based approach for multi-trophic level analysis of observational data, spanning a range of organisms from bacteria to macrozooplankton; examines how the environment shapes ecosystem interactions by conducting the analysis along a spatial gradient, from nutrient-limited open ocean to the coastal upwelling zones.

Conference presentations:

Kenitz, K., P. Mariani, A.W. Visser, K.H. Andersen: "*Seasonal succession of copepods feeding traits.*" at the workshop for Trait-based Approaches to Ocean Life, Waterville Valley, NH, USA, 5–8 Oct 2015 (poster)

Kenitz, K., K.H. Andersen, P. Mariani, A.W. Visser: "*Vertical distribution of motile and non-motile phytoplankton and implications for optimal feeding mode of zooplankton.*" at Aquatic Sciences Meeting, Granada, Spain, 22–27 Feb 2015 (oral)

Future conference presentations:

Kenitz, K., K.H. Andersen, T. Kiørboe, M.D. Ohman, M.R. Landry, A.W. Visser: "*Trait-based approach to food-web interactions across environmental gradients.*" at Aquatic Sciences Meeting, Honolulu, Hawaii, 26 Feb – 3 Mar 2017 (Session: "006 - New Directions in Plankton Ecology")

6.24 Analysis of Trait-Based Models in Marine Ecosystems

Irene Heilmann, PhD student (75% position);
Employment period: 1 November 2012 – 31 July 2017
Supervisors: Mads Peter Sørensen (DTU Compute), Uffe Høgsbro Thygesen (DTU Aqua), Ken Haste Andersen (DTU Aqua) and Jens Starke (Institute of Mathematics, University of Rostock, Germany)

Description of project:

We have completed the part of this project pertaining to the investigation of a size-structured population model of a daphnia population feeding on an algae food resource. The response to a periodic variation in the food resource has been investigated for a physiologically structured population model. This problem is of particular interest for species living in the northern or southern hemisphere. For the case of self-induced internal oscillations in the population, external forcing close to the internal self-oscillating frequency can phase lock the dynamics of the population. The forcing is a time varying growth rate of the algae. Secondly, we found appearance of period two cycles where the daphnia population peaks every second year and similarly for period 4 cycles with population peaks every 4th year. Chaotic dynamics and bifurcation dynamics also appear (Ref. 1).

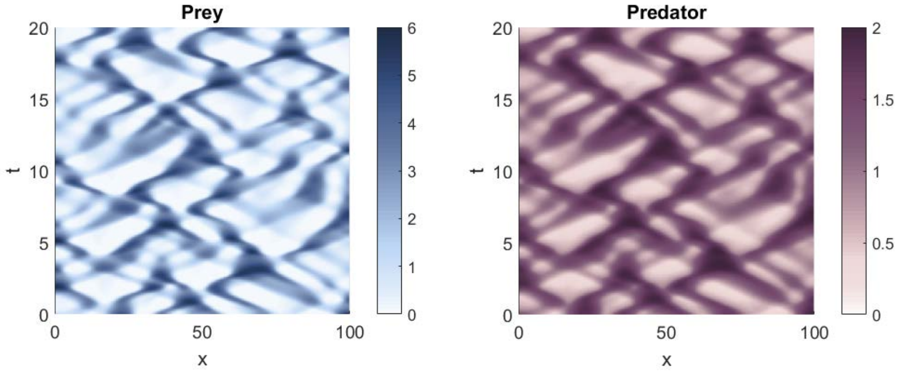


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Figure 4. Predator-prey model with fitness taxis, nonlocal hunting strategy and diffusive wandering of animal species. Birth and death rates are described by the Bazykin model, which couples the birth and death rates in a highly nonlinear fashion.

Currently, our focus is on predator-prey models of marine species adding fitness taxis leading to heterogeneity in the spatial pattern formation of the animal densities. Inspired by chemo taxis we have introduced fitness taxis where movements of species are in the direction of the spatial gradients of the specific growth rates. The animals move to places, where there are better conditions for growth and survival. To this is added diffusion of animal species, modeling random wandering. The highly nonlinear birth and death rates are described by the Bazykin model. A uniform and constant equilibrium solution exists for this model and stability analysis has revealed complex regions of instability of the equilibrium state. This in turn leads to highly complex pattern formation. A particular feature of the model is instability of high wavenumber perturbations, which eventually diverges. We refer to this as an ultraviolet catastrophe. It is linked to the fact that the model is local in the sense, that predators only hunt prey on point wise encounter, that is predator and prey are placed at the same spatial position.

Aims for the final part of the thesis project:
In order to prevent instability for high wavenumber disturbances in space, we have derived a nonlocal model, where the growth rate of predators at position x depends not only on the prey density at x, but depends on the prey density in a neighborhood of the predator. This is achieved by introducing a nonlocal predator growth rate through a suitably chosen integral over the prey density multiplied by a space dependent kernel. The kernel decrease as the distance from the predator increases. Biologically this is interpreted as the predators can search and hunt prey in a neighborhood of their positions. Stability analysis of this nonlocal model again reveals complex regions of instability. However, now growth of high wavenumber spatial disturbances leads to patterns with finite amplitudes in time and space without divergence. A thorough analysis of pattern formation and classification is conducted.

Outlook:
In the oceans currents are present leading to advection of animal species. To include advection is a main goal for future investigations of the fitness taxis and nonlocal model in the studies of the influence of advection on pattern forming density structures. Secondly, we wish to adopt the nonlocal fitness taxis model to marine data.

Dissemination:

Scientific publications:

[1] Heilmann I, Starke J, Andersen KH, Thygesen UH, Sørensen MP. (2016) Dynamics of a physiologically structured population in a time-varying environment. Ecological Complexity 28: 54-61.

[2] Heilmann I, Thygesen UH, et al. Nonlocal predator-prey models for marine species with fitness taxis. In preparation.

Significance and relevance: a) Provides mathematical methods applicable to a big class of problems within nonlinear applied mathematics in general and marine ecosystems in particular. b) Results give insight into the biological mechanisms of size-structured populations and their behavior under seasonal forcing of food resources. c) Classification of pattern formation in predator prey models with fitness taxis and nonlocal hunting strategies.

Presentations at conferences, seminars etc.: September 15, 2016, until February 15, 2017, the project on fitness taxis includes Astrid Helene Bro Christensen on the team. Astrid works on her master thesis project at DTU Compute entitled: *Fitness taxis in reaction diffusion systems.* Main supervisor: Mads Peter Sørensen, co-supervisors: Uffe Høgsbro Thygesen (DTU Aqua) and Jan Hesthaven (EPFL, Switzerland).

6.25 Trait ecology of plankton in a changing marine environment

Agnethe Nøhr Hansen, PhD student
Employment period: 15 December 2014 – 15th October 2018
Supervisors: André W. Visser (DTU Aqua), Ken Haste Andersen (DTU Aqua)

Description of project:

Living conditions in the oceans are changing as a response to climate change. This affects all lifeforms from the largest predators down to the simplest plankton cells. Like all other organisms a plankton cell needs to invest its energy resources in a manner to achieve the best fitness under the given environmental conditions. This raises several important questions on what traits to prioritize and fine-tune: What is an appropriate size? How efficient must light and nutrient harvesting be? Should energy be spent on rapid growth or defense mechanisms such as toxicity or a shell? And how does one trait exclude another; what are the trade-offs between different traits? The objective of this project is to investigate and model how in particular the traits of size, nutrient and light harvesting investment develop and distribute in a changing environment.

The ocean is a continually changing environment, light availability differs both spatially and temporally, turbulence and stratification depend on current atmospheric weather conditions and the nutrient availability is regulated by both biologic and physical processes in the water column. The size of an organism is an important trait that can regulate how cells react to changes in stratification and turbulence. Stronger stratification and deeper mixed layers are predicted as a response to climate change, resulting from increasing temperatures and more frequent extreme wind events. The more mixed conditions will make it easier for large cells to stay floating in the water column. The traits of nutrient and light harvesting are essential and these two mechanisms are good indicators of competitive ability of the species in most parts of the ocean, why they are obvious to include when examining plankton traits.

The investigation of the traits will be conducted using a mechanistic modeling approach that develops in three stages:

A trait model that includes the traits and trade-offs concerning size, nutrients and light harvesting investments in a phytoplankton cell. This model is based on an earlier model (Bruggeman and Kooijman, 2007) that only takes into account the traits of nutrient and light harvesting investments, but it will be expanded with the trait of size. The underlying assumptions on the trade-offs that drive the fine-tuning of the traits will instead of the rather complicated approach used by Bruggeman and Kooijman (2007) be modeled by a simpler mechanistic approach. In addition, trade-offs like photo harvesting repair (as a trade-off for light harvesting investment) and antiviral defense (as a trade-off for nutrient harvesting investment) will be included in the trade-off model.

A physical model which is a one dimensional water column model tuned for the North Sea/ the English Channel. This model acts as the physical setting within which the trait model will run. This model is based on a General Ocean Turbulence Model and will provide estimated seasonal cycles of stratification, light, nutrient distributions and turbulence. The physical model represent the environment that regulates the abundance of the different trait combinations and the trade-offs.

A climate model that provides artificial information on light, nutrient, turbulence and stratification from a specific point in the North Sea from today and from a future scenario e.g. year 2100. This data is generated by OGCM's for example at DMI, where they have large models that generate predictions of the physical conditions in the oceans.

When forcing the trait model with the physical model the actual abundance of a certain trait combination will be a function that depends only on the traits (and the hind laying trade-offs) and the environment. In this way a mechanistic model is created that directly links the trait space and the abundance of the traits, i.e. it predicts the appearance and abundance of traits only from knowledge on physical parameters in the environment. This gives the possibility to move the model into a scenario of predicted future conditions from the climate model, where the respond of the plankton community can be assessed. The trait ecology will in this manner be investigated both in a seasonally changing environment, but also consequences of long term changes will be included.

Dissemination:

Scientific publications:

4 publications where the first is based on earlier finished work and 3 directly related to the project milestones set out in the project plan:

Hansen, AN, & Visser, A. W. (2016). Carbon export by vertically migrating zooplankton. Limnology and Oceanography, 61(2), 701–710. doi:10.1002/lno.10249
Significance and relevance: Presents a model of vertical migrating zooplankton based on optimal behavior, and provides a trait based estimate of the active transport of carbon to the deep ocean by migrating plankton.

Hansen AN, Visser AW, Size, Nutrient and Light Harvesting Traits of Plankton; a Mechanistic Trait and Trade-off Approach.
Significance and relevance: Provides the theoretical rationale for a trait-based model of phytoplankton; how they should optimize the allocation of resources to light and nutrient harvesting, and how they are related to cell size.

Hansen AN, Visser AW, Andersen KH, Kenitz KM. Plankton Trait Ecology in the English Channel; Validation of a Mechanistic Trait and Trade-off Model.
Significance and relevance: Provides a comparison and analysis of the trait-based plankton model against a long time series of observations in the English Channel.

Hansen AN, Visser AW, Andersen KH, Kenitz KM. Plankton Trait Ecology in a Modeled Future Ocean.
Significance and relevance: Provides a comparison of size, nutrient and light harvesting traits in today's ocean against a modeled future ocean in order to assess differences.

References:

Bruggeman J, Kooijman SALM (2007) A biodiversity-inspired approach to aquatic ecosystem modeling. Limnology and Oceanography, 52(4):1533--1544.

6.26 Past and future changes in functional trait diversity

Anna Törnroos, visiting Postdoctoral researcher (August 2014 – December 2017), Maternity leave: 26.2-5.12.2016.
Supervisors: Martin Lindegren, Brian MacKenzie and Ken Haste Andersen (DTU Aqua) as well as Erik Bonsdorff (Åbo Akademi University)

Description of project:

A need to move beyond species richness in understanding patterns and changes of biodiversity has lead to the inclusion of functional diversity in ecological studies. Functional diversity refers to the range, degree and distribution of traits among species in communities and ecosystems. Utilizing multiple traits linked to specific ecosystem functions (such as production and biogeochemical cycling) has proven a successful method for assessing functioning over spatial scales. However, less is known about the temporal variability of functional diversity, which is particularly important if we are to predict future changes in ecosystems.

Within this project past and future changes of functional structure and diversity under various environmental and anthropogenic drivers are studied on a community level. The aim is to assess this on multiple trophic levels and thus, focus on the major taxonomic and trophic groups: benthic invertebrates, fish, zoo- and phytoplankton. In this project, the Baltic Sea is used as a case study area, because of its natural environmental and diversity gradients, a well-known biology and ecological history as well as availability of long-term data series.

The project consists of the following parts i) compilation of quantitative time series data (1970-present) and trait information on benthos, fish, zoo- and phytoplankton, as well as environmental variables (completed, manuscript in prep), ii) assessment of past variability in trait expression and functional diversity in the different taxonomic groups using statistical models (completed, manuscript in prep), iii) application of climate models to project future changes in functional (trait) diversity (2017).

Dissemination:

Two scientific publications are planned within the project above:

Törnroos A., Olsson J., Gårdmark A., Pécuchet L., Blomqvist M., Lindegren M., Bonsdorff E. *Long-term functional trends in Baltic Sea coastal macrofauna and fish* (January 2017)

Törnroos et al. Future predictions of functional diversity under different climate scenarios.(December 2017).

Scientific publications (two from previous project and one paper relating to this project outputs)*:*

Pedersen M.W., Kokkalis A., Bardarson H. Bonanomi S., Boonstra W.J., Butler W., Diekert F.K., Fouzai N., Holma M., Holt R.E., Kvile K.Ø, Nieminen E., Ottosen K.M., Richter A., Rogers L.A., Romagnoni G., Snickars M. Törnroos A., Weigel B., Whittington J.D., Woods P., Yletyinen J., Ferreira ASA. (2015) *Trends in marine climate change research in the Nordic region since the first IPCC report.* Climate change 134:147-161

Pecuchet L., Törnroos A., Lindegren M. (2016) Patterns and drivers of fish community assembly in a large marine ecosystem. Mar. Ecol. Prog. Ser. 546:239-248.

Törnroos A, Nordström MC, Aarnio K, Bonsdorff E. Environmental context drives trophic trait variability in a key species, the tellinid clam *Macoma balthica* L. J. Ecol. Mar. Biol. Ecol. 472:32-40.

Scientific presentations:

Törnroos A. 2016. Introduction to trait modelling. The Ocean's Seafloor – One Bio-Geo System. (12-14.10.2016, Hannover, Germany).

Törnroos A. 2016. *Describing key traits and trade-offs of marine benthos: towards a mechanistic trait-based approach.* Trait-based approaches to Ocean Life, an international workshop (Waterville Valley Resort, New Hampshire, USA 5 8.10, poster).

Törnroos A., Olsson J., Gårdmark A., Pécuchet L., Blomqvist M., Lindegren M., Bonsdorff E. *Long-term functional trends in Baltic Sea coastal macrofauna and fish.* ICES Annual Science Conference (21-25.9.2015, Copenhagen, Denmark).

Törnroos A., Bonsdorff E. *Interpreting ecological functioning in coastal waters: spatial and temporal trait patterns across the Baltic Sea.* 10th Baltic Sea Science Congress, BSSC (Riga, Latvia, 15-19.6.2015).

Törnroos A., Multiple traits and benthic functioning: from toolbox to application in a system rich in functions but poor in species. Invited speaker (Oral presentation), International workshop on Trait-based approaches to Ocean Life, (August 2013 Copenhagen).

Outreach and other activities:

Popular science article: Törnroos A. 2016. Høj funktionel rigdom trods få arter i Østersøen. Aktuel Naturvidenskab 1: 16-19.

Popular science Blog under the BONUS project site:
"Baltic Diversity Notes" (http://www.bonusprojects.org/bonusprojects/blogs/baltic_diversity_notes)

Invited talk: Törnroos A. Fish - more than just food? Their functional roles, diversity and long-term trends in the Baltic Sea. FishBase Symposium- The Baltic Sea (17.10.2016 Stockholm, Sweden)

Invited guest lecturer at Roskilde University, 3 November 2014: Analysing functional aspects of benthic communities: a trait-based approach.

6.27 Trait based models of marine primary production

Subhendu Chakraborty, Post Doc.
Employment period: 1 November 2014 – 31 December 2017
Supervisors: Ken Haste Andersen (DTU Aqua)

Description of project:

The appearance of the "trait-based" approach to model plankton dynamics promised a deliverance from the "curse of dimensionality" by replacing discrete functional groups with a structuring around continuous trait-distributions. Centered on the concept of functional traits, the trait-based approach is essentially a marriage between a classic NPZ model and "cost-benefit" type of models. As an example, consider the allocation to chloroplast as a trait. Investing in chloroplasts leads to a higher photosynthetic rate. This investment though, comes with costs in terms of resources (nutrients, carbon) needed to synthesize the chloroplasts and fuel their maintenance; resources that may otherwise have been invested in other traits (e.g. affinity for nutrient, food). The advantage and the costs (investment, maintenance and reduced function elsewhere) constitute the trade-off associated with the trait. Similar considerations can be made for traits related to dissolved nutrient uptake, feeding (phagotrophy), investment into defense, cell-size, temperature, and resistance to pathogens.

On the other hand, the size of an individual organism is another important key trait describing individual physiology across major taxa through power-law functions: metabolism, leading to the celebrated ¾ law for the scaling of resting metabolism with size, population growth rates, predator-prey relationships in terms of functional response and predator-prey ratios, fluid-mechanical forces, swimming speed, vision, diffusive uptake affinities and, for phytoplankton, affinities for photosynthesis and maximum uptake rates. Size has also been used to describe macro-ecological patterns of size-dependent species diversity and the "size spectrum" describing the biomass distribution of individuals as a function of size across major taxa has been explained theoretically using the size relationships describing individual physiology. Using size one can develop a single universal theory or empiric relation that covers all life, though some recognize differences between major taxa.

The main objective of the project is to investigate how characteristic sizes of plankton affect vital rates of individuals and finally the whole community. The effects of different environmental conditions will also be observed. The project implements models representing unicellular organisms that can take up carbon from photosynthesis, dissolved nutrients by diffusion feeding and organic carbon and nutrients by phagocytosis on other organisms. The organisms' ability to perform these uptakes (the affinities) are determined by investment in organelles associated with each function, and described by traits. Moreover, being another vital trait, size of an individual affects affinities for different resources, maximum uptake rates, and mortality. In accordance with the central idea in trait-based modelling, functional groups are thus neglected, i.e., the traditional distinction between phytoplankton (plants) and heterotrophs zooplankton (animals) are discarded. Here, the model structure allows for a range of mixotrophic strategies from autotrophy to heterotrophy; and realized trophic strategy then becomes an emerging property of the model. After considering the trade-offs, the model constitutes a mechanistic approach to derive the vital rates of the individual cell. Finally, embedding these descriptions in a dynamical model of the resource and the consumer structured by the trait, it would be possible to simulate the trait-space of the phytoplankton community throughout the seasonal succession. The actual parameters governing the processes within the community are therefore not prescribed *a priori*, but are emergent outcome, which depends on the environmental forcing and the outcome of competition.

Results:

First we have formulated a trait-based model for mixotrophy with three key resource-harvesting traits: photosynthesis, phagotrophy and inorganic nutrient uptake, which predicts the trophic strategy of species throughout the seasonal cycle [1]. Assuming that simple carbohydrates from photosynthesis fuel respiration, and feeding primarily provides building blocks for growth, the model reproduces the observed light-dependent ingestion rates and species-specific growth rates with and without prey from the laboratory. The combination of traits yielding the highest growth rate suggests high investments in photosynthesis and inorganic nutrient uptake in the spring and increased phagotrophy during the summer, reflecting general seasonal succession patterns of temperate waters. This novel model presents a simple and general approach for the inclusion of mixotrophy, succession and evolution in ecosystem models.

Further, we have shown that how optimal trophic strategies depend on cell size under various environmental conditions, including seasonal succession [2]. We identify two mixotrophic strategies: ‘generalist mixotrophs’ investing in all three investment-traits and ‘obligate mixotrophs’ investing only in phototrophy and phagotrophy. We formulate two conjectures: 1) most cells are limited by organic carbon, however, small unicellulars are co-limited by organic carbon and nutrients, and only large photoautotrophs and smaller mixotrophs are nutrient limited; 2) trophic strategy is bottom-up selected by the environment, while optimal size is top-down selected by predation. The focus on cell size and trophic strategies facilitates general insights into the strategies of a broad class of organisms in the size range from micro-meters to millimeters which dominate the primary and secondary production of the world’s oceans.

Ongoing scientific work:

We have several manuscripts in preparation. Currently we are exploring how trophic strategies mentioned earlier interact in a fully dynamical model. In the new model, competition and predator-prey interactions are represented explicitly. Moreover, this model also embraces the feedbacks between food availability and optimal strategies, since they undoubtedly influence each other. We expect to achieve richer and more complex results, along with the general result – optimal trophic strategies shift with body size. Our aim is to present the size-based trade-offs as the hidden keys to understand the rich variety of trophic strategies proliferating among unicellular plankton, from pure phototrophs to pure heterotrophs. We have two different aims with this dynamic model: (1) The organisms in our model are able to instantaneously adjust their investments in different resource harvesting strategies to maximize their fitness depending on the environmental conditions. However, these kinds of problems are generally dealt with using models based on adaptive dynamics. Complex adaptive dynamics models involve a huge number of parameters and equations and make the computation expensive. In contrast, our model based on instantaneous adjustment in investments requires less number of parameters and equations and thus computation becomes easier. Here, we aim to compute both the systems under seasonal variation of light and some other environmental factors in a 1D water column to investigate how much accurate information can be provided from our approach compared to the model based on adaptive dynamics [3]. (2) Furthermore, we would like to compare our modelling results with real data obtained from station

L4 [4]. In this case we aim to compare how trophic strategies of different size classes of plankton change with seasonal variation and compare with the information obtained from data.

Apart from the main project, I am also involved in a project related to the annual routines of marine organisms that are organized around the seasonal variation of resource availability [5]. Here we seek to find and understand patterns in the various seasonality traits – e.g. migration, dormancy, reserves, resting stages – by which organisms contend with these annual cycles of feast and famine. A series of simple life history models are formed for the hypotheses that are tested against a large assemblage of observations reported in the literature. The main aim is to investigate how body size, intensity and duration of seasonal highs and lows, and trophic level are related to seasonal trait patterns. Specifically, we are looking at how the reserves (percent lipid weight) stored by marine organisms are related to latitudinal variation, seasonal amplitude and body size.

I am also involved in a project where we are investigating the seasonal succession between non-toxic and toxin producing phytoplankton [6]. Here the ability to produce toxin is considered as a trait. Investing in toxin production reduces mortality from grazing. However, toxin production comes with a cost in terms of resources (nitrogen, carbon) needed to synthesize toxin and maintenance of the corresponding machineries. The advantage and the costs constitute the trade-off associated with the trait. Here we aim to investigate the environmental conditions under which toxin production becomes useful and how it promotes the seasonal succession between non-toxin and toxin producing phytoplankton.

Dissemination:

Scientific publications:

Published:

[1] Berge T, Chakraborty S, Hansen PJ, Andersen K (2016) Modeling succession of key resource harvesting traits of mixotrophic plankton populations. *ISME Journal*, (published online), doi: 10.1038/ismej.2016.92.
Significance and relevance: Provides general seasonal succession patterns of trophic strategies in temperate waters. Important for the understanding of how trophic strategy changes at different environmental conditions.

[2] Chakraborty S, Nielsen LT, Andersen K (accepted) Trophic strategies of unicellular plankton. American Naturalist.
Significance and relevance: Provides optimal trophic strategies depending on cell size under various environmental conditions, including seasonal succession. Important for the understanding of how trophic strategy changes with the size of unicellular planktonic organisms at different environmental conditions.

Planned:

[3] Chakraborty S, Andersen K. A new approach to trait-based plankton modelling.
Significance and relevance: This is completely a new approach to trait-based plankton modelling. This approach will save lots of time involved in computation especially when one would like to model real world scenarios involving several variables.

[4] Chakraborty S, Bruggeman J, Andersen K. Seasonal succession of unicellular plankton organisms in station L4.
Significance and relevance: Succession of planktonic organisms occur in both size and trophic strategies. We will compare our model outcome with the data available from station L4.

[5] Visser AW, Brun PG, Jonasdottir SH, van Denderen PD, Nielsen LT, Pancic M, Chakraborty S, Thygesen UH, Heilmann I, Kenitz K, Dencker TS, Pécuchet L, van Gemert R, Schnedler-Meyer NA, Holm MW, van Someren Gréve H, Mariani P, Payne M, Kiørboe T, Törnroos A, Andersen KH. Traits and trade-offs of seasonal strategies in the marine environment.
Significance and relevance: The study is devoted to understand patterns in the various seasonality traits – e.g. migration, dormancy, reserves, resting stages – by which organisms contend with these annual cycles of feast and famine..

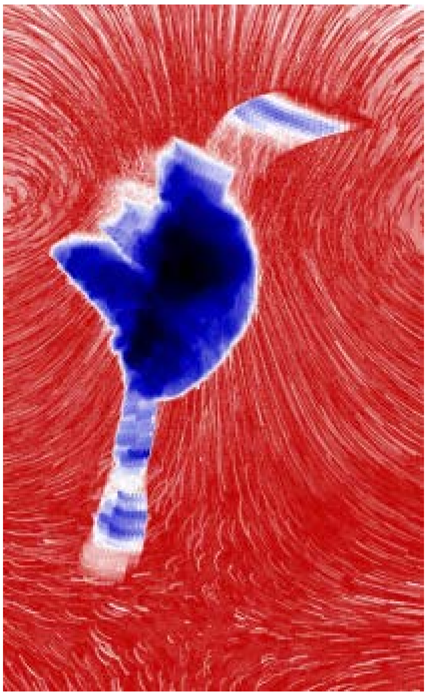
[6] Chakraborty S, Pancic M, Andersen KH. Seasonal succession of toxin and non-toxic dinoflagellates.
Significance and relevance: Generally, spring and autumn are dominated by non-toxic phytoplankton whereas nutrient deplete summer conditions are favourable for some toxic phytoplankton. We try to find the main factor that drives such seasonal succession pattern.

Presentations at conferences, seminars etc.:

Chakraborty S, Nielsen LT, Andersen K (5-8 October 2015) Correlation between organism size and trophic strategies. International conference on “Trait-based approaches to ocean life”, Waterville Valley, New Hampshire, USA.

6.28 Prey detection and capture in zooplankton

Rodrigo J. Gonçalves, visiting scientist
Stay period: 23 May 2012 - 20 May 2014
Supervisor: Thomas Kiørboe (DTU Aqua)



Description of project:

One of the most important groups within zooplankton is that of feeding-current feeding copepods, which capture prey entrained in a microcurrent generated by their feeding appendages. These appendages move so quickly that it's been traditionally hard to quantify, leaving place for different interpretations of their feeding mechanisms (ie during many years copepods were considered as passive filter feeders). Pioneer studies using high-speed cinematography (ie film cameras) yielded initial observations which changed this notion. Now it's accepted that copepods can manipulate their prey in not-so-simple behavior which results in sometimes highly selective feeding. However those first reports also spread notions which were not always supported by extensive and conclusive evidence, for example long-distance chemodetection of prey. It is well known that copepods have a preferred size range of prey, but this has not been well explained once the passive filter idea was discarded.

We use well-established techniques (ie. high-speed videography and digital image particle velocimetry) but with newer technology to shed light into details of particle detection, capture and handling in feeding-current feeding zooplankton using the copepod *Temora longicornis* as model organism. We combine these high temporal- and spatial-resolution observations with traditional feeding experiments to obtain a mechanistic description of the feeding patterns of this species.

Dissemination:

Scientific publications:

Gonçalves RJ, van Someren Gréve H, Couespel D, Kiørboe T. (2014) Mechanisms of prey size selection in a suspension feeding copepod, *Temora longicornis*. Marine Ecology Progress Series 517: 61-74.
Significance and relevance: Provides a mechanistic description of size range of food in the copepod *T. longicornis* based in prey detection and capture combining individual observations of feeding events and traditional feeding experiments.

Andersen KH, Berge T, Goncalves R, Hartvig M, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer A, Olsson K, Payne M, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N,

Kiørboe T. (2016) Characteristic sizes of life in the oceans - from bacteria to whales. Annual Review in Marine Science 8: 217-241.
Significance and relevance: Provides a comprehensive explanation for the emergence of traits and general relationship as a function of size across the full marine animal kingdom.

Gonçalves RJ, Hylander S (2013) Marine copepods and solar radiation. In: Seuront, L. (ed). Copepods: Diversity, Habitat and Behavior. Nova Science Publishers, USA.
Significance and relevance: Provides a review of current knowledge of effects of solar ultraviolet radiation on marine copepods, and the gaps to consider in future studies.

Kiørboe T, Jiang H, Gonçalves RJ, Nielsen LT, Wadhwa N (2014) Flow disturbances generated by feeding and swimming zooplankton. Proceedings of the Natural Academy of Sciences of USA 111(32):11738-11743.
Significance and relevance: Shows two different mechanisms of feeding-swimming in zooplankton which account for a tradeoff between risks of being detected by rheotactic predators and energy gain from feeding.

Presentations at conferences, seminars etc.:

Andersen KH, Berge T, Goncalves R, Hartvig M, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer A, Olsson K, Payne M, Prowe F, Sainmont J, Traving SJ, Visser AW, Wadhwa N, Kiørboe T. Characteristic sizes of life in the oceans - from bacteria to whales. International workshop on Trait-based approaches to Ocean Life, 2013, Copenhagen. Conference abstract for conference

Hylander S, Sylvander P, Gonçalves RJ, Friis Møller L, Kiørboe T, Leijonmalm PS. 2013. Deficiency syndromes in Baltic Sea top predators and the importance of zooplankton as producers of vitamins and pigments. ASLO Ocean Sciences Meeting. Honolulu, Hawaii, Feb 23-28, 2014 – talk

Kiørboe T, Gonçalves RJ. Detecting the algae: how copepods detect their prey. ASLO Aquatic Sciences Meeting, Granada, Spain. Feb 22-27, 2015 – talk

Gonçalves RJ, van Someren Gréve H, Kiørboe T. Prey capture and food size spectra in a current-feeding copepod. International workshop on Trait-based approaches to Ocean Life, 2013, Copenhagen. Poster

6.29 Marine Ecosystem Climate Services - Forecasting the marine biological environment

Anna Katharina Miesner, PhD student
Employment period: 1 September 2016 - 31 August 2020
Supervisors: Mark R. Payne and Brian MacKenzie (DTU Aqua)

Description of project:

The PhD in “Marine-Ecosystem Climate Services” will build on top of the tremendous advances in observing and modelling of the ocean that have occurred in recent decades: today it is possible to make accurate forecasts of physical oceanographic variables, such as temperature and salinity, several years into the future. However, the next step of converting these forecasts of the physical environment into forecasts of the biological environment, and therefore into variables that are directly relevant for stakeholders and society has yet to be taken. Developing these so-called “climate services” for marine ecosystems represents one of the new challenges in marine science.

The PhD project will conduct research with an aim of developing predictions of marine ecosystem parameters on a seasonal to decadal scale. Appropriate biological models relating physical and biological variables will be identified and/or developed within the project, coupled to existing seasonal and decadal forecast systems, and their skill assessed.

Previous studies have shown that changes in the spatial distribution of spawning of blue whiting are associated with changes in the North Atlantic sub-polar gyre, which alters water masses and thus the marine climate in blue whiting’s spawning region (Hátún et al. 2009). This reliance on physical cues can lead to extensive shifts in spawning distributions in time and space, creating problems for both the monitoring and management of blue whiting. Understanding of the underlying mechanisms at the local and individual level is limited, however. The first project of my PhD, will aim at understanding the underlying mechanisms behind the changes in blue whiting’s spawning distribution.
Based on this knowledge it will then be assessed whether it is possible to predict the spawning distribution of blue whiting passed on the physical conditions (i.e. temperature and salinity) in their spawning region, which could be used to enhance the management and annual design and execution of scientific monitoring surveys of this species.

However, models are only simple approximations of complex reality (Anderson 2008, Zuur et al. 2010) and moreover uncertainty present in physical climate models can propagate into ecological models (Payne et al., 2015). Accordingly, there is an inherent risk associated with forecasting, that needs to be evaluated in order to assure the quality of biological forecast. While a comprehensive assessment of model as well as forecast skill requires more than one verification metric (Stow et al. 2009, Jolliffe and Stephenson 2012, Matei et al. 2012), there is no common protocol for estimating the skill of forecasts of the biological environment, yet.
Therefore, building on the knowledge of forecast validation metrics used i.a. in meteorology and physical oceanography a review of statistical tools relevant in assessing the quality of forecasts of marine ecosystem variable and their forecast horizon will be carried out. This literature review will illustrate these statistical metrics with examples where these are successfully applied in the context of fisheries oceanography, such as forecasts of fish distribution or productivity (recruitment).

Dissemination:

Scientific publications:

At least 3 publications directly related to the project are planned.

Presentations:

Miesner A.K., Payne, M. R. Forecasting the spawning distribution of blue whiting (Micromesistius poutassou). ICES Annual Science Conference, Riga 19-23 September 2016

6.30 Functional trait biogeography of fish: linking traits, environment and ecosystem functioning

Esther Beukhof, PhD student
Employment period: March 2016 – March 2019
Supervisors: Martin Lindegren and Ken Haste Andersen (DTU Aqua)

Description of project:

Marine ecosystems are exposed to both environmental and anthropogenic stressors, e.g. climate change and fishing, leading to concerns about the influence of such stressors on ecosystem processes, goods and services. Traditionally, fisheries management has focused on single species and populations. However, more emphasis is now put on developing management tools that can aid in assessing whole fish communities and their relation to ecosystem functioning. Trait-based approaches are a promising way to increase our understanding of fish community dynamics. Functional traits related to size, growth, diet and reproduction are believed to hold information on how organisms will respond to change and will impact ecosystems with regards to ecosystem functions, e.g. food web dynamics, productivity and fisheries yield. Therefore, the main aim of my PhD is to gain insight into the spatial and temporal distribution of functional traits in marine fish communities around the globe, and relate them to ecosystem functioning. By collecting and combining data of fish species distributions, fish traits, environmental conditions and ecosystem functions, relationships between them will be tested through statistical modelling.

Current projects

My first project focuses on the North Sea fish community. By using international survey data I investigated the spatio-temporal patterns of several traits of fish to see how and if these trends are related to environmental and anthropogenic drivers. I calculated community mean traits weighted by their biomass and found that most of them had strongly declined during the last three decades. Declines were most strongly in the central western North Sea, whereas in other areas no significant change in community traits seems to have occurred. The trait patterns showed relationships with environmental variables such as annual variability in temperature and phytoplankton biomass, depth and salinity. Fishing effort was of lesser importance, revealing that the fish community as a whole is not impacted as strongly as individual targeted populations by fishing.

The first project has given me some initial understanding of how traits of fish at the community relate to their environment. In my second project, I will elaborate on these trait-environment relationships by exploring them on a larger scale. I will make use of a dataset of European fish communities – ranging from Greenland and Iceland to the Mediterranean – which has been collected by Laurène Pécuchet and her collaborators. I started a collaboration with Romain Frelat from University of Hamburg to analyze the data using two novel approaches (RLQ and fourth-corner analysis) that can link traits and environment through information on the spatial distribution of species. We expect our work will result in the first general trait-environment relationships for marine fish. A recently set collaboration with Malin Pinsky from Rutgers State University will expand our dataset to North American waters. We could then explore to what extent the trait-environment relationships we have found in the East Atlantic also hold in waters of the West Atlantic and the Eastern North Pacific.

Future projects

A third will build on the understanding of trait-environment relationships gained from Project I and II. The goal is to investigate how community means of fish traits are spatially distributed across the globe. Trait values for species present in a global Aquamaps database will be collected together with environmental variables (e.g. temperature) that match up with the resolution of the fish species occurrence data. First, community weighted means of the traits will be calculated for each site. Next, regression models will be constructed to relate the community weighted mean traits to the environmental variables. Once the best model for each trait has been selected, global environmental data can be inserted in the model equations to calculate community weighted means across the Earth's oceans. These results can then be plotted to generate global maps of community mean fish traits.

The final project will investigate the link between functional traits of fish and ecosystem functioning. A thorough literature study will be done on existing information on functional traits of fish, ecosystem functions to which fish contribute and the potential links between traits and ecosystem functioning. Once a coherent set of functional traits has been chosen and hypotheses have been made on links between traits and ecosystem functions, a study area will be selected for which the following data exist or can be collected:

- Time series of species abundances with corresponding trait values
- Time series of environmental variables that are linked to functional response traits
- Time series of an ecosystem function(s)

An appropriate statistical model will be chosen to model the ecosystem function data by the community mean traits and environmental variables. The model output will be evaluated to compare the strength of the relationships between traits, environmental variables and the ecosystem function. This will shed light on the importance of functional trait diversity of fish on ecosystem functioning – knowledge that is presently lacking.

Dissemination:

Planned papers:

Beukhof ED, Dencker T, Pécuchet L and Lindegren M. Spatio-temporal patterns and drivers of the North Sea demersal fish community: a trait-based approach
Significance and relevance: 1) investigates both spatial and temporal patterns of community traits of a fish community; 2) gives new insights into the structure of the North Sea fish community in terms of traits rather than species; 3) it demonstrates which traits of marine fish respond most strongly to environmental and anthropogenic stressors.

Beukhof ED, Frelat R, Pécuchet L, Möllmann C and Lindegren M. Exploring trait-environment relationships in European and North American marine fish communities.
Significance and relevance: provides general trait-environment relationships for marine fish using a unique large scale datasets, and tries to identify mechanisms between how fish respond to the environment in terms of their traits.

Beukhof ED et al. Trait biogeography of marine fish.
Significance and relevance: attempts to demonstrate how traits of fish are distributed around the globe.

Beukhof ED et al. Linking functional traits of marine fish to ecosystem functioning.
Significance and relevance: attempts to identify if traits of fish can be linked to one or several ecosystem functions to which fish contribute. This knowledge will aid the identification of functional traits of fish that can be used in studying biodiversity and ecosystem functioning relationships.

Presentations at conferences:

Beukhof ED, Dencker T, Pécuchet L and Lindegren M. Spatio-temporal changes in life-history traits of the North Sea fish community under climate change and fishing. ICES Annual Science Conference, Riga, 2016.

6.31 Parallel pathways of energy in marine ecosystems

P. Daniel van Denderen, Post Doc.
Employment period: 5 October 2015 – 31 December 2017
Supervisors: Martin Lindegren (DTU Aqua) and Ken H. Andersen (DTU Aqua).

Description of project:

Marine systems support global food security through fisheries. Marine fish and fisheries production varies largely between ecosystems in the world. Most of the ocean primary production occurs only in the surface pelagic layer. Yet sufficient carbon reaches the benthos via sinking and other downward transport processes to support high benthic and fish production in some regions. The proportion of primary production which reaches the benthos varies latitudinally and bathymetrically throughout the global ocean, and this variation determines whether local fish communities are dominated by benthic or pelagic fish biomass (see Fig. 1). The **main goal** of this project is to assess these differences in the structure of fish communities and fish production along the pelagic and benthic energy pathway.

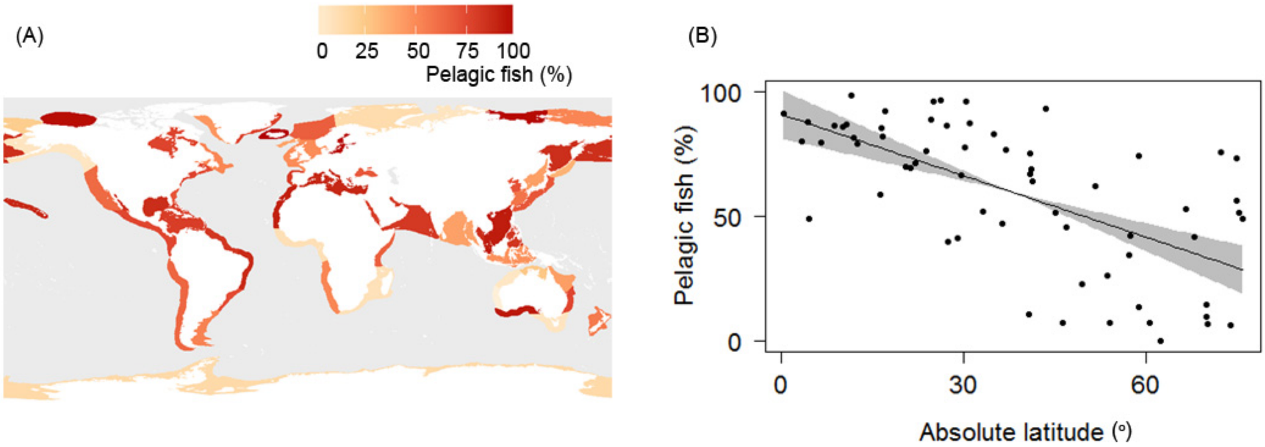


Fig. 1 Preliminary analysis of fisheries catches from 63 large marine ecosystems showing the proportion (in %) of pelagic fish compared to fish that (partly) rely on the benthic pathway for feeding in the catch (a) on a map and (b) across absolute latitude. The proportion of pelagic fish in the fisheries data is much higher in tropical areas than in polar and temperate regions, suggesting structural differences in the flow of energy to fish across latitude.

Results

Patterns in the productivity of the pelagic and benthic fish component of marine systems were studied using global empirical data of fisheries landings, stock-assessments and fish surveys. Fish was classified into different size-classes and feeding strategies and spatial patterns in fish communities (following Fig. 1) were related to predicted fluxes of energy in the pelagic and benthic pathway. The results show that a large part of the variation in the relative productivity of pelagic and demersal fish (especially large predatory fish) can be explained by latitudinal differences in the fraction of net primary production that sinks out of the photic zone and to the seabed. The amount of large fish species within the pelagic zone is higher in tropic-subtropical regions where the proportion of primary production retained in the surface layer is high, than in boreal-temperate regions, where large fish biomass is concentrated in benthic-feeding fish species. Using a food-web model that incorporates region-specific fluxes of energy to the seabed, we make the case that the observed patterns in large predatory fish correspond to a classical generalist-specialist interaction, where a low benthic channel favors large pelagic species, while an equal productivity of pelagic and benthic resources favors large demersal generalists, which then outcompete large pelagic specialists. This highlights that the dominant feeding strategy of marine fish predators is largely determined by the difference in inflow of energy at the base of the pelagic and benthic food web. Our understanding of these biogeographic patterns in fish communities in response to primary production variability can be used to characterize the structure of fish communities and their production across global ecosystems.

Ongoing scientific work

Coming year, I will continue to examine how the structure of fish communities varies across ecosystems with different strengths of the pelagic and benthic energy pathway. I will do this using a fish community model developed within the Centre for Ocean Life. The model will be used to investigate the emergence of fish communities, by allowing fish to invade from a small population density, across ecosystems with different structures of energy fluxes. The model will also be used to assess how exploitation by fisheries affects fish communities with differently structured energetic pathways.

Dissemination:

Scientific publications:

van Denderen PD, Rijnsdorp AD, van Kooten T. (2016) Using marine reserves to manage impact of bottom trawl fisheries requires consideration of benthic food-web interactions. Ecological Applications 26 (7): 2302-2310

Significance and relevance: Review article about the importance of food-web interactions between target and non-target species for an effective implementation of marine reserves.

Rijnsdorp AD, Bastardie F, Bolam SG, Buhl-Mortensen L, Eigaard OR, Hamons KG, Hiddink JG, Hintzen NT, Ivanovic A, Kenny A, Laffargue P, Nielsen JR, O'Neill G, Piet GJ, Polet H, Sala A, Smith C, van Denderen PD, van Kooten T, Zengin M. (2016) Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. ICES Journal of Marine Science 73: i127-138.

Significance and relevance: This paper was prepared under the FP7 project BENTHIS. The study describes a method to assess the impact of bottom trawl fishing on a large spatial scale.

Manuscripts in preparation:

van Denderen PD, Lindegren M, MacKenzie B, Watson R, Andersen KH. Energy pathways in the oceans determine functional composition of global fish communities.

Significance and relevance: This paper describes global patterns in the relative productivity of marine fish along the pelagic and benthic energy pathway. It demonstrates how the dominant feeding strategy of marine fish predators is largely determined by the difference in inflow of energy at the base of the pelagic and benthic food web.

Van de Wolfshaar K, Schellekens T, van Denderen PD, van Kooten T. Direct and indirect effects of fishing gear on a marine benthic food web.

Significance and relevance: This paper was prepared under the FP7 project BENTHIS. The study describes a food web model to assess the direct and indirect effects of bottom trawl fishing on different functional groups (suspension feeder, deposit feeder, predator) of benthic invertebrates.

van Denderen PD, Rijnsdorp AD, van Kooten T. Exploring the trade-off between fisheries yield and conservation of the benthic ecosystem in trawled fish stocks.
Significance and relevance: The study describes a food web model to explore trade-offs between fish and fisheries production and the conservation of benthic ecosystems using fishery effort restrictions and marine protected areas.

Presentations at international science meetings:

van Denderen PD, Lindegren M, MacKenzie B, Watson R, Andersen KH. Global patterns in the feeding ecology of large marine fish Gordon research conference and seminar “Unifying ecology across scales” University of New England, Biddeford, Maine, July 2016

van Denderen PD, Bolam SG, Hiddink JG, Jennings S, Kenny A, Rijnsdorp AD, van Kooten T. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. British Ecological Society annual meeting. Glasgow, Scotland, December 2015

6.32 Defense mechanisms in phytoplankton: Traits and trade-offs

Marina Pancic, PhD student
Employment period: 1 November 2015 – 30 October 2018
Supervisors: Thomas Kiørboe (Ocean Life, DTU Aqua) and Andy Visser (Ocean Life, DTU Aqua)

Description of project:

Phytoplankton is a highly diverse group of microscopic photosynthetic algae and cyanobacteria, which contributes to approximately 50% of the global carbon dioxide fixation. The composition of the microbial community, which directly influences the requirements for carbon, nitrogen, phosphorus, and other elements, profoundly affects the biogeochemical cycles in the ocean. The fact that many phytoplankton species coexist in the same space and at the same time on few resources (nutrients and light) together with the strong top-down selective pressure, demands for identification of the traits that determine their ecological niche. However, the ever-present trade-off in phytoplankton seems to be the one between competitive advantage and grazer resistance. For instance, resistance to grazing can often be attained by colony formation, which either decreases nutrient competitive abilities due to higher surface-to-volume ratio, or decreases competitive abilities for light due to increased sinking rates, which consequently creates a trade-off. Phytoplankton has developed a variety of physical, chemical, and behavioral defenses to reduce predation from higher trophic levels, and was additionally found to be highly flexible in traits that affect their edibility. These defense mechanisms decrease per capita consumption rates of grazers, albeit it appears that there is not a single mechanism that has a 100% success rate against the predators. Most of the mechanisms were suggested to either affect the grazer's clearance rates or its growth rates. Based on the theory, the grazer's handling times or attack rates were proposed to increase as a result of such mechanisms. In addition, a few studies have reported viable algae within copepod fecal pellets and remains of feeding pallium of dinoflagellates, suggesting that the defense mechanisms increase the chance of algae survival after being ingested by the predators.

Although many studies reported various defense mechanisms in phytoplankton, both the benefits and costs remain poorly understood and still unquantified. Hence, an important task of this project is to quantify the trade-offs of defense mechanisms. The initial focus is on the thickness of the silica walls in diatoms, which is known to vary widely among the diatom species. Moreover, the thickness of the silica shells was found to be a plastic trait, meaning that it can also be induced by the presence of herbivores, and as such, it may allow perceiving and measuring associated benefits and costs to organisms, thus making it an appropriate subject of investigation.

The overarching research question of this study is to identify important defense mechanisms in phytoplankton and to quantify the benefits, costs, and associated trade-offs. The first step is an extensive review of the existing literature, and based on that analysis, the following step is experimental quantifications of trade-offs. Since all existing biogeochemical models assume some sort of defense trade-offs in phytoplankton (as there is very little experimental demonstration or quantification of the actual trade-offs), such hard-core information is thus badly needed, and I have designed experiments to approach this issue. The final phase of this project is a formulation of general models of defense trade-offs in phytoplankton.

Dissemination:

Scientific publications directly related to the project:

At least 3 publications directly related to the project are planned, and the working title of the first one is:

[1] Pancic M and Kiørboe T. "Defence mechanisms in phytoplankton: Traits and trade-offs. A review" (in prep)
Significance and relevance: Provides an overview of existing work on the topic of defence traits and associated trade-offs in phytoplankton.

Other manuscripts in preparation:

[2] Visser AW, Brun PG, Jonasdottir SH, van Denderen PD, Nielsen LT, Pancic M, Chakraborty S, Thygesen UH, Heilmann I, Kenitz K, Dencker TS, Pécuchet L, van Gemert R, Schnedler-Meyer NA, Holm MW, van Someren Gréve H, Mariani P, Payne M, Kiørboe T, Törnroos A, Andersen KH. "Traits and trade-offs of seasonal strategies in the marine environment" (in prep)
[3] Chakraborty S, Pancic M, Andersen KH. "Seasonal succession of toxin and non-toxic dinoflagellates" (in prep)

6.33 Traits in the context of biodiversity – drivers and patterns

Tim Spaanheden Dencker, PhD Student
Employment period: 1 September 2015 – 31 August 2018
Supervisors: Martin Lindegren (DTU Aqua, Centre for Ocean Life), Mark Payne (DTU Aqua), Peter Grønkjær (Aarhus University).

Description of project:

The overall aim of the project is to investigate how the use of ecologically important traits can give us relevant information on biodiversity and ecosystem functioning in marine ecosystems. Biodiversity is nearly always equated to species numbers and relative abundance. However, we wish to expand the concept of biodiversity to include measures of trait diversity, as these have been shown to better reveal the mechanistic links that form the effects biodiversity has on ecosystem functioning. Trait-based biodiversity measures have only up until recently been used in terrestrial systems and have not been applied in marine environments. The three suggested sub-projects of the PhD will elucidate the patterns and drivers of such biodiversity. This will form the starting point for further research into ecosystem functioning and vital management and protection of biodiversity.

Results:

Sub-project one of the PhD is nearing its end, and a manuscript is currently being written, aiming for publication early Spring 2017. The most important finding of the sub-project was the identification of temporal and spatial matches and mismatches between taxonomic diversity and trait diversity in the North Sea fish community. Two extensive data sets were combined to form the basis of the project. A 32 year data set originating from ICES North Sea International Bottom Trawl Survey, and a unique trait data set, compiling information on traits of 80 North Sea demersal fish species, ranging from body size over fecundity to diet. One of the results of the project is shown in figure 1. The region of highest diversity differs between the two measured indices (species richness and trait richness), though, the same Southeastern to Northwestern gradient dominates, with the lowest values near Germany and Denmark. Additionally, different environmental drivers were found for the two measures. The results together suggest that different mechanisms drive different facets of the demersal fish diversity in the North Sea.

Future work:

The first sub-project forms the stepping stone and inspiration for the next two sub-projects. The highlighted mismatch between different facets of biodiversity found will be investigated further along a latitudinal gradient along European and North American coastlines in both Atlantic and Pacific waters. Specifically, I will look at shifts in taxonomy, traits and phylogeny in fish communities across said geographical gradient to identify areas of high turnover and whether this turnover is reflected in all three facets of diversity. Environmental drivers will be included to investigate potential drivers. The work will contribute to research on latitudinal regional gradients of biodiversity and potentially elucidate mechanisms behind community assembly and how different facets of biodiversity affect each other. The work will be done in collaboration with Professor Malin Pinsky, Rutgers, Princeton, New Jersey, where a planned external research stay is being organized.

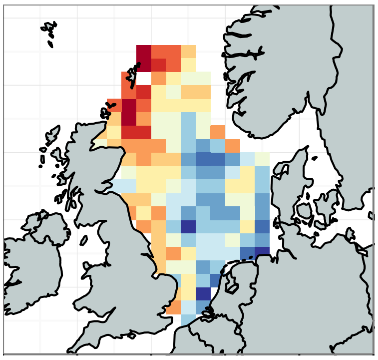


Figure 5 Spatial patterns of species richness and trait richness in the North Sea demersal fish community shown as mean values per ICES rectangle over 32 years.

Dissemination:

Scientific publications:

Dencker TS, Lindegren M, Richardson K, Payne MR (2017).Temporal and spatial mismatches and matches between taxonomic diversity and trait diversity in the North Sea fish community. *Submitted* **Significance and relevance:** Highlights the differences between two widely used metrics of biodiversity (richness and evenness) from two different angles, taxonomy and traits. First description of the North Sea trait diversity at the community level over three decades. Highlights the importance for incorporating multiple facets of biodiversity into management and conservation.

Pecuchet L, Reygondeau G, Beauchard O, Beukhof E, Brun P, Cheung W, Dencker TS, van Denderen D, Licandro P, Törnroos A, Payne MR, Lindegren M. Spatial structuration of life history traits: congruence between multiple taxa and environmental drivers in the North Sea. *Submitted*

Beukhof ED, Dencker TS, Pécuchet L and Lindegren M. Spatio-temporal patterns and drivers of the North Sea demersal fish community: a trait-based approach. *Submitted*

Sand-Jensen, K., Hammer, KJ, Madsen-Østerbye, M, Dencker, TS, & Kragh, T. (2014). Positive interactions between moss cushions and vascular plant cover improve water economy on Öland's alvar, Sweden. Botany, 93(3), 141-150.

A number of internal and external collaborations have also been initiated. A cross- Centre for Ocean Life paper on Seasonality in the Ocean is underway, which I have contributed to with data on fat storage in fish communities. Two external collaborations have been initiated with other young career researchers from North America, South America and Europe.

Conference presentations:

Dencker TS, Lindegren M, Richardson K, Payne MR (2017) Temporal and spatial mismatches and matches between taxonomic diversity and trait diversity in the North Sea fish community. ICES Annual Science Conference, September 2016, Riga.

Courses:

Aquatic science and living resources-research communication (25801), PhD course.
IMBER ClimEco5 Summer school, Natal, Brazil 2016, PhD summer school
Ocean Life Meeting Series, PhD Course

Other activities:

Representing Centre for Ocean Life and DTU Aqua in the ICES working group for biodiversity, WGBIODIV in 2016 in San Sebastian, Spain.

Student PhD-representative on the PhD-committee for Life Sciences at DTU, 2016-2017, nominated for same position 2017-2018.

Guest presenter, Physical Oceanography course, DTU Aqua. Quick presentation of potential topics for Msc. thesis students.

6.34 Copepod life cycles, population dynamics and trophic interactions in marine systems

Floor Soudijn, Postdoctoral Research Fellow
Employment period: 15 September 2016 – 15 September 2018
Supervisors: Ken Andersen, Andre Visser and Thomas Kiørboe (DTU Aqua)

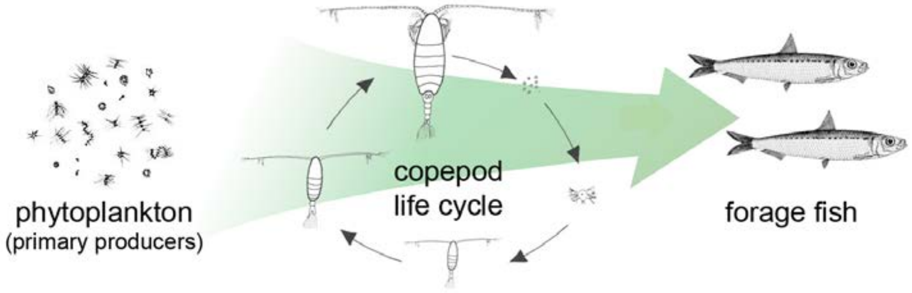


Figure 6. Phytoplankton-copepod-fish model

Description of project:

Small zooplanktivorous fish, or forage fish, support the largest fisheries in the world. At the same time, forage fish form an essential element of marine ecosystems as the main food source for large predatory fish, seabirds, and marine mammals. Forage fish are themselves supported by herbivorous copepods, the absolutely dominating group of marine zooplankton. However, it is unknown how copepod dynamics affect the flow of energy from primary producers to forage fish and thus, what drives global scale spatial and temporal patterns in forage fish production. This knowledge gap results from a dichotomy in marine science: research focuses either on biochemistry and plankton dynamics or on fish physiology and fish dynamics. Moreover, models of marine food webs typically contain a poor representation of copepods. Therefore, my project aims to predict global patterns in forage fish production by connecting fish and primary producers with the missing link: the population dynamics of copepods. I am planning to develop a phytoplankton-copepod-fish model and test the effect of copepod traits, seasonality, temperature and productivity on copepod dynamics and fish production.

The global patterns of forage fish production remain in general, poorly understood. Recent work on the global distribution of copepod traits shows large spatial variation in the average size of copepods. This variation in copepod size is likely to have a major impact on their forage fish predators as foraging is strongly size selective. Environmental conditions are expected to affect optimal copepod traits. So far it is unclear which mechanisms lead to the observed patterns in the global distribution of mean copepod body size. In addition, it is unclear how copepod traits affect the flow of energy to forage fish. Understanding the link between environmental conditions, copepod (trait) dynamics and forage fish production is essential for reliable predictions of the effect of global change on fish production. In addition, it may better fisheries management predictions in general.

Individual body size is one of the main traits that shapes other species charachteristics, such as ecological role, prey availability and predation pressure. Also energetic charachteristics such as basal metabolism and maximum food ingestion are strongly body size dependent. In copepods, between species differences in body mass of up to 2 orders of magnitude are observed on a global scale, while intraspecific variation in body size can be as large as 3 orders in magnitude. Still, intraspecific differences in body size are usually ignored in foodweb models that include zooplankton. I am therefore planning to develop a phytoplankton-copepod-fish model that includes the copepod life cycle, based on a previously developed modeling framework for animals with complex life cycles.

Achieved results & Future plans:

The first months of the project have lead to a clear definition of the first steps in the project. In addition, we have established which data is necessary for parameterization of the models that will be used to study the research questions. We have decided on a two-fold approach. On the one hand, I will study the importance of multicellular zooplankton for plankton community dynamics, using a model that includes Nutrients, Phytoplankton, Unicellular Zooplankton and Size-structured multicellular Zooplankton. Using this model I will: (i) study the dynamical feedback between the size distribution of phytoplankton and zooplankton, and, (ii) assess the effect of environmental conditions, such as seasonality, on the zooplankton size-distribution.

Second, I will study the importance of copepod traits for zooplankton dynamics, using a model with phytoplankton and a detailed copepod life-cycle model. In this model I will assess the effect of feeding strategies and body size on copepod dynamics. Using the model, I aim to predict optimal copepod trait strategies depending on different environmental conditions. The model outcomes will be confronted with data of the geographical patterns in copepod traits. This step in the project will lead to a mechanistic understanding of the global trait-distribution of copepods.

The ultimate aim of this project is to make a full link from primary-productivity to zooplankton to fish production. Once I have developed a basal understanding of the importance of copepod traits for copepod dynamics, I will proceed by extending the model with a fish predator. Using the phytoplankton-copepod-fish model, global productivity and temperature data (http://www.noaa.gov/) and global copepod trait distribution data (Centre for Ocean Life) I aim to finally predict global patterns in forage fish production.

Dissimination:

Scientific publications:

Planned papers (with tentative title and authors):

Optimal copepod feeding strategies and body sizes depend strongly on environmental conditions: dynamics of copepod size-distributions from the arctic to the tropics.
F.H. Soudijn, A. Visser, T. Kiørboe and K.H. Andersen

Shifts in community dynamics of Zooplankton in the light of climate change.
F.H. Soudijn, J.P.A. Pinti and K.H. Andersen

A mechanistic understanding of the global trait distributions of copepods based on size-structured copepod population dynamics.
F.H. Soudijn, A. Visser, T. Kiørboe and K.H. Andersen

The link between global forage fish production and copepod trait dynamics.
F.H. Soudijn, A. Visser, T. Kiørboe and K.H. Andersen

Presentations:

So far I have presented some of my previous work at the Ocean life work meeting and Ocean Life modelers meeting.

Planned presentations:

I am planning to present my work at the Dutch Ecological Society Meeting (2016/2017), The American Ecological Society Meeting (2017) and the Meeting of the Association for the Sciences of Limnology and Oceanography (2018).

Scientific outreach:

I am currently organizing the Annual Retreat of the Center for Ocean Life. In addition, I have presented some of my previous work as part of a Course for Masters Students in Marine Ecology.

I am planning to develop a broader scientific outreach, by creating a popular science video of my work and also organize a lecture for high school children about the importance of ontogenetic development in marine animals.

6.35 Density dependence in marine fish stocks: Influence on fisheries reference points

Rob van Gemert, PhD student
Employment period: November 2015 – November 2018
Supervisors: Ken H. Andersen and Martin Lindegren (DTU Aqua)

Description of project:

The aim of this PhD project is to investigate how density-dependent processes within a fish stock can influence the stock's fisheries reference points. Density dependence can affect vital rates within a population, such as growth, reproduction, and survival. If these rates change as a result of a change in population size, they are density-dependent. By influencing vital rates, density dependence is an important factor in shaping population structure and dynamics (Brook & Bradshaw, 2006). However, in almost all current fisheries models and stock assessments, density dependence is taken into account only during the larval stage of the fish (Brodziak et al., 2011). This density dependence is described with the so-called stock-recruitment relationship. All processes outside of this relationship are assumed to be density-independent. This is contrasting with empirical observations, which have shown that many fish species are subject to density-dependent processes throughout their lives (Rose et al., 2001). The first aim of this project is to understand how density dependence manifests itself in fish populations. Incorporating density-dependent processes other than stock-recruitment in fisheries models will likely influence fisheries reference points. The second aim is therefore to describe how fisheries reference points depend on the type of density dependence and when in life density dependence occurs. This will allow for more sustainable fisheries exploitation. During this PhD project different mechanisms of density dependence in fish stocks and their effect on fisheries reference points will be investigated. This will be done using size- and trait-based models, both on the single-species and multispecies level. These models will then be fitted to empirical data, allowing for model validation and testing the model's predictive capabilities.

My first project focusses on intraspecific competition for resources. Whenever there is intraspecific resource competition present within a population, it is possible that growth, reproduction, and mortality experience a density-dependent effect. The magnitude of this effect will likely depend on multiple variables, such as resource growth rate (Andersen et al., 2015) or asymptotic body size. By varying such variables, this project aims to investigate how density-dependent competition for resources can influence stock structure and dynamics, and what this will mean for maximum sustainable yield and optimal size-at-entry. The outcome of this project was a dynamic single-species size-based model, able to describe density-dependent resource uptake as observed in fish stocks, and its influence on growth and reproduction.

The aim of the second project is to investigate how cannibalism can influence a stock's fisheries reference points. Fishery models that use a Ricker stock-recruitment relationship describe the cannibalism on fish larvae, but not on juveniles and adults (Ricker, 1954). For species that experience cannibalism on juveniles, this means that a portion of the stock's mortality is not taken into account when determining its fisheries reference points, leading to the risk of overfishing. Furthermore, the interaction between density-dependent resource uptake and cannibalism is very interesting to study. The initial hypothesis would be that cannibalism partly negates the effect that density-dependent resource uptake has on the population, by removing competitors. To test this hypothesis, the model used in my first project will be expanded to include cannibalism. This new model will also be fitted to empirical data as a means of validation and testing its predictive capabilities. The outcome of this project will be a dynamic single-species size-based model that describes the interactions between cannibalism and other density-dependent processes as observed in fish stocks, and is able to calculate fisheries reference points that result in the optimal exploitation of the stock.

The aim of my third project is to investigate how inter-species interactions influence the functioning of density-dependent processes, and how this in turn can influence fisheries reference points. Individuals within a fish stock do not only interact with other individuals of the same species, but also with those of other species. These interactions can have a significant impact on the functioning of density-dependent processes (Persson et al., 1996, Hixon & Jones, 2005). Therefore, a multispecies dynamic size- and trait-based model will be constructed, incorporating the density-dependent processes included in the models of project 1 and 2. The initial hypothesis is that the density-dependent effects on a species are diminished when that species experiences strong interactions with another species, such as predation and competition for resources. It is expected that the biomass ratio between the species plays an important role in determining the strength of these interactions.

Dissemination:

Planned publications:

van Gemert R, Andersen KH. Implications of late-in-life density dependence on maximum sustainable yield and size selectivity.

Significance and relevance: Currently, almost all fisheries reference points and mesh size regulations are based on the assumption that density dependence only occurs early-in-life. We show that several species appear to experience most density dependence late-in-life, resulting in a wide range for optimal size-at-entry. Therefore, this study encourages a re-evaluation of the use of stock-recruitment relationships as the sole means to characterize density dependence in fish stocks.

Conference oral presentations:

van Gemert R, Andersen KH. Late-in-life density-dependence: catching smaller fish for higher yields. ICES Annual Science Conference, September 2016, Riga.