A PROPOSAL FOR THE EXTENSION OF CENTRE FOR OCEAN LIFE

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SUMMARY

The vision of the Centre for Ocean Life is to develop a fundamental understanding and predictive capability of marine ecosystems. Trait-based approaches have emerged as an efficient way to describe the overwhelming complexity of marine ecosystems in a relatively simple way: rather than describing the *many* interacting *species*, trait ecological approaches consider interacting *individuals* characterized by a *few* essential traits that are interrelated through trade-offs. During the first 5 years of the Centre for Ocean Life, we have developed and implemented the trait-based approach to marine ecosystems and, specifically, taken it from a discipline that considered only phytoplankton, to encompassing all trophic levels. We have successfully achieved this by: (i) identifying and mechanistically quantifying the key traits of important marine life forms (bacteria, phytoplankton, zooplankton, fish) and quantifying their associated trade-offs; (ii) used that information to develop the first trophic trait-based models of simple marine ecosystems; and (iii) developed the first ever global trait biogeographies of important higher trophic level marine organisms (e.g., zooplankton, fish).

The next phase of Centre for Ocean Life will project our vision to a new level. Specifically, having laid the foundations of our trait-based approach, we are poised to extend our focus beyond a mechanistic description of ecosystem structure towards understanding and predicting ecosystem function. That is, we can address not only how ecosystems self-assemble through trait interactions, but how they function in terms of biomass production, nutrient cycling and carbon sequestration. Further, we will pursue the logical outcome of this approach to investigate how ecosystem structure and function respond to perturbations, such as global change. In this context, our work will evolve around our two main hypotheses:

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

ii. *Dynamics of populations and ecosystems emerge from mechanistic descriptions of the functioning of the individuals and the properties of the environment,*

amended with a third hypothesis to highlight the focus of the second phase:

iii. *The function of marine ecosystems and their responses to perturbations can be predicted from the mechanistic descriptions of trait distribution and how traits serve to create ecosystem structure.*

In the second phase we will (i) fill knowledge gaps that are important to make the trait-based approach more complete and better suited to address global change issues, (ii) develop new trait-based models and test predicted trait distributions against those observed in nature, (iii) explore the relation between

trait composition and ecosystem function, and (iv) test the predictive capability of trait-based models by exposing them to perturbations, notably climate change, fishing, and invasive species.

Imbedded within this research agenda, we will pursue a second but equally important mission, namely the training of young scientists in quantitative marine ecology. We will continue to do so by maintaining the vibrant international scientific environment that has been created at the Centre, continue to organize international summer schools, workshops, and group retreats, host visiting scientists and students to interact with us, and by organizing joint projects to maintain the strong team spirit that has developed within the Centre.

INTRODUCTION

The fundamental issue of how marine biota will respond to global change was recently identified by the *National Academy of Sciences* as one of the most pressing questions in ocean sciences (*Sea change: 2015-25 decadal survey of ocean sciences*, February 2015). Although the question has been on the agenda for decades, traditional species-centric approaches have clearly failed to provide an answer. Instead, trait-based approaches have been promoted as a promising tool: rather than describing the *many species* and how they interact with each other and their environment, trait ecological approaches consider interacting *individuals* characterized by a *few* essential traits that are interrelated through trade-offs (Anderson 2005; Litchman et al. 2013). This approach thus has the potential to tackle the overwhelming complexity of marine ecosystems in a relatively simple way and address the issues of global change with a novel approach.

Trait-based approaches to describe communities and ecosystems were proposed by theoretical ecologists (McGill et al. 2006) and were originally developed in plant ecology based on empirical trade-offs (Westoby and Wright 2006). They have since been used to describe and model marine phytoplankton communities (Bruggeman and Kooijman 2007a; Follows et al. 2007; Monteiro et al. 2010), planktonic ecosystems (Pahlow et al. 2008), and fish communities (Andersen and Pedersen 2010)). The main contributions of the Centre for Ocean Life during its first 5 years of existence have been (i) to replace empirical trade-offs with mechanistically based and quantified trade-offs for the key traits of the most important marine life forms; (ii) the development of *trophic* trait-based models that describe interactions between several trophic levels rather than *competition* models that considers only one trophic level (e.g., the MIT Darwin model, Follows et al. 2007); and (iii) development of the first ever global and regional trait biogeographies of important life forms (zooplankton, fish, benthos) that can be used to test predictions of trait based models in addition to having a value on their own. While these tasks cannot be considered fully explored, our work has progressed far enough to allow us to take the next step and ask: **How the functions of an ecosystem relate to its trait composition and structure and how environmental perturbations affect ecosystem function** (Fig. 1)? In this endeavour, trait-based, rather than species-centric approaches are particularly relevant, because the function of a system can only be assessed from the species that make up that system if the traits of all these species are known. Our trait based approach, on the other hand, concentrates directly on functional traits and how they are interlinked by trade-offs, simplifying and directly addressing the issue of how the functions of ecosystem arise.

The work until now has been governed by testing (in a general sense) two fundamental hypotheses:

1. Interactions between individual marine organisms can be derived from organism characteristics and from the fundamentals of physics, chemistry, and evolutionary biology.
2. Dynamics of populations and ecosystems emerge from mechanistic descriptions of the functioning of the individuals and the properties of the environment.

With the additional and new focus of our work, we will explore and test a third hypothesis to highlight the focus on ecosystem function:

3. The function of marine ecosystems and their responses to perturbations can be predicted from the mechanistic descriptions of trait distributions and how traits serve to create ecosystem structure.

The research agenda and scientific goals outlined here provide the setting for an equally important mission of the Centre, which is to educate a new generation of young researchers. The day-to-day life in the Centre creates a vibrant intellectual environment for training young researchers, and they represent the main workforce and recipients of Centre funding through the PhD and post docs stipends. In addition to the projects funded directly by the Centre, there is a large body of affiliated young researchers, attracted to the work and working environment of the Centre from all over the world. The principle investigators of the Centre are dedicated to a high level of engagement in education, training and mentoring to ensure a high quality of research, exposure to a broad range of concepts and methods, and environment to encourage the very best transfer of knowledge to our young researchers.

OVERVIEW

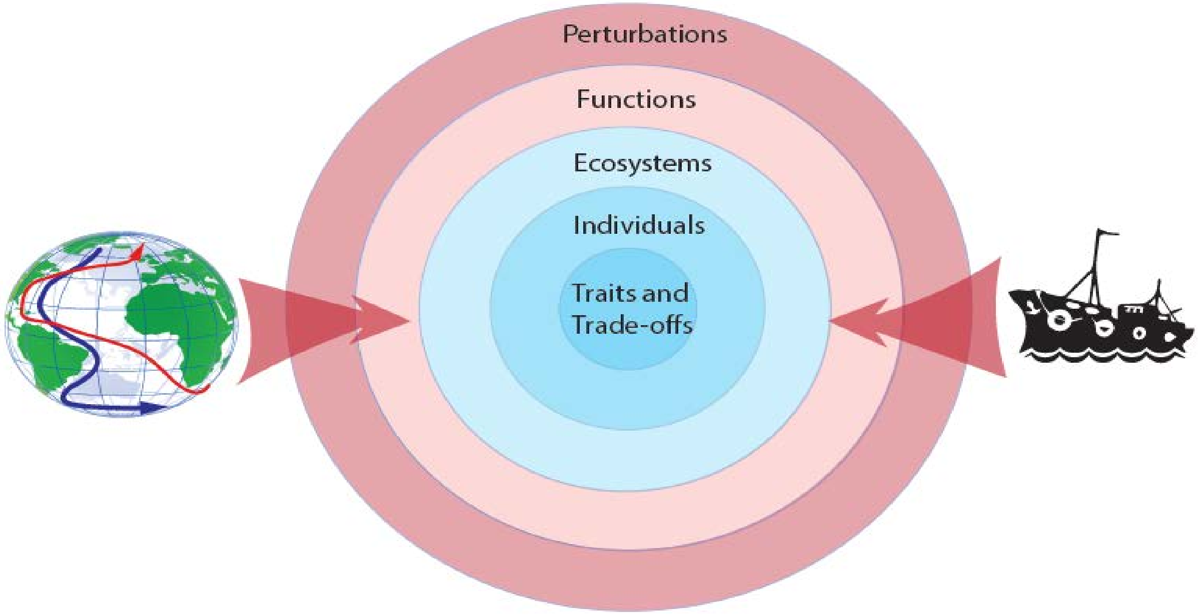
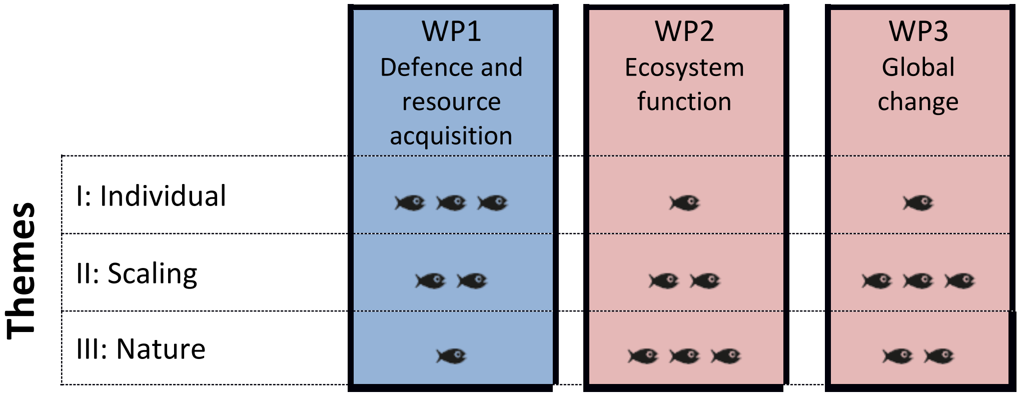


Figure 1. Conceptual representation of the main aim of the prolongation of the Centre: To use and further develop our trait-based approach to understand, model and predict the functioning of marine ecosystems under multiple, interacting perturbations (e.g., climate change, fishing, and invasive species). Changes in the environment affect the trade-offs that organisms face and therefore shift the optimal traits values. The trait distributions change to adapt to the new conditions, thus affecting ecosystem structure and key functions (biomass production, nutrient cycling and carbon sequestration). Taken

together, the trait-based approach provides a solid and novel scientific framework to successfully achieve our aim of understanding and predicting the functioning of marine ecosystems under global change.

The main aim of the prolongation of Centre for Ocean Life will be to project our vision to a new level, extending our focus beyond a mechanistic description of ecosystem structure towards understanding and predicting ecosystem functions, (i.e., how energy and carbon flow through an ecosystem, how fast nutrients are recycled, how much carbon is exported; Fig. 1). At the core lays the traits and the trade-offs upon which evolution acts. These determine individual fitness and ecosystem structure. These three core aspects have been the principle focus of the first phase of the centre (blue). In the next phase we will additionally focus on ecosystem function and on how external perturbations on individuals change ecosystem structure and function (red).



Themes	WP1 Defence and resource acquisition	WP2 Ecosystem function	WP3 Global change
I: Individual	🐟🐟🐟	🐟	🐟
II: Scaling	🐟🐟	🐟🐟	🐟🐟🐟
III: Nature	🐟	🐟🐟🐟	🐟🐟

Fig. 2. The three themes described in the original Centre proposal define the methods used to address the questions defined by the three work packages of this proposal. The number of fish in each cell of the matrix indicates the importance of each theme in realizing the work packages.

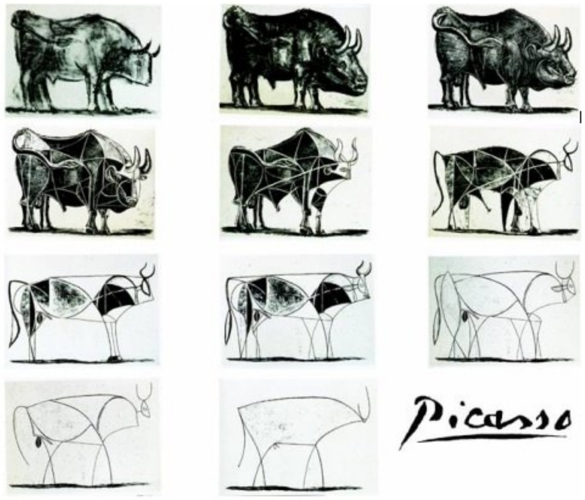
We will organise the work in three work packages (WPs): 1) Defence and resource acquisition traits, 2) ecosystem function, and 3) global change (Fig. 2). The first WP is our continued development of the core of the trait-based approach (blue), while the two other WPs are our extended focus on ecosystem function and response to perturbations (red). Each of the WPs relies on work on the three central components (Themes) of the trait-based approach: the individual, scaling, and nature.

Before detailing the WPs, we will first describe the philosophy behind the trait-based approach (“What is the trait-based approach?”) and briefly outline how we have indeed successfully developed the trait-based approach to describe life in the ocean (“Where are we now?”). We next provide a description of the visions and goals of the future work and how we plan to pursue these goals (“Where are we going and how are we getting there”). Our methodology is summarized as the “trait-based toolbox” for each of the three component themes. We finally describe Centre organisation and management, budget requests, implementation and training, dissemination and outreach, international collaboration and infrastructure. Outlines of specific PhD and post doc projects are provided in Appendix 1.

WHAT IS THE TRAIT-BASED APPROACH?

The trait-based approach aims to describe how structure and function of ecological communities emerge from properties of the individual organisms. The approach differs fundamentally from the traditional description of ecosystems which focuses on *differences* between *species*. In contrast, the trait-based approach focuses on *similarities* between *individuals* and strives to identify only the essential differences. In this way, the trait-based approach seeks to exclude unnecessary detail to retain only the important differences, allowing manageable (mathematical) descriptions of marine ecosystems.

The trait-based approach generally ignores that individuals belong to species. While species offer an immensely useful description of life, the species concept can become a distraction when we want to understand the structure and function of complex and diverse (species rich) systems. Instead of describing individuals as belonging to species we describe individuals by a few taxa-transcending properties: their key *traits*, i.e., the few properties that best describe the fitness of an individual. An individual is characterized by a combination of many traits and can thus be described as a point in a high-dimensional trait space. By projecting that space down on one or a few dimensions, given by the most important traits, we reduce the complexity of the description of life immensely.



Pablo Picasso, Bull (plates I - XI) 1945

Just as Picasso's few inspired pen strokes clearly depict a bull, the art of the trait-based approach lies in the skilful selection of the few key traits that best describe the fitness of an individual.

In the trait-based approach the fundamental axiom is that the dominant traits will be those that result in the highest fitness in the given environment. This dominance may be established by behavioural adaptation, phenotypic plasticity, ecological succession, or evolution by natural selection. To make this axiom operational, we identify key fitness components, such as survival and resource acquisition, and establish the trade-offs between these conflicting objectives that an organism faces. For example, a cell's investment in chloroplasts determines its ability to photosynthesize but comes at the energetic cost of forming and maintaining the chloroplast. Likewise, the active feeding by an animal comes with the risk of being eaten by a predator. The trade-off quantifies these costs and benefits. Trade-offs are described at the level of the individual and are ideally derived from a mechanistic understanding of the underlying processes. That is, they are based on observations and experiments that, e.g., quantify the predation risk of foraging, or through physical constraints, e.g., that a large cell sinks faster than a small cell. The trade-offs constrain the individuals' attempts to maximize their fitness through behaviour and phenotypic plasticity and, ultimately, natural selection and evolution. It is the ability of trait-based models to accommodate trade-offs that makes them so powerful, essentially providing them with extra information inspired by the laws of evolution that traditional species-centric models are ill-equipped to handle.

One fundamental aspect of trade-offs is that they are impacted by physical and biotic features of the environment. For instance, a particular feeding mode may only become effective when certain prey traits abound, or the investment in expensive defence traits may only pay-off when predators exceed some critical abundance. That is, the optimal trait combinations of certain groups of organisms will influence the optimal trait combinations in others (and vice versa). The overall (functional) diversity of an ecosystem is governed by such trade-offs and their interactions, as they allow the coexistence of species with similar fitness utilizing the same resource (Thingstad et al. 2005; Winter et al. 2010).

Community and ecosystem composition is described by *trait distributions*. The trait distribution characterizes the average abundances of individuals with particular traits in an ecosystem, or it may be spatially explicit, i.e.., describing the local or global distribution. The structure and function of an ecosystem emerges as the result of interactions between individuals and with the environment according to the principle of survival of the fittest as determined by the key traits and their associated trade-offs. If the trade-offs are known, trait distributions can be derived as predictions of mathematical models. Alternatively, trait-distributions can be obtained from observational data. Either way, trait distributions offer the possibility of evaluating ecosystem function (see below)

From the above philosophical manifesto a comprehensive trait-based approach emerges that consists of three components (themes) that have guided our work during the past 5 years:

I) *The individual*: identification of key traits and quantification of the associated trade-offs through experiments, observations, fitness optimization models, and theoretical considerations of physical constraints.

II) *Model*: developing trait-based models of the trait distribution on the basis of trade-offs.

III) *Nature*: exploring the distribution of traits in nature through observations and statistical trait-distribution models.

These three themes are inter-related: Theme I informs trait-based models (theme II) and the selection of key traits for statistical trait-distribution models (theme III), theme III offers a way to test predictions of trait-based models (theme II), and all three themes are required to assess ecosystem function from trait distributions. The three themes emphasise that the trait-based approach is much more than mathematical models. We use models throughout our work, but the trait-based approach is incomplete without established trade-offs from experiments, physiology or theory, and without reference to the realized trait distributions observed in nature.

We are not alone in championing a trait-based approach to describing life on earth. A focus on traits has been developed in plant ecology (Westoby and Wright 2006) but despite an early focus on trade-offs as being fundamental in structuring ecosystems (Tilman 1990) the approach has mainly been empirical (Edwards et al. 2011; Kremer et al. 2016; Kunstler et al. 2016) and only recently have models of trait distributions been developed (Falster et al. 2015). In marine ecology, trait-based models have focused on unicellular phytoplankton (Bruggeman and Kooijman 2007a; Follows et al. 2007; Edwards et al. 2013; Martiny et al. 2015) or other trophic levels (Record et al. 2013). In most cases, the focus has been on competitive interactions between individuals and with few attempts to consider multiple trophic levels (Smith et al. 2014). The Centre for Ocean life is unique in embracing a comprehensive approach that emphasises a mechanistic rather than a heuristic basis of emerging trait distributions from the constraints in the trade-offs. Further, we aim at covering many life-forms in the ocean, from bacteria to fish, with an emphasis on pelagic organisms and ecosystems. Finally, we recognize that predator-prey interactions are important in structuring marine systems. Marine communities are not only structured through competitive interactions, as is implicitly assumed in most trait-based descriptions, but equally through the evolutionary arms race between feeding and defence traits. We therefore put an emphasis on developing trophic models that span more than just a single trophic level.

WHERE ARE WE NOW?

During the first phase of the Centre our emphasis has been on establishing the above three components (themes) of the trait-based approach for marine ecosystems, and we have made significant progress in that endeavour. The achievements are described in the progress report, but are summarized here for each theme.

Within theme I, our efforts constitute the first attempt to systematically characterize taxa-transcending key traits for the main life forms in the ocean and to quantify their associated trade-offs. The latter quantification has been achieved through a mechanistic description of traits, and we have thus moved beyond the heuristic descriptions of trade-offs based on statistical analyses of correlation (Follows et al.

2007; Edwards et al. 2011). The mechanistic approach to quantifying trade-offs is rare and has previously been attempted mainly for phytoplankton (Shuter 1979; Toseland et al. 2013a) or phytoplankton groups, e.g., diazotrophs (Pahlow et al. 2013). In principle, a mechanistic understanding allows generalizations beyond the few species that we have been able to examine experimentally and permits the construction of trait-based models with better predictive power. This work has crystalized into the identification of three groups of **life-form transcending key traits**: **resource acquisition mode**, **defence**, and **body size**. Body size determines the order of magnitude of all vital rates (feeding, growth, metabolism, mortality, etc.) and defines the main physical constraints of an organism (Kiørboe and Hirst 2014). Body size also largely governs the mode of resource acquisitions and can thus be considered a master trait (Andersen et al. 2015c). The resource acquisition-cost-defence trade-offs govern the diversity of communities as they allow the co-existence of many trait-compositions with similar fitness (Tilman 1990; Våge et al. 2013), as expressed by the ultimate Darwinian mission of reproduction. We thus argue that these three 'traits' capture the most important aspect of the ecology of an organism, and that they provide a sufficient basis for a trait-based description or model of an ecosystem.

The three groups of traits materialize differently for different life forms. For example, bacteria need to produce specific enzymes to utilize certain organic molecules and, thus have to pay for enzyme synthesis to be rewarded (Traving et al. 2015); phytoplankton must invest in a photosynthetic apparatus to fix inorganic carbon (Chakraborty et al. 2016a); protozoa, zooplankton, and other animals may have to swim to encounter food, but are penalized by higher metabolic and mortality cost (Kiørboe et al. 2014a). These selected examples constitute only parts of our work but serve to illustrate how we have approached the resource acquisition-defence trade-off complex for different life forms.

While traits are properties of individuals, trait distributions describe properties of communities or ecosystems. Within theme II, we have utilized the insights and quantifications of trade-offs to formulate a suite of mechanistically underpinned trait-based models to predict trait distributions: *i*) We have used fitness optimization to study resource acquisition strategies among unicellular plankton (Berge et al. 2016; Chakraborty et al. 2016b). This work has created the foundation to build a size- and trait-based model of the entire uni-cellular plankton complex; *ii*) We have developed game-theoretic approaches to describe the offspring size strategies of life in the ocean (Olsson and Andersen 2016; Olsson et al. 2016); *iii*) We have made dynamic models involving the resource acquisition-defence trade-off for the seasonal succession of zooplankton (Mariani et al. 2013; Kenitz et al. 2016) and for the global distribution of gelatinous plankton (Schnedler-Meyer et al. 2016). *iv)* We have developed fully dynamic size- and trait-based models of the trait distribution of fish communities (with an open-source implementation: Scott et al. 2014), which have been used by us (e.g. Jacobsen et al. 2016) and others (e.g. Jennings and Collingridge 2015) to describe the effects of fishing on a global scale.

Several other groups have during the same period developed trait-based models of marine systems, but these are mainly *competition* models considering only one trophic level, typically phytoplankton (e.g.

Terseleer et al.; Toseland et al. 2013b) or using body size as the sole trait (Banas 2011; Ward et al. 2012). Ours are *trophic* models that emphasize the trophic interactions, and which go beyond just using body size as the trait.

With this suite of approaches, from fitness optimization to fully dynamic models of trait-distributions, we have now a comprehensive toolbox of trait-based models with demonstrated utility at our disposal. While we will continue to develop our trait-based modelling toolbox (described in "Methods: the trait-based toolbox") our modelling work will be focused on application of the existing toolbox.

Within theme III, we have made significant progress in describing trait distributions in the ocean from observations. We have utilized regional and global databases on species distributions that are available for many groups of organisms (mainly phytoplankton, zooplankton, and fish), and we have compiled our own extensive trait databases for fish (in progress) and zooplankton(Kiørboe and Hirst 2014; Brun et al. 2017). The trait databases have allowed us to 'translate' species distributions into trait distributions at the level of communities, and our efforts thus represent the first comprehensive attempts to develop regional and global trait biogeographies for important marine organism groups, e.g., fish (Pecuchet et al. 2017) and zooplankton (Brun et al. 2016a). Organisms distribute along environmental gradients according to their traits and their responses to the environment, not their taxonomic affiliation. We have utilized this to fill observational gaps on global trait maps from correlations with environmental drivers. Since trait biogeography in general is still in its infancy (Van Bodegom et al. 2014; Violle et al. 2014) and particularly poorly known in the marine environment (Barton et al. 2013), we count our accomplishments in this emerging research field as ground-breaking.

GOALS: WHERE ARE WE GOING AND HOW ARE WE GETTING THERE?

The three transcending themes of our trait based approach – the identification of key traits and quantification of trade-offs, the utilization of this in the construction of models to predict trait-distributions, and the observation and statistical description of trait distributions in nature – will continue to form the methodological basis of our new activities (see below) but the work will be organized in three work packages (WPs) that reflect the overarching goals of the continuation of the Centre (Fig. 2): 1: Defence and resource acquisition, 2: Ecosystem function, 3: Ecosystem response to perturbations. The general contents of the work packages are described below and the specific projects in Appendix 1.

The first WP is the direct extension of the first phase of the centre. It is concerned with developing trade-offs for traits related to defence and resource acquisition. As described in "Where are we now?", we have established these as central traits across all life forms in the ocean, but still have important work to do. This WP is dominated by theme I (traits and trade-offs of individuals).

The next two work packages directly target our new goals of **assessing ecosystem function from trait distribution and interactions** to evaluate the **effects of global change** on individual performance and ecosystem function (Fig. 1). This was also formulated as the future target in our original proposal, and we have made significant progress in that direction for selected systems, e.g., elevated risk of jelly blooms due to fishing and eutrophication (Schnedler-Meyer et al. 2016) or the response of fish communities to fishing (Jacobsen et al. 2016). Our success in these pilot applications provide us both with the road map and confidence to tackle some of the most pressing and complex questions of marine ecology: namely those related to the re-configuration of marine ecosystems in response to the varied and accelerating pressures to which they are exposed.

Within the trait-based approach, ecosystem function and response to perturbations have been addressed by distinguishing between *response*, *effect*, and *interaction* traits. This tradition grew out of plant ecology (Violle et al. 2007), and it has been partly adopted by the marine science community (Garvel et al. 2016; Hébert et al. 2016). This distinction is though, somewhat artificial, as all traits evolve by natural selection in response to the biotic and abiotic environment, and all traits also have some effect – large or small – on the ecosystem, including those that focus on interaction (defence, predation). To date, we have focused on the response and interaction aspect of traits: this is what has allowed us to both model trait distributions and to relate observed trait distributions to environmental conditions. The assessment of ecosystem structure and function, on the other hand, focuses rather on the effect aspects of these traits. The overarching hypothesis is that **ecosystem function and response to perturbations emerge from trait distributions and interactions**.

In addressing ecosystem response to perturbations, (i.e., global change) we realize that we are pursuing a line of research that has become a "catch-phrase" in research proposal over the past decades. However, we argue that our approach is novel and has potential to provide new insights. Due to the complexity of the ecosystems and the sensitivity of ecosystem models, a species-centric approach has not succeeded to provide robust predictions of system-wide effects. Furthermore, marine ecosystems do not just respond to climate change, but make an important component in the carbon cycle (see WP2 in the following) and therefore contribute to the complex feedback dynamics of the global climate. Our work to date however has cemented our view that a trait-based approach is uniquely suited to provide robust system-wide predictions. It speaks directly to the matter of the self-assembling of ecosystems based on the principles of evolution, and can thus describe how ecosystem structure can re-emerge after a disruption. Our ambitions on this front remain curiosity driven, but the tools that we will develop are an integral part of this research challenge. This is a central motivation, shaping our vision to move on from an understanding of what determines trait distributions (the scope of our work till now) to an understanding of how trait distributions impact ecosystem function and its response to perturbations.

Below we describe the three work packages, while concrete projects of each WP are outlined in Appendix 1.

WP1: Defence and resource acquisition

Our work till now has come a long way in mechanistically describing key traits and quantifying trade-offs for several marine life forms but has revealed a large and surprising gap in the understanding of defence traits and trade-offs in unicellular eukaryotes (Pancic and Kiørboe *in prep*). The competitive exclusion principle predicts that there can be only one species per resource, yet, there are typically many co-existing species of protists, all living on the same few resources. The diversity that never-the-less exists is believed to be driven both by a diversification in resource acquisition mode (autotrophs, heterotrophs, mixotrophs, diazotrophs, osmotrophs, phagotrophs), and by predation and parasitism and the associated evolution of costly defence mechanisms. Diversity is then generated by co-existing species that distribute themselves along a gradient from competition to defence specialists (Thingstad et al. 2005; Winter et al. 2010)). This idea is rather well developed for prokaryotes competing for dissolved organics and defending themselves against virus attacks and grazing (Våge et al. 2013), and work at the Centre has successfully examined this for metazoan zooplankton. However, even though many potential defence mechanisms have been described for unicellular eukaryotes, particularly phytoplankton (toxicity, shell armour, colony formation, etc), the trade-offs are poorly understood and rarely quantified. The trait-based models of eukaryotic plankton communities that have nevertheless been developed have solved this lack of information pragmatically (e.g., by assuming a trade-off, or by introducing constant immigration, (Bruggeman and Kooijman 2007b; Banas 2011).

Another surprising realization is that despite a great wealth of information and knowledge on fish traits, particularly regarding the effect of size on fish community dynamics, a mechanistic understanding of the key traits and trade-offs involved in the fundamental process of feeding, growth, survival and reproduction is largely lacking. Hence, under this work package we will modify and adapt a generic framework of key “ecological functions” previously developed for phyto-and zooplankton (Litchman and Klausmeier 2008; Litchman et al. 2013) to broadly characterize the primary traits and trade-offs of fish related to feeding, growth, survival and reproduction. This information will be used to set up conceptual models summarizing the key traits and trade-offs in fish, providing the understanding needed to fully explore and investigate their dynamics and trophic interactions in mechanistic trait-based models.

Thus, the first work package will include the quantification of **defence trade-offs** and **trade-offs associated with resource acquisition** in unicellular eukaryotes and fish, to complement our former work on mechanistically characterizing key traits and their associated trade-offs in bacteria and zooplankton.

WP2: Ecosystem function

Perhaps one of the most important strengths of trait based ecology is that it provides a framework where we can examine, analyse, and predict the structure and function of communities and ecosystems. Specifically, the traits and trade-offs of organisms are inherently interrelated through either direct (e.g. predator-prey) or indirect (e.g. competition) trophic interactions. In this, communities can be seen as a self-assembling and dynamic system where certain trait combinations are promoted to the detriment of others. While our development so far has facilitated descriptions of abundance in time and space, it is also evident that this approach can address the overall functioning of a community. Ecosystem functions are defined in terms of the fluxes of energy, nutrients, and organic matter through an ecosystem (Cardinale et al. 2012a), and although a broad range of functions exist in marine ecosystems (Strong et al. 2015), we will, at least initially, focus on two key functions, **carbon sequestration** and **biomass production** and to a lesser degree also on **nutrient cycling** (Fig. 3). Below we will illustrate the approach through a few examples

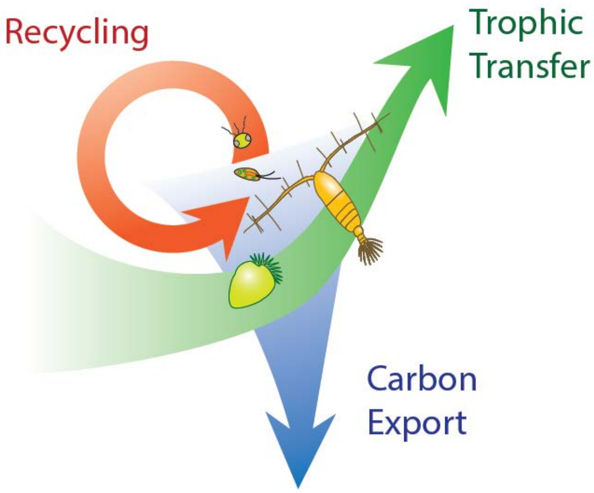


Fig. 3. Marine ecosystems can be viewed as networks through which energy (or organic matter) is channelled from its primary production in autotrophic unicellular organisms along one of 3 different pathways: (1) to higher trophic levels such as zooplankton, fish and marine mammals, (2) through a microbial loop that recycles much of its mineral content, or (3) into export to the deep oceans. The primary goal is to quantify how ecosystem functions such as carbon export, nutrient cycling, trophic transfer and biodiversity emerge from and relates to trait the composition of the community.

Biological processes **sequester carbon** through the action of the ‘biological pump’, perhaps one of the most important functions provided by marine ecosystems with regard to global climate. Essentially, phytoplankton fix inorganic carbon in the surface of the ocean, a fraction of which is transported to the ocean interior through various processes: (i) the coagulation of small phytoplankton cells into rapidly sinking marine snow aggregates (Burd and Jackson 2009), (ii) through the consumption of phytoplankton by zooplankton and the subsequent excretion and rapid sinking of faecal pellets (Stamieszkin et al. 2015) or particle loaded mucus feeding webs (Lombard and Kiørboe 2010), and (iii) through diel and seasonal vertical migration of the zooplankton (Jónasdóttir et al. 2015). One of our ambitions is to develop a mechanistic, trait-based description of the biological pump, a development that would have far reaching implications for the modelling of the global carbon cycle. We know for instance, how the flux of marine snow can be estimated from the concentration and size distribution of the phytoplankton (Burd and Jackson 2009) that in turn, can be derived from trait-based models (Follows et al 2007) or satellite observations (Boyce et al. 2015). The contribution of zooplankton to the biological pump depends strongly on their size: Larger zooplankton produce larger and faster sinking fecal pellets (Stamieszkin et al. 2015), they undertake deeper diel vertical migrations (Ohman and Romagnan 2016), thus bringing respired carbon to greater depths, and they hibernate at great depth in arctic areas, where they leave very significant amounts of inorganic carbon (Jónasdóttir et al. 2015). Thus, the size distribution of the zooplankton plays a pivotal role for the vertical material flux, and we can quantify all the component process from existing mechanistic studies by ourselves and others. The global pattern of the size distribution of zooplankton can be derived directly from our observation-based zooplankton trait biogeography(Brun et al. 2016a)or be predicted from trait-based model that we are developing (Hansen and Visser 2016). This way an important ecosystem function can be assessed from trait distributions, whether the latter are derived from mechanistic modelling, from observations and derived trait biogeography, or both.

Biomass production can mean various things, ranging from primary production to production of ecosystem components of particular interest, e.g., fish production. Energy predominantly enters ecosystems as carbon fixed by photosynthesis. This primary production is passed on to the next trophic levels through predation. Eventually energy reaches the higher trophic levels that are of most interest to human consumption: fish and larger crustaceans. Three aspects of production have our attention: *i)* The widespread occurrence of mixotrophy increases the efficiency of trophic energy transfer between the primary and secondary production (Ward and Follows 2016) – how will this efficiency depend on the degree to which organisms invest in mixotrophy vs. phototrophy? *ii)* The production of energy towards higher trophic levels can either occur efficiently via the short grazing food chain or inefficiently via a longer food web. The conditions that favours either mode are qualitatively understood (Kiørboe 1993), but a generic model-based understanding is lacking. *iii)* The fisheries production of higher trophic levels depends on the trait composition of fish communities, on their resilience to fishing, and on whether they rely on energy from pelagic or benthic production. These three aspects of production can be explored via observed trait distributions or by trait-based modelling.

Nutrient cycling in the euphotic zone helps maintain a high biomass of living organisms in the upper ocean. This function is largely carried out by an extensive microbial community (Azam and Worden 2004; Falkowski et al. 2008) that lives off the discards of the trophic chain from primary producers to zooplankton and to fish. These discards include dissolved organic material, faecal pellets and aggregates of detrital material that rains from the surface ocean and carry with them a fraction of the vital nutrients required by primary producers. The rate at which the microbial community breaks down dead organic material and converts it to mineral nutrients determines in a large part, the efficiency of the biological pump as well as the trophic transfer efficiency to higher trophic levels. Nutrient cycling is thus a vital process in the context of carbon sequestration and production of harvestable biomass. We will develop microbial community models that can describe the breakdown and recycling of organic matter by bacteria.

WP3: Ecosystem responses to perturbations

Marine ecosystems are constantly subject to a variety of perturbations such as changes in the physical environment, or the removal or addition of organisms (e.g. invasions, harvesting, extinctions). Our overriding aim here is to use the trait-based approach to address how ecosystems respond to such perturbations. Our work will primarily focus on perturbations related to global change, in particular climate change and the effects of harvesting. The individual organism may respond to a perturbation by altered physiological rates (e.g. increased rates in a warmer ocean), by increased mortality (e.g. under fishing), or by adaptation through changes in behaviour or investments in different functions. The ecosystems response may be observed as a reduction or even loss of certain traits and, hence, functions. Other traits may take over through colonization or even invasion, thereby potentially giving rise to alternative ecosystem functions. While investigating some specific key processes at the organismal level, the overarching goal is to understand system responses and implications to ecosystem functions. We will explore these and related issues through a combination of experiments and modelling.

Trait-based models are a potent tool to examine how marine ecosystems may respond to change. Standard ecological models implicitly assume that the perturbed system contain the same species with the same adaptations as in the unperturbed system. Trait-based models are free from these constraints; the models allow all trait-combinations and adaptations to occur in the perturbed system, subject only to the constraints laid down in the trade-offs. While the trait-based models do not predict the extinction or invasion of specific species, they provide credible predictions of how the trait distribution changes, i.e., which types of species will benefit or suffer under a perturbation. In this way trait-based models provide credible assessment of the future state of marine ecosystems.

Perturbations are introduced into the models as changes in the forcing. Climate change, for example, can be imposed on optimization models as changes in the ambient temperature (Shuter 1979; Toseland et al. 2013a), in larger dynamical models by changes in temperature and mixing, or in global circulation models by IPCC scenarios of climate change (Follows and Dutkiewicz 2011). The effects of fishing are imposed simply as elevated mortalities.

The **global warming** of the oceans have already had measurable effects on the spatial distribution of species that are reported to move mainly pole-wards (Cheung et al. 2013; Pinsky et al. 2013). This does not immediately imply a change in ecosystem function since the biogeography of traits may change (or not) independent of changes in species biogeography (Zhang et al. 2016). Some organisms may be able to adapt to higher temperatures over multiple generations by changing their temperature reaction norms (Dam 2013; Padfield et al. 2016) preventing a geographical relocation of those organisms. However, different traits or processes, such as photosynthesis, metabolism, and feeding rates may scale differently with temperature (Wilken et al. 2013; Toseland et al. 2013b), thus changing the trade-offs at the level of individuals in response to changes in temperature and consequently ecosystem functions in non-trivial ways. For example, photosynthesis appears to be less dependent on temperature than phagotrophy among aquatic eukaryotes, implying changed investments allocation in resource acquisition and consequent potential changes in food web structure with changes in temperature (Rose and Caron 2007). Anthropogenic greenhouse gas emissions are simultaneously warming and acidifying the oceans (Kirtman et al. 2013). While temperature affects all biological processes (but not at the same rate), ocean acidification primarily affects the rate of photosynthesis through increased availability of inorganic carbon, as well as the precipitation of calcium carbonate in, e.g., calcifying algae (Rost et al. 2008; Kroeker et al. 2010). Increased availability of inorganic carbon may favour diazotrophs that engage in energy-expensive N_2-fixation, thus causing changes not only to the carbon – but also the nitrogen – mass balance (Eichner et al. 2014). Further, climate change may imply a higher frequency of extreme events (e.g., oxygen depletion, heat waves, freshwater waves; Cheng et al. 2016; Hobday et al. 2016), and impact the structure of ecosystems and their biogeochemical functions in a different way than the more gradual changes in the average environmental conditions, as documented for terrestrial but not marine system (e.g., Easterling et al. 2000). The aspects of climate change are dealt with in several of our proposed project, and the focus on climate change, will be a large theme in the next phase of the centre.

Fishery is probably the largest perturbation of most marine ecosystems. Fishing profoundly affects the demography and resilience of fish stocks, it induces an evolutionary response (Jørgensen et al. 2007), and it leads to trophic cascades that affect the entire ecosystem beyond the fish (Daan et al. 2005). Within that context there is a need to make credible impact assessments of fishing and identify the strategies that balance the trade-offs of food production, profit, and conservation of biodiversity. This is particular relevant for a large part of the world's oceans for which only limited data exist and which are not covered by the complex analytical stock assessment used in the western world. The trait-based model that we have developed in the first part of the Centre has proven to be successful in particular in data-poor regions. We will continue to develop and apply our trait-based fish community model to predict the effects of fishing and participate in the contemporary debate on the global effects of fisheries.

METHODS: THE TRAIT-BASED TOOLBOX

The methods used within the three components of the trait based approach will partly be further developments of methods used during the past 5 years, but we will also harness new approaches. Here, we focus on new methods, while 'old' methods described in the original proposal and the 5-year report will be only briefly mentioned.

Theme I: The individual

The focus will here be on (i) quantifying resource acquisition and defence trade-offs mainly in unicellular organism (WP1) and (ii) on adaptive responses of individual organisms to gradual and abrupt environmental changes (temperature) (WP3).

Defence trade-offs in unicellular eukaryotes will be examined by utilizing the feature that many defences are inducible. That is, they are expressed more strongly in the presence of predators and typically in response to chemical cues. Recently discovered molecules exuded by copepods, known as copopodamids, or solutes from other grazers can induce a large variety of defences in their phytoplankton prey, ranging from toxin production and increased shell thickness to swimming activity and colony formation (Pondaven et al. 2007; Selander et al. 2011, 2015). This offers an experimentally accessible means to quantify both the efficiency (how much is grazing mortality reduced) and the cost of the defence (e.g., how much is the growth rate reduced) as well as the environmental dependency of the trade-off. We will also approach the defence trade-off through resource allocation optimality modelling, much the same way as we have quantified the trade-offs associated mixotrophy (Chakraborty et al. 2016b). By examining a variety defence mechanisms we hope to be able to extract more general rules to quantify trade-offs that transcend taxa and maybe even defence mechanism and that will make the results more useful for the modelling (Theme II).

To explore *resource acquisition trade-offs* in heterotrophic unicellular organisms we will apply the approach we developed to examine this trade-off in zooplankton. Resource acquisition efficiency (feeding efficiency) in representative phagotrophic protists with different feeding strategies will be quantified from visualizations of feeding currents using micro-Particle Image velocimetry that we have developed for this application (Nielsen and Kiørboe 2015) as well as by novel micro holography. The associated predation risk will be evaluated from fluid disturbances generated by feeding organisms, generalized by fluid mechanical modelling, and tested in simple incubation experiments. Again, by exploring in detail the mechanism in selected forms we hope to be able to generalize the findings in simple ‘rules’ much as we have done for zooplankton.

The work on resource acquisition *trade-offs in diazotrophs* (nitrogen fixing organisms) will again combine experimental and modelling approaches. We will use data on bacterial growth and nitrogen fixation in continuous seawater cultures with cultivated strains of diazotrophs (Farnelid et al. 2014) to constrain a trait-based based model at the single-cell level. We will adapt and develop a recent model on a soil diazotroph (Inomura et al. 2016) to marine diazotrophs, and use the model to analyze key environmental drivers of nitrogen fixation: concentrations of carbon substrate, reduced nitrogen and oxygen (Bombar et al. 2016). The idea is that this gained mechanistic understanding of the autecology of diazotrophs will facilitate prediction of nitrogen fixation at micro- and macro-scales in the marine environment. This information is essential for our understanding of marine nitrogen cycling and, consequently, a prerequisite for any prediction of overall ocean productivity, from bacteria to fish production.

We will in addition develop and use *trait-data bases* to test the general validity of the trade-offs identified through experimentation and modelling and to identify (other) trade-offs. A trait-data base is simply a table with a list of species that are each characterized by a number of trait (values), e.g. their size, resource acquisition mode, maximum feeding rate, etc. Positive correlations between traits offer a means to simplify a trait-based description (two or more inter-correlated traits can be combined in a composite trait), and negative correlations suggest trade-offs that may be further explored and quantified through experimentation or optimality modelling. Traits that separate invasive from non-invasive species may be identified as 'invasion' traits. Trait data bases are also essential in the development of trait biogeographies (Theme III, see below). Trait databases of variable quality exist for some marine groups, e.g. phytoplankton (Bruggeman et al. 2009; Edwards et al. 2015), corals (Madin et al. 2016), copepods (Brun et al. 2017), and fish (Froese and Pauly 2015), and for selected life-form-transcending traits (Hirst and Kiørboe 2014; Kiørboe and Hirst 2014; Horne et al. 2016; Neuheimer et al. 2016), several of which are our own. However, to constantly expand and improve the quality of these data bases is a community effort to which we will continue to contribute. Some of the existing trait data-bases include properties that are not really traits, and traits that have no immediate and obvious significance for the fitness of the organism. Traits have often been selected because they are easy to measure. Thus, a particular challenge is to obtain traits that are both relevant and measurable; or measurable proxies of relevant traits (e.g., 'myelination' in copepods, which is a good proxy for the ability to escape predators). We will expand with further species and traits by trawling the literature for information, a boring but important and rewarding task.

The *adaptation to changing temperatures* will be quantified through the incubation of organisms during many generations in different temperature regimes and examine how and whether their temperature reaction norm changes (= performance as function of temperature). The underlying hypothesised trade-off is that increased performance at higher temperatures is at the cost of lower performance at lower temperatures, or that a broadening of the reaction norm (temperature generalist) will make the organism less competitive at specific temperatures (i.e., the area under the reaction norm curve is constant). Such experiments are feasible mainly for organisms with short generation times such as bacteria and phytoplankton, which has provided an understanding of the mechanisms governing the potential for adaptation (Dam 2013; Padfield et al. 2016). We will use copepods as multicellular model organisms because of their relatively short generation times that allow us to experimentally examine the potential for evolutionary adaptation on short time scales. Also, we can revive former population of copepods by hatching eggs of known age from the sediment where they have been dormant for up to many decades, and thus examine changes in reaction norms of natural populations along known changes in the temperature of the sampling location. And we can examine the genetic underpinning of any changes by molecular approaches, thus potentially allowing some more general insights in adaptation potential that may help explain and predict changes in biogeography. Individuals' adaptation to higher or lower temperature will also be explored through optimality modelling: how will resource allocation change when different fundamental processes scale differently with temperature and how do this change the environmental dependency of the fitness of the organism? Examples include mixotrophs and diazotrophs, where investment in machineries for phagotrophy, phototrophy, and diazotrophy may change differently with temperature and availability of inorganic carbon.

Theme II: Individuals to trait distributions and community structure

The trait-based approach allows us to mathematically describe the complex interactions that shape real communities, to make predictions of how traits are distributed in nature, and to predict community structure and function. This capability builds from the individual (Theme I) that can be viewed mathematically as a point in multidimensional trait space, and a given community structure can be viewed as a density function within the same trait space (Bruggeman and Kooijman 2007a). Given a mechanistic understanding of the risks and costs that specific trait combinations are subject to, a relatively simple mathematical expression can be written that describes the dynamics of the community in trait space (Cressman and Hofbauer 2005; Petchey et al. 2008).

Theme II develops models based on the trade-offs established in Theme I. While the mathematical methods rest on established techniques from theoretical ecology, there are considerable technical challenges. For example, size-based models of unstructured models tend to create “lumpy” size-distributions (Banas 2011), game-theoretical models of multiple trophic levels are still largely unexplored, and many trait-distribution models often have problems maintaining trait diversity. The centre involves dedicated mathematicians as PIs to assist in tackling some of these problems. Further, the use of fitness optimization arguments is still considered controversial. We are well aware of the pitfalls of optimization but use it (as one of multiple tools) with a keen eye to its limitations because we find that it does provide valuable insight into the trait distributions we observe in nature. The mathematical details of our approaches, including equations, are given in the 5-year report (section 3.2.1: Modelling principles). Here we provide a conceptual overview.

At the core of the models are the processes representing the fundamental vital rates: growth (through encounter, metabolism etc.), reproduction, and survival (Fig 4). What makes a model “trait-based” is the dependence of the vital rates upon the set of traits ϕ that describe individuals. How each vital rate depends on a trait embodies the trade-off for that trait. From the vital rates the fitness can be calculated using standard techniques, as described in the 5-year report, and in our publications, (Andersen et al. 2015b) for unstructured models and (Andersen et al. 2016a) for structured models.

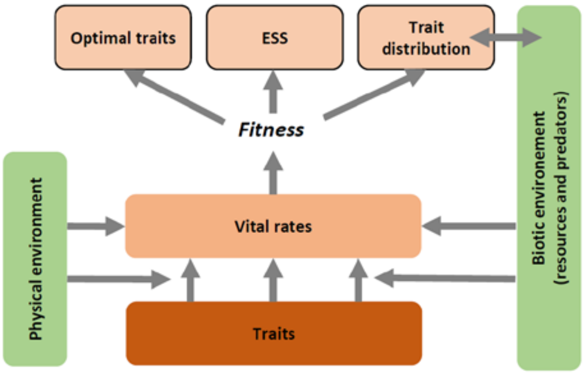


Fig. 4. The trait-based modelling toolbox. Vital rates (e.g. growth, mortality) are determined by the traits of the organism in concert with the biotic and abiotic environment. These rates in turn determine the Darwninian fitness of the organism, i.e., the lifetime reproductive success. This allows prediction of optimal traits, evolutionary stable trait distributions (EES), or the dynamics of trait distributions.

The calculation of fitness forms the basis of three modelling approaches: *i)* fitness optimization; which trait combination results in the maximum fitness in a given environment (Fig. 5) (see 5-year report for a discussion of limitations), *ii)* adaptive dynamics to find the evolutionary stable strategy, and *iii*) fully dynamic models of the entire **trait distribution** $N(t, \phi)$ that specifies how the abundance of individuals as a function of their traits change over time.

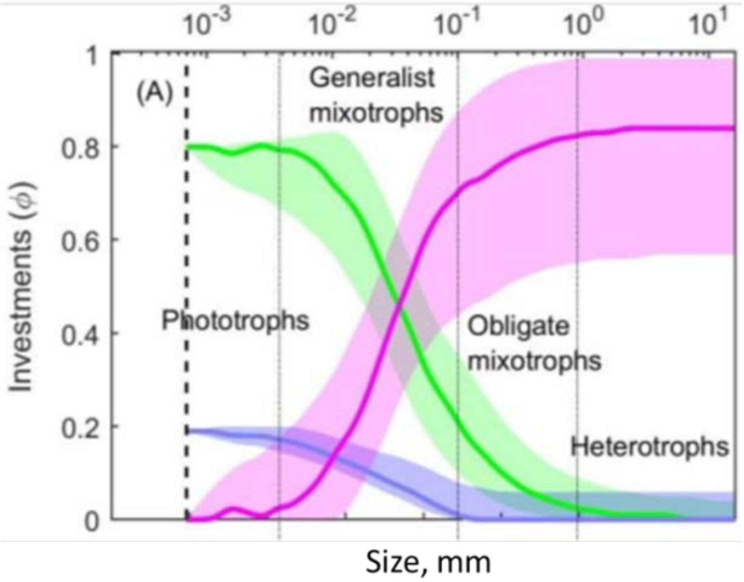


Fig. 5. Example of output from an optimization model. Optimal investments in resource acquisition traits: phototrophy (green), nutrient uptake (blue) and phagotrophy (magenta) as a function of cell size (Chakraborty et al. 2016b)

Supplementing these three approaches to trait-based modelling established during the first period, we will develop two additional approaches:

Dynamic optimization: Models with several trait dimensions become computationally heavy to resolve. To overcome this, we only resolve one trait dimension explicitly, e.g. body size, while other traits are assumed to adjust continuously to their optimal value. The utility of this approximation is based on the observation by Terseleer et al. (2014) and Falster et al. (2015) that the peak of emergent trait distribution often are very close to the optimum predicted by simple optimization.

Hybrid modelling: The Holy Grail in ecosystem modelling is the generation of so-called ‘end-to-end’ models. That is, models that describe the entire ecosystem from primary producers and bacteria to fish and mammals, all embedded in a physical setting (Rose et al. 2010). This is also the ideal long-term goal of trait-based modelling. However, there are several challenges in such an endeavour. First of all, model robustness and predictive capability decreases with model complexity. The trait-based trophic models that we have produced so far consider only few trophic levels, e.g., fish communities with internal predation (e.g. Andersen et al. 2016c) or models considering only phytoplankton and zooplankton in a physical setting (Mariani et al. 2013). A short-cut to produce simpler models that none-the-less produce robust results, is to use observations of drivers or trait distributions at one trophic level to make predictions of trait distributions at the next trophic level(s). An example of this is the simple multi-trophic level trait based model describing the ecosystem in a physical setting from phytoplankton to zooplankton to fish and jellyfish that we have developed (Schnedler-Meyer et al. 2016). The model allows analytical solutions and provides fundamental insights in mechanism. However, to predict the global distribution of the susceptibility of ecosystems to outbreaks of jellyfish blooms, we use observed rather than modelled distributions of phytoplankton (Fig. 5). We use this approach also to predict the global size distribution of zooplankton from satellite-observed global biomass and size distributions of phytoplankton from a simple trait-based model (work in progress), and see many more applications of this short-cut to make robust predictions of trait distributions.

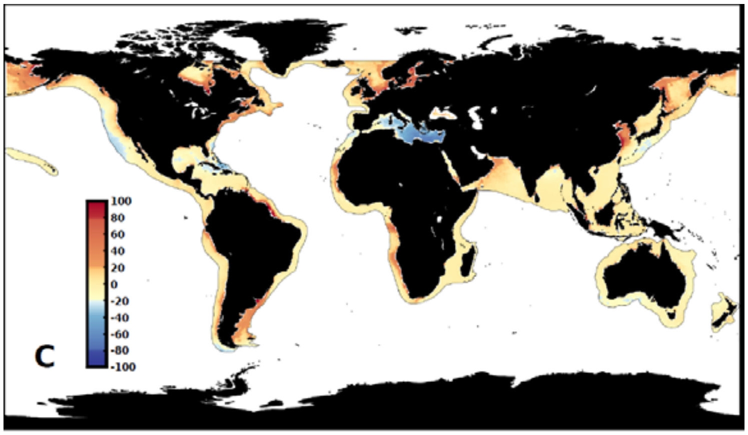


Fig. 6. Example of a ‘hybrid-model’ to predict the global distribution of the susceptibility of coastal ecosystems to jellyfish dominance, expressed as an index between -100 to +100. A simple ‘end-to-end’ model is used to understand mechanisms,

but a simpler model driven by observed rather than modelled phytoplankton distribution is used in the actual prediction. From (Schnedler-Meyer et al. 2016).

These two examples also demonstrate how predicted trait distributions can be used to assess ecosystem function: The jellyfish example directly predicts an ecosystem function (the susceptibility to eutrophication and fishing of the system to flip to jellyfish dominance), and the global zooplankton size distribution can be used to quantify an important component of the 'biological pump', as exemplified in the previous.

Model systems

The models need to be embedded in a model system that describes the environment, e.g., nutrient dynamics, light, and/or advection and mixing. We use several systems depending on the application. Two approaches of increasing complexity will be used within the centre:

1) A 0-dimensional chemostat model that represents the dynamics of the upper mixed layer of the ocean. The model is forced by light variation as given by latitude and by influx of nutrients from the deep ocean. The model is a modified version of the classic "Evans and Parslow" model (Evans and Parslow 1985).
2) A 1-dimensional water column model that represents the entire water column in a location. The model is forced by light, wind stress and tides. The physics in the model – light, temperature and turbulence – is described by the General Ocean Turbulence Model (GOTM) system (Burchard et al. 2006).

The use of more complex 3-dimensional Global Circulation Models may be employed through collaborations with the MIT Darwin group (Mick Follows and Stephanie Dutkiewicz) and with the NOAA Geophysical Fluid Dynamics Laboratory (Charles Stock).

Theme III: Trait distributions in nature

The fundamental test of our trait-based approach is to confront our theoretical predictions (via Themes I and II) with observations from nature (Theme III). The general aim here is to i) extract and document patterns of the temporal and spatial distribution of key traits in nature, ii) to indicate potential trade-offs, iii) inspire mechanistic descriptions and iv) to test and verify model predictions.

The description of trait distributions in nature and how they vary in time and space is conceptually simple but may be challenging in practice. In general, the idea is simply to combine observational data describing the spatio-temporal distribution of species with trait data bases that lists the traits of each species to generate trait distributions at the level of communities. Spatial trait distributions can be considered 'trait biogeographies', akin to traditional species biogeographies. We have already successfully used this approach to produce the first copepod and fish trait biogeographies (see 5-year report). The challenges in this approach include the availability and quality of relevant data bases and the application of relevant statistical tools to fill gaps in the observations and relate traits to environmental variables. There are several global and local species data-bases (e.g. FishBase, Froese and Pauly 2015) and national and international programs (e.g. the Continuous Plankton Recorder Survey; the CalCofi program) describing the spatio-temporal distribution of species. In contrast to species databases, there are much fewer good trait databases available and we will thus continue to develop high quality trait data bases, as discussed above.

Even the best databases do not allow complete global trait biogeographies, and empirical modelling approaches are required to fill spatio-temporal gaps. The most successful of these approaches thus far involves the application of empirical environmental trait distribution models with spatial autocorrelation terms (Brun et al. 2016b),. Also, we focus on the most important traits – or proxies of these – that are direct concrete realizations of our core traits: body size, resource acquisition and defence. In these models, knowledge on the relationships between a trait and the environment gathered in themes I and II is expressed in formal statistical terms. The values of a given trait observed in time and space are then used to parameterize a model describing their distribution as a function of the environment (e.g. temperature, salinity, nutrient concentrations), and a spatial auto-correlation term is used to allow for local deviations from the model and absorb the effect of variables that cannot be included directly in the model. The parameterized model is then used to extrapolate the expected value of the traits into regions where observations are missing based on the environmental conditions found there, thereby filling the gaps in the most appropriate manner (e.g., Fig. 7). These approaches also have the added bonus that they reveal relationships between trait distributions explicitly. Furthermore, being steeped in a rigorous statistical framework, such approaches allow for formal hypothesis testing to be performed.

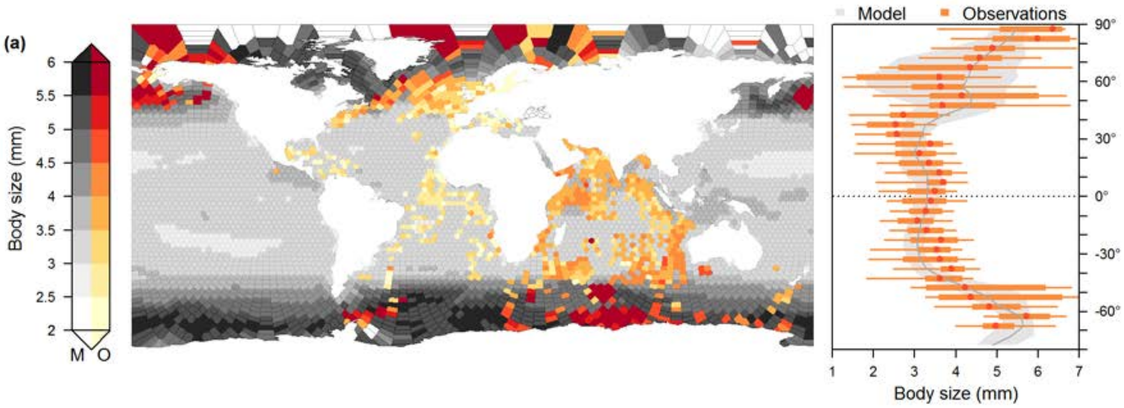


Figure 7: Global distributions of copepod community-mean body size. Coloured polygons are data-based estimates; polygons in grey scales are predictions with the environmental models. The panels on the right show trait distributions per latitude (Brun et al. 2016b).

Another way of combining species and trait databases with environmental variables is the so-called 4th corner approach. From a methodological point of view, this requires methods capable of linking three data matrix tables to jointly investigate the unknown 4th corner (i.e., the trait-environment table) (Fig. 8): a table L with abundance or presence–absence values for species at a series of sites, a table R with variables describing the environmental conditions of the sites, and a table Q containing “response traits” of the species. We will investigate the trait-environment relationship using RLQ-analysis, a recently modified multivariate technique that provides ordination scores to summarize the joint structure among the three tables, as well as the 4th corner method that primarily tests single trait-environment relationships at a time (Dray et al. 2014).

Finally, we will use advanced hierarchical random effect models, based on the generalized linear mixed model (GLMM) framework, that have recently been introduced to examine the relationship between (terrestrial) plant traits and the environment (Pollock et al. 2012; Jamil et al. 2013).These approaches allow us to model relative abundances or the probability of occurrence of a species at a given site as a function of its traits, the environmental variables, and the interaction between traits and environments, representing the trait–environment relationship.

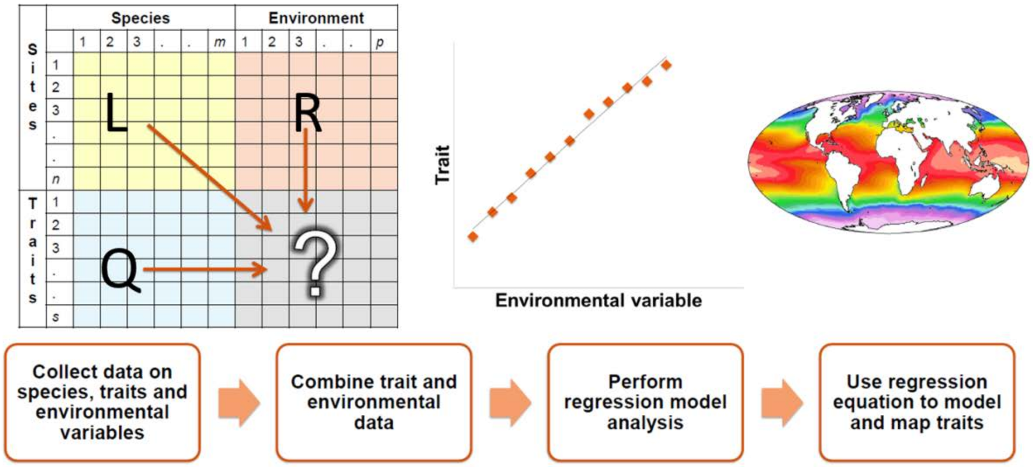


Fig. 8. A schematic representation of the so-called 4th corner problem, in this case illustrated by the unknown relationship between traits and the environment (denoted by a question mark). Resolving this issue requires methods capable of linking three data matrix tables to jointly investigate the trait-environment table; namely a table **L** with abundance or presence–absence values for species at a series of sites, a table **R** with variables describing the environmental conditions of the sites, and a table **Q** containing traits of the species. After having identified the key traits responding to these drivers, as well as described their functional relationships (e.g., through regressions), the models can be used to map current or future trait distributions.

WORK PLAN

Appendix 1 provides outlines of concrete projects that together describe the actual work contents of the Centre. The realization of individual projects depends on the availability and interests of qualified candidates, and we do not expect that all projects will necessarily be realized. Also, some new projects may become relevant as the work progresses, while others may indicate “spin-off” projects. The lesson from the past 5 years is that one often cannot successfully force candidates to conduct a very specific project unless s/he is enthusiastic about it, and so there is a weak conflict between academic freedom and training on the one hand and the obligation to pursue a very specific goal on the other. We prioritize scientific creativity and talent over very specific skills, and will balance the above conflict in our selection of candidates such that the overarching goals of the Centre are reached through the work of enthusiastic candidates without necessarily realizing all the projects described.

Nevertheless, an outline work plan that describes the division of time and effort between work packages and projects can be constructed as a starting point. The plan distinguishes between projects that we consider highly likely to be realized (yellow), and projects that are likely to be realized (blue):

Workpakage\Year		*1*	*2*	*3*	*4*	*5*
WP1: Defence and ressource acqusion trade-offs						
Costs and benefits of defence in diatoms	*1.1*	🟨	🟨	🟨		
Chemical defence trade-offs in phytoplankton	*1.2*		🟦	🟦	🟦	
Risk versus resource acquisition in heterotrophic nanoflagellates	*1.3*	🟨	🟨	🟨		
Trade-offs of microbial N2 fixation	*1.4*	🟨	🟨			
End-to-end model of planktonic life in the ocean	*1.5*			🟨	🟨	🟨
WP2: Community trait assemblages and ecosystem function						
Bacteria traits and the recycling of organic matter	*2.1*		🟨	🟨		
Predator-prey games and ecosystem functions	*2.2*			🟦	🟦	🟦
Zooplankton and the oceanic carbon pump	*2.3*		🟨	🟨		
Global model of fish production and benthic-pelagic coupling	*2.4*	🟨	🟨			
Biomass production across trophic levels	*2.5*		🟨	🟨		
Macro-scale biogeochemical fluxes across trophic levels	*2.6*		🟨	🟨		
WP3: Fish						
Temperature and the vital rates of plankton communities	*3.1*		🟦	🟦		
Interacting effects of temperature and resources on marine phytoplankton	*3.2*	🟨	🟨			
Plasticity of temperature adaptation in copepods	*3.3*		🟦	🟦	🟦	
Response of fish physiology to climate change	*3.4*		🟨	🟨		
Food-web response to climate change	*3.5*		🟦	🟦	🟦	
Operationalize size-spectrum models of fish communities	3.6	🟨				
WP7: Management & Outreach						
Administration, management	*4.1*	🟨	🟨	🟨	🟨	🟨
Visiting Scientist Centre	*4.2*	🟨	🟨	🟨	🟨	🟨

ORGANIZATION, MANAGEMENT, AND RESEARCH GROUP

The central challenges for the Centre management is to align the effort across a broad range of scientific disciplines, several institutes, and two universities towards the overarching goals of the Centre. The interdisciplinary nature of the PI group requires that the central management has scientific credibility across disciplines to make respected decisions about e.g. hires. The cross-institutional nature requires a central management that can act independently on a daily basis. We have gained experience in managing all of these challenges during the past 5 years, and have been successful in most aspects. We, therefore, make only slight changes to the management structure and base these on our past experiences. We will implement a three-level management structure:

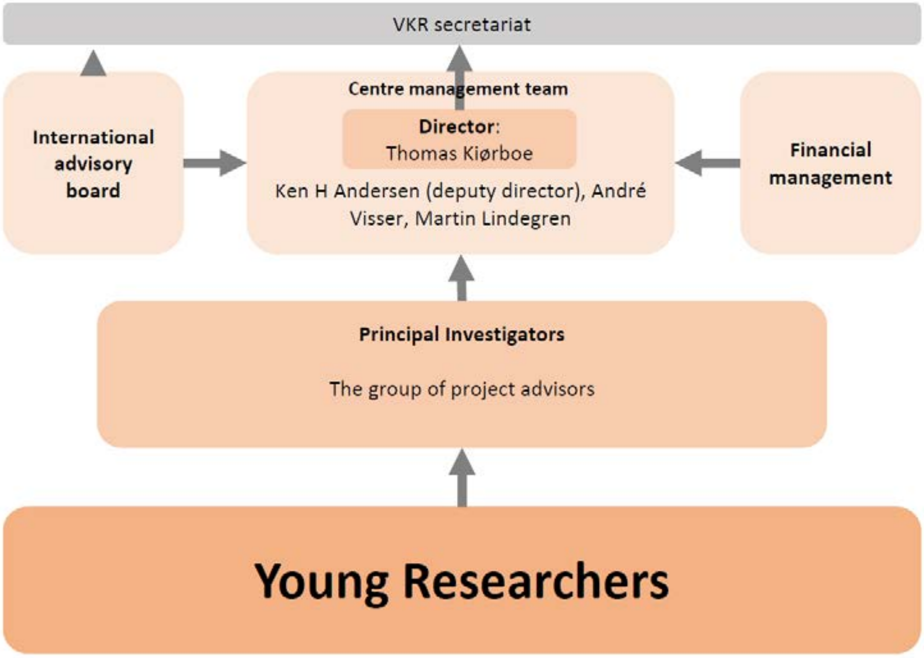


Fig. 9. Schematic outline of the structure of Centre management

The management team is led by the director Thomas Kiørboe supported by deputy director Ken H Andersen. The team is supplemented by André W. Visser and Martin Lindegren, all from DTU Aqua. All members of the management team are trend-setting researchers within marine ecology but each comes from different disciplinary backgrounds: TK is an experimental oriented marine biologist; KHA comes from theoretical physics but has established himself as a theoretical ecologist; AWV is trained as a physical oceanographer and has experience in integrating biology and ecology with physics; ML works in the field of statistical marine biology. The expertise in the group represents the full range of disciplines involved in the Centre. Decisions about hires of PhDs and post docs are taken by the management team in consultation with the PI group, in particular potential supervisors. In case of disagreement in the management team the director has the final decision. The members of the management team are responsible for the daily scientific management: weekly meetings, annual meetings, ad hoc working groups, etc. (details given below in “implementation”).

The Principal Investigator group, including the management team, consists of the scientists that are responsible for the young researchers. The group consists of scientists from 4 university departments at two universities (DTU, KU) and includes biologists, mathematicians, chemists, physicists, as well as engineers and so is truly interdisciplinary. As the pool of young researchers changes with new hires and finishing PhD, so does the PI group. Initially, the group is made up of those responsible for a project description (see CVs in Appendix 2): A. Andersen (Physics), C. Stedmon (Chemistry), P. Mariani (Environmental Science), L. Riemann (Microbiology), U.H. Thygesen (Mathematics), P.J. Hansen (Plankton ecology), J. Hemmer Hansen (Population genetics), S.J. Sigrunsdottir (Plankton ecology), M. Payne (Chemical engineering). The PIs are responsible for supervising and overseeing the scientific progress and well-being of their assigned young researchers and for co-supervising other young researchers. In this capacity they are expected to inform the management team of irregularities, significant delays, or other aspects relevant to the Centre.

The young researchers form the bulk of the Centre and are doing the bulk of actual research: master students, PhD students, and post docs. Each young researcher is formally associated with the institute where their PI supervisor is employed. The young researchers are primarily responsible for the progress of their scientific project within the Centre. They are also expected to be involved in the supervision or realization of other relevant project – this is particular relevant for the more senior young researchers (post docs), but we expect PhD students to help supervise MSc and bachelor projects. Further, the young researchers contribute to the practical work: they are giving presentations during weekly, annual, and ad hoc working group meetings (see Implementation), they provide peer feedback to other young researchers, and assist with practical organization of annual meetings and scientific workshops. Finally, the young researchers participate in the scientific environment at their institute – in this way they are anchored in their core scientific discipline and thereby distribute knowledge of the work in the Centre throughout the Danish research landscape.

The Centre management is supported by an international advisory board. The board plays the dual role of providing advice to the management team, and independent contact to the VKR secretariat. In the latter capacity they provide short reports to the VKR secretariat, as requested. Further, the board acts as a network that assists in spreading information about open positions and workshops and provides feedback to individual young researchers during the annual meeting. We plan some changes to our board and have assembled a group that reflects the cross-disciplinary nature of the Centre and its novel focus. Further, we have emphasized a mix of experienced and younger researchers – it is our experience that younger researchers are more actively engaged in the Centre's work. So far, the following scientists have been invited and have accepted to serve on the board (pending approval from the Villum Foundation): Øyvind Fiksen (Univ. Bergen; theoretical marine ecology, http://bio.uib.no/modelling/of/), Andrew Barton (plankton ecology and trait-based modelling, https://scripps.ucsd.edu/profiles/adbarton), Elena Litchman (Univ. of Michigan; plankton ecology, http://preston.kbs.msu.edu/), Stephanie Dutkiewicz ((MIT; numerical modelling of biogeochemical cycles, http://ocean.mit.edu/~stephd/). Mick Follows (MIT; trait based approaches and numerical modelling, https://eapsweb.mit.edu/people/mick), Adam Martiny (Univ. of California; experimental marine microbiology, http://www.ess.uci.edu/researchgrp/amartiny/adam-martiny-lab), Simon Jennings (CEFAS, UK; marine ecology, with a focus on fish and fisheries management, https://www.uea.ac.uk/environmental-sciences/people/profile/simon-jennings ,Charlie Stock (NOAA; global numerical modelling, https://www.gfdl.noaa.gov/charles-stock-homepage/).

Financial management is provided by the DTU central economy centre which allocates a person to follow and report the project. Decisions on allocation of funds are taken by the director in consultation with the management team. The director reports on the state of financial affairs at the annual meeting and in particular on the possibilities for new hires during the coming year.

DTU provides support for the Centre from the international office. In a Centre with a strong influx of international young researchers and visitors their support on matters of immigration, housing and other matters of relevance to non-Danish citizens is indispensable.

IMPLEMENTATION AND EDUCATION

Centre for Ocean Life is an inherently multidisciplinary effort. In this respect the central challenge for success is to foster collaboration between young researchers and PIs from different disciplines. This challenge is accentuated by our ambition to educate the next generation of quantitative marine ecologists, with a focus on both *quantitative* and *ecology*. This means exposing young researchers with a classic biology background to mathematical modelling and those with a “hard” natural science background to the perplexing complexity of the living nature. Realizing both aims requires a common language to create insight and respect across disciplines. This insight permeates our implementation, from hiring strategy and supervision, over joint projects, to organized meetings and social activities.

Hiring strategy: We want to hire the most talented young researchers. We therefore favour open calls for positions but also head-hunt candidates through our networks. We then develop a project with the prospective candidates based on their skills and interests. In this respect, our formulated project outlines (Appendix 1) serve as inspiration and starting points for defining actual projects. Due attention is however paid to achieve a balance in the Centre between the three central themes and three focal areas, such that, taken together, the overarching aims of the Centre are fulfilled. For post docs we will prioritize a 2+1 year type of contract. We initially offer a two year position – it is our experience that it takes a while for post docs to get fully started partly because they carry some legacy work with them from their PhD that they need to finish, and partly because it takes time to adjust to a new topic. We will offer successful post docs a 1 year extension, typically already after the first year to avoid that they spend too much time looking for the next position.

Supervision: Each project has a main supervisor who oversees the scientific progress. The supervision is assisted by a co-supervising PI from a complementary discipline, again to ensure collaboration across disciplines. We further involve young researchers in relevant supervision to prepare them for the next steps in the career, i.e., PhD students in the supervision of master students and post docs in the supervision of PhD students. As a mandatory part of the PhD education in Denmark, students are expected to spend some time with another research group, and both students and post doc are therefore encouraged to stay and work with our international collaborators. Finally, PhD students are associated with a PhD school at their home institution through which mandatory course work etc. is organized.

Cross-cutting collaborative projects: In the first period of Ocean Life we have developed collaborative projects with great success. The first, '*Size in the Ocean'*, resulted in 6 high profile papers (see 5-year report). We are currently finalizing work on the second project, '*Seasons in the Ocean'*. The projects are coordinated by senior PIs but involve all young researchers and multiple seniors. Besides being scientific successes with high international exposure, these projects have shown to be immensely important for the cross-disciplinary integration and the sense of common purpose within the Centre. The reason is that the projects force the young researchers into actual work and direct communication with other young researchers from different disciplines. One new concrete project is planned ('*Defense in the ocean'*); we expect other topics to emerge during the period.

Meetings and social activities: The organized meeting activities in the Centre are: "Ocean Life" meetings, study groups and ad hoc working groups, annual meetings, and social activities.

The most important activity in the Centre is the weekly meetings. All young researchers in the Centre are required to be present, regardless of their institutional affiliation. The content of the meetings is discussions, typically organized around a young researchers' presentation of scientific progress or ideas for future work. The meetings run in the spring and fall semesters and are formalized as an official PhD course to give PhD students credit for attendance.

Study groups and working groups involve people with shared interests. They may be continuous and organized around a broad topic, such as "trait-based modelling", or ad hoc groups working towards a shared interest or collaborative project, such as "fish traits". These groups do not necessarily have a cross-disciplinary aspect, but they ensure that young researchers obtain broader research experience than their own projects. It is also a means of mutual supervision, where students can share their often very different skills and help one another in the pursuit of their 'personal' projects

The annual retreats are a celebration of the years' work, mostly revolving around presentation by young researchers. The meeting involves the entire Centre, young researchers and PIs, with attendance from the international advisory board and special invited international guests.

Finally, we are conscious of the importance of social activities, in particular among the young researchers coming from abroad. This supports them in the integration into a new culture and in the difficult phases of their work where progress is slow – very common among PhD students – and generally contributes to a positive and enthusiastic working environment. The Centre supports social activities that involve all young researchers, such as biannual barbecues or ad hoc outings, with or without PI attendance. These activities also serve as kernels for further self-organized activities.

Career development: Upon request from our young researchers we will implement an annual 'career day' where we invite possible future employers from industry and academia to inform on career possibilities and organise a workshop to discuss and explore career options.

DISSEMINATION AND OUTREACH

Dissemination of research results will be through (i) scientific publications and presentations at meetings and workshops; (ii) the organization of international workshop and conference sessions; (iii) summer schools; and (iv) public outreach.

Publications and presentations: The most important output from the Centre is in the form of scientific publications in international journals. We also encourage young researchers to attend international meetings and workshops to present their work to get immediate feedback from their peers (other than their supervisors) and to help them establish their own international network

International workshops and conference sessions: As in the past 5 years, we will continue to organize international workshops and conference sessions. In particular, the biannual international workshops on ‘Trait-based approaches to Ocean Life’ will continue to be our main activity in this endeavour. These workshops have now been established as the international meeting place for scientists working in this discipline. The core organizing group includes our international board.

Summer schools: We will continue to organize and help teach international summer schools on topics relevant to the Centre, including a summer school on trait based approaches to ocean life.

Web site and social media: As till now we will maintain a web site that provides basic information about the Centre (who we are and what we are doing) and where we can publish ‘News’. We encourage young researchers to produce ‘pitch videos’ as part of the web site presentations of their research. We will also continue to be active on social media (Facebook, Twitter).

Public outreach: We consider public outreach as an important part of our missions for a number of reasons. First, researchers have an obligation to share their knowledge with the general public, and in these post-factual times, the dissemination of the scientific way of thinking and testing ideas seems more important than ever. Second, public outreach offers an important training opportunity for young researchers. Whatever their future career they need to be able to communicate complicated knowledge to non-experts, orally as well as in writing, and doing so also helps them to put their own (maybe nerdy) science into a larger context to make it interesting and relevant to lay people (and tax payers). We encourage the young researchers to write popular articles, give popular presentations, help organizing ‘open university’ days, and to produce material for our web site and social media platforms, etc. With the help of the communication officer at DTU Aqua we also organize training workshops in popular writing and presentations.

INTERNATIONAL COLLABORATION

Our international network is large and will be maintained through (i) the bi-annual international workshops on trait-based approaches and other international meeting activities, (ii) exchange of students and post docs with collaborating groups, (iii) collaboration on concrete projects (see commitment letters from most important collaborator in Appendix 4), and (iv) by maintaining a Scientist visitors Centre.

INFRASTRUCTURE

Experimental facilities are available at DTU Aqua and at University of Copenhagen (Marine biological laboratory). The facilities at the University of Copenhagen have just been updated and DTU Aqua will move into brand new facilities (laboratories and offices) at the DTU main campus during spring 2017. In addition, all necessary equipment, cold rooms, culture facilities, etc. to conduct the planned experimental activities are available and of very high standard. The move of DTU Aqua to the main campus also bring the three DTU departments that participate in the Centre in closer vicinity.

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APPENDICES

1. WPs and project descriptions

APPENDIX 1. WORKPACKAGE AND PROJECT DESCRIPTIONS

In the following, we outline a series of projects to demonstrate how the aims of each work package can be realized in practise. The projects generally represent a single PhD or post doc project. Some projects are smaller and will likely only fill part of a young researchers time, e.g. 3.6; others are large and can be realized by several young researchers, e.g. 2.6; or related projects in two work packages will be merged into a single project, e.g. 3.1 and 3.2. In most cases, the projects will be modified to fit with the skills and interests of the most talented candidates that apply for positions in the Centre. We prioritize scientific creativity and talent over very specific skills in our hiring strategy, and will balance our selection of candidates such that the overarching goals of the Centre are reached without necessarily realizing all the projects described below

Some projects have been or will be initiated during the present contract.

Work Package 1: Defence and resource acquisition trade-offs in marine organisms

In this work package we investigate traits and trade-offs associated with defence and resource acquisition. Why, for instance, do so many planktonic species produce toxins that diffuse away in the environment, providing limited benefit for the individual that produced it while encouraging a host of freeloaders? What is the role of building an expensive shell? Is it really just for protection from grazers or does it serve other subtle purposes? What are the economics of biochemical production of enzymes in the acquisition of resources? Working with examples we will build a general understanding of the type of trade-offs involved in defence and resource acquisition. The examples are mainly from microbial systems, i.e., bacteria and protists. This is because we have successfully covered this for zooplankton during the first phase of the Centre, where we have generated a mechanistically underpinned and experimentally verified generic description of zooplankton, from defence to competition specialists, that transcend all zooplankton taxa, and build that insights into trait-based models (see report). However, to our surprise, defence mechanisms and their trade-offs are poorly understood for protistan plankton. Even though many defence mechanisms have been suggested, particularly for phytoplankton, there are only very few examples where the trade-offs have been quantified. We will experimentally quantify costs and benefits. The experimental studies are complemented with optimality modelling to generalize the results and understand under which conditions different types of defence traits can be expected to prevail. This will follow the recipe from our successful studies from the first phase (Berge et al. 2016; Chakraborty et al. 2016b).

Defence traits examined include shell formation in diatoms (1.1) and toxin production by phytoplankton (1.2). The costs are the direct costs of the defence, such as the matter needed to construct a shell or produce toxin, and the metabolic costs associated with the defence. Expected benefits are lowered predation risk, which we will quantify by exposing the plankton organisms to predation by copepods. The trade-off are examined for the resource acquisition traits protist feeding (and its associated risk; 1.3) and nitrogen fixation by heterotrophic bacteria (1.4).

The last projects (1.5) will explore the community level consequences of defence trait through trait-based models of the predator-prey interactions. The aim is to gain insight into the types of patterns that emerges from the interactions between organisms with different defence and resource acquisition traits, and thereby pave the way for the larger models in WP2 and WP3. The insights from Projects 1.1-1.4 together with the large body of work already carried out during the first phase is used to formulate plausible generic trade-offs. The project synthesises the insights about defence and resource acquisition traits into a simple model of the entire planktonic ecosystem in the oceans.

Project 1.1: Costs and benefits of defence in diatoms

Many phytoplankton have a shell that is generally understood to provide protection against grazing (Monteiro et al. 2016). The shell can be characterized as a defence trait. Pelagic diatoms, a highly successful taxon responsible for a significant fraction of global primary production are probably the best example of this. The thicker the diatom shell, the more pressure is required to crush it and, presumably, the better the cell can survive the passage of the gut of a grazer (Hamm et al. 2003; Assmy et al. 2013). Indeed elevated shell thickness can be induced by grazer chemical signals (Pondaven et al. 2007), underlining the defence attribute of this trait. However, surprisingly, there is very little direct demonstration, neither of the efficiency of the grazer resistance that the shell provides (Carroll Lohan et al. 2016), nor of the cost required to build and maintain the shell and suspend the cell. We will manipulate the silica content of diatoms (e.g., via light) and experimentally examine how gut survival and grazing resistance to various grazers vary with the thickness of the shell. The costs of having a silica shell include the cost of forming it, elevated sinking losses and the formation of a vacuole to counter sinking, and the dependency on silica availability (see map). We will evaluate these costs through biochemical considerations, optimality modelling, and direct experiments by examining growth rates of cells in the absence and presence of grazer cues and under different environmental conditions.

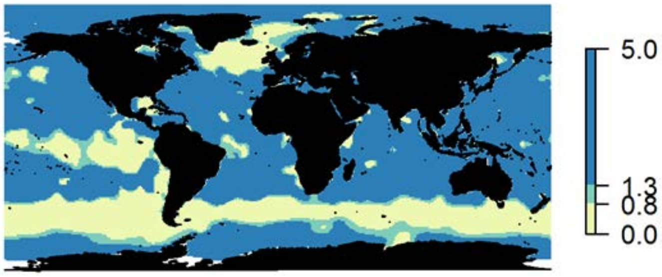


Figure. Global map of Si:N ratio. Values <0.8 in yellow mark the areas where Si rather than N is a growth limiting nutrient for diatom growth. This area coincides with the regions where diatoms dominate the phytoplankton (Pancic in prep)

Supervisors: **Thomas Kiørboe**, **André W Visser**, **Per Juel Hansen**

Project 1.2: Chemical defence trade-offs in phytoplankton

Many species of phytoplankton produce substances (toxins) that have defensive implications (Jonsson et al. 2009), because they impact the grazers directly (Tillmann 2004). The production of such toxins may be induced by grazer cues (Selander et al. 2006), and may have lethal or sub-lethal effects on zooplankton grazers, or may allow the grazer to actively deselect toxin producing cells, as revealed by our direct observations of individual zooplankton responses(Xu et al. 2017) . We will focus on quantifying the costs and benefits of toxin production (the trade-off). Previous experimental attempts to quantify the costs of toxin production have been unsuccessful, and induced cells appear to grow as fast as un-induced cells (Bergkvist et al. 2008). However, we hypothesize that costs will become apparent only when nutrients are limiting, as they typically are in nature. We will quantify the costs of chemical defences through direct experiments with nutrient limited cells, and through stoichiometric resource allocation optimization modelling.

Supervisors: Per Juel Hansen, Thomas Kiørboe, Ken H Andersen. Collaborators: Hans Dam (University of Connecticut)

Project 1.3: Risk versus resource acquisition in heterotrophic nanoflagellates

In the low Reynolds number world of protists, viscosity impedes predator-prey contact, and the physics of how protists nevertheless clear huge volumes of water for bacterial and phytoplankton prey is not understood for most significant forms (Langlois et al. 2009; Nielsen and Kiørboe 2015). Also, the processing of water for prey capture implies fluid disturbances that will allow flow sensing predators to detect the feeding protist (Kiørboe et al. 2014b), and feeding mechanisms will differ in their efficiency and risk. We will combine experimental and modelling approaches to achieve a mechanistic understanding of the feeding mechanisms in representative forms, and to make quantitative estimates of the associated trade-offs, largely following the approach used to explore resource acquisition trade-offs in zooplankton (see report). We will use high-speed video-microscopy to observe prey encounter and capture, and micro-PIV and particle tracking to estimates feeding currents and the fluid disturbances. Simple analytical models will provide insights in the underlying physical mechanisms (how flows are generated by beating flagella and cilia), and computational fluid dynamics models (CFD) will provide quantitative estimates of flows and clearance rates and, hence, feeding-mortality trade-offs, that will also be quantified experimentally. By resolving the underlying mechanisms of feeding and mortality risk, we will be able to generalize our results beyond the relatively few forms that we can study.

Supervisors: Thomas Kiørboe, Anders Andersen, Collaborators: Roman Stocker (ETH, Zürich), Stuart Humphries (University of Lincoln, UK), Jens Walter (DTU/ETH Zürich).

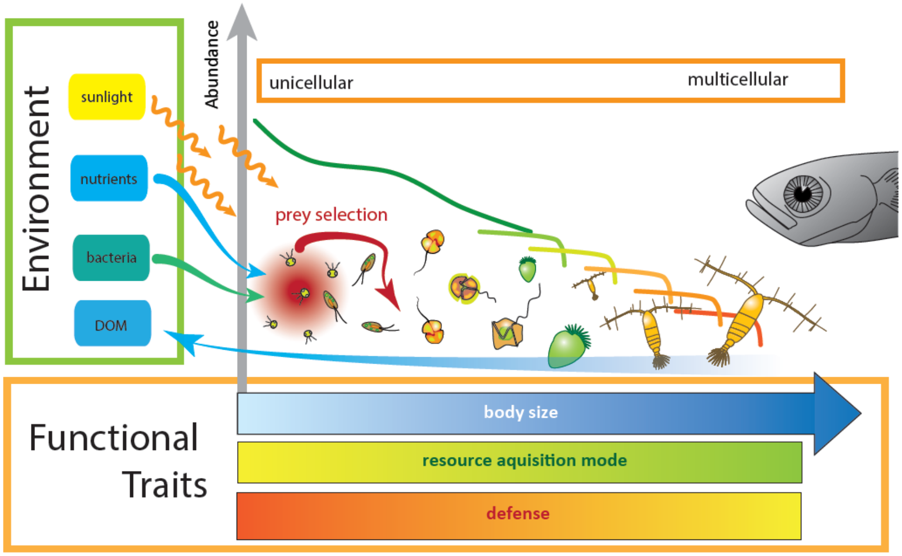
Project 1.4. Trade-offs of microbial N2 fixation in the oceans

The availability of nitrogen (N) limits biological production in vast areas of the global ocean. Availability of N is therefore tightly linked to the fixation of atmospheric CO_2 and export of carbon from the ocean's surface (Zehr and Kudela, 2011). N is the second most abundant element in living organisms, but although its most common form, N_2 gas, is found at high concentration in seawater it can only be used by specialized microorganisms (*diazotrophs*) capable of converting dissolved N_2 into "fixed" N available for growth and fixation of CO_2. The prevailing belief is that cyanobacteria using light are the only relevant N_2 fixing organisms. It has, however, now become evident that N_2 fixing bacteria with a fundamentally different ecology, the heterotrophic non-photosynthesizing bacteria, are widespread and active in marine waters, and that they play a role in marine biogeochemistry (e.g. Bentzon-Tilia et al., 2015b). Still, how they carry out the energetically expensive and anaerobic process of N_2 fixation in aerobic marine waters is not understood (reviewed in Bombar et al., 2016). We will combine experiments with key isolates (Bentzon-Tilia et al., 2015a) and models to constrain the energetic trait-offs associated with N_2 fixation. Our hypothesis is that the main energetic expenditure is associated with strategies to avoid oxygen, rather than the reduction of N_2 *per se*, and that suitable environments for N_2 fixation therefore are defined by both oxygen, resource (energy) and reduced inorganic N conditions. The mechanistic description of the energetics associated with N_2 fixation is essential for understanding and predicting the distribution, importance, and ecology of diazotrophs – and is consequently fundamental for an improved understanding of the presently unbalanced N budget of the global ocean.

Supervisors: Lasse Riemann, Ken H Andersen. Collaborators: Mick Follows (MIT)

Project 1.5: End-to-end model of planktonic life in the ocean

What is the trait structure of planktonic life in the ocean? In this project we will build a trait-based model that bridges from physics – light and nutrients – towards fish. The aim is to explore how the physical forcing shapes structure and function of the planktonic system and to create a basis for the models in WP2 and WP3. It is a realization of the vision outlined in (Andersen et al. 2015a). The model resolves three traits: 1) body size that determines predator-prey interactions (big eat small); 2) resource acquisition model (auotroph, mixotroph, heterotroph, cruising or ambushing); 3) investment in defence (see illustration). Technically, the model will be structured with size as a continuous variable, while the two other traits will adapt towards their optimal value (as in project 1.7). This minimizes the number of state variables and makes the model tractable. The unicellular part of the model will build on our previous work on strategies of unicellular planktonic organisms (Chakraborty et al. 2016a). The addition of multicellular organisms (copepods) is a true novelty. Here we use our expertise in developing size-based models of fish as a basis for resolving the copepod life cycle (Andersen et al. 2016a).



Supervisors: Ken H Andersen, André Visser, Thomas Kiørboe.

Work package 2: Community trait assemblages and ecosystem function

This work package focuses on ecosystem functions: the rate of organic carbon production, nutrient cycling, trophic transfer efficiency, and carbon export. In this, we view marine ecosystems as channels of energy along one of three different pathways: (1) to higher trophic levels such as zooplankton, fish and marine mammals, (2) through a microbial loop that recycles mineral nutrients, or (3) into export to the deep oceans (see figure).

Figure: marine ecosystems channels energy from primary production towards higher trophic levels, towards recycling of nutrients, or export it to depths (carbon sequestration).

The primary goal of this work package is to quantify how these ecosystem functions emerge from and relates to the trait composition of the community. We will do so across trophic levels, from bacterial recycling of dissolved organic carbon (2.1), over different aspects of the carbon export by copepods (2.2 -2.3), to fish production (2.4). The projects targeting specific trophic levels are complemented by two projects addressing several trophic levels, either through observations (2.5) or theoretical models (2.6). In all cases, the hypothesis is that ecosystem function is more accessible and better predicted from trait-composition than from species composition.

Project 2.1. Bacteria traits and the recycling of organic matter

Heterotrophic microbial communities are essential components of marine ecosystems (Azam & Worden 2004, Falkowski et al. 2008). They breakdown particulate organic matter (POM), recycle dissolved organic matter (DOM), mineralize carbon and nutrients, and serve in turn as a food source for micro zooplankton. The focus of this project is to develop a microbial community model that can describe the breakdown and recycling of organic matter by bacteria. The traits and trade-offs associated with extracellular enzymes define their acquisition strategy for resources (energy, carbon, nutrients) from the mixture of dissolved organic compounds in the environment (Vetter et al. 1998; Alison 2012; Travig et al 2015). Importantly, different enzymes target different fractions of the DOM pool. We will quantify the costs and of enzyme production, and the return on enzyme investments in meeting energy, carbon and nutrients demands. These trade-offs determine the fitness of a given trait combinations, so that under different conditions (e.g. temperature, POM supply, substrate concentration and stoichiometry) certain trait combinations will prevail. It also follows that the resulting community structure will determine overall community functions such as the net rate of carbon uptake from DOM, its changing chemical profile as different DOM fractions are targeted, and ultimately nutrient re-supply to autotrophic plankton. The overall outcome of this project will reveal the controlling factors influencing microbial production and turnover of dissolved organic material in the oceans, a large yet poorly understood component of the global carbon pool

Supervisors: Colin Stedmon, André W Visser; Collaborator: George Hagström (Princeton University)

2.2 Predator-prey games and ecosystem functions

Trophic interactions are ultimately strategic games played out between predators and prey (Maynard Smith 1976). The rationale for the rules of these games can be found in natural selection, and can be embodied in either physiological traits (e.g. size, defence) or behavioural traits (e.g. migration, selective feeding). While we have the ambition of exploring the game theoretic aspects of tropic traits and trade-offs in a general frame work, this project will concentrate on a specific case, that of vertical migration and its associated ecosystem functions. Vertical migration is a common behaviour of life in the ocean, being exhibited by wide range of organisms from marine mammals to fish and plankton. It has important consequences for key ecosystem functions: the trophic transfer efficiency of the community as well as the carbon export (Steinberg et al. 2008; Hansen and Visser 2016), oxygen budget (Bianchi et al. 2013) and nutrient cycling (Dam et al. 1995). Migrations can be rationalised in terms of a trade-off between growth and survival; for a grazer, this would involve a balance between visual predation risk in the surface and the vertical abundance of food. The predators that in some sense provoke the migration of grazers, have in turn their own imperatives to optimize fitness; they can follow their prey or not, or adopt some other distinct migration pattern depending for instance on water clarity, competition with non-visual predators, and their own mortality risk (Sainmont et al. 2013). This triggers a cascade of interlinked migration patterns throughout the food web (Bollens et al. 2011) where the optimal choice for one affects the optimal choice for the other and vice versa (Hugie and Dill 1994). More strategically within a trophic chain, this can promote predators and prey of an intermediate consumer to seek out each other's company – the one acting as bait the other as protector - in a mutually beneficial arrangement (Schmitz et al. 2004; Kaartvedt et al. 2005). That is, there is a game of strategies being played out between predators and prey that ultimately shapes the patterns of diurnal vertical migration that emerge in nature. While this trophically linked behavioural game is of interest in its own right, the aim of this project is to quantify the importance of vertical migrations for ecosystem functions.

Supervisors: André W Visser, Uffe H Thygesen. Collaborators: Øyvind Fiksen (University of Bergen), Hans Dam (University of Connecticut).

Project 2.3. Zooplankton and the oceanic carbon pump.

Zooplankton contribute significantly to the downward transport of carbon in the ocean and, hence, to carbon sequestration, through three main processes: (i) by packaging grazed phytoplankton into large rapidly sinking fecal pellets (Turner 2002; Stamieszkin et al. 2015), (ii) by undertaking diel vertical migration and metabolizing part of the phytoplankton grazed in the surface layer at depth (Hays 1994; Hansen and Visser 2016), and (iii) through the accumulation of large lipid reserves which partially fuel overwintering in deep ocean basins (Jónasdóttir et al. 2015; Visser et al. 2016). Each of these contributions depend strongly on the size of the zooplankton: the larger the zooplankton, the larger and faster sinking are their faecal pellets (Stamieszkin et al. 2015), the deeper their diel vertical migration (Hansen and Visser 2016; Ohman and Romagnan 2016), and the easier it is for the organisms to accumulate enough reserves to hibernate at depth (Maps et al. 2014; Visser et al. 2016). Hibernation is also dependent on latitude, being much more pronounced in arctic regions than elsewhere (including Antarctica) (Dahms 1995) where productivity is strongly modulated seasonally. This project will combine novel trait-based modelling frameworks and spatiotemporal statistical tools to obtain unique insight into the zooplankton-mediated processes of the biological pump, and their response to recent climate change. Specifically, will produce global maps of zooplankton size distributions based on (i) the copepod trait biogeography that we have generated already(Brun et al. 2016a)(Brun et al. 2016a)(Brun et al. 2016a)(Brun et al. 2016a) (Brun et al. 2016a), and (ii) a simple trait-based model that predicts zooplankton size from satellite-derived estimates of phytoplankton biomass and sizes (Boyce et al. 2015). The expected result is a global assessment of the magnitude carbon sequestration due to zooplankton grazing.

Supervisors: Andre Visser, Sigrún Jónasdóttir, Thomas Kiørboe

Project 2.4. Global model of fish production and benthic-pelagic coupling

The productivity of the pelagic and benthic fish component of marine ecosystems varies largely between different areas (Suess 1980). Yet, it is so far unclear what drives global spatial patterns in the productivity of fish feeding, and how benthic and pelagic production will shift under climate change. This project aims to investigate the role of the parallel pathways of pelagic and benthic energy for the structure of fish communities and their production. The energy flux in marine systems can be broadly divided into a pelagic and benthic pathway (see figure). Energy is generated by phytoplankton that is either consumed directly by secondary producers in the water column (pelagic pathway) or sinks to the bottom, where bottom-dwelling organisms consume the phytoplankton (benthic pathway). Both energy pathways support fish species, however, most species are specialized on either benthic pathway, e.g., flounders and angler fish, or the pelagic pathway, e.g. small forage fish. Feeding on these resources and the energy pathways are generally coupled by fish species at higher trophic levels (fish predators) that use both pathways for feeding (Rooney et al. 2006).

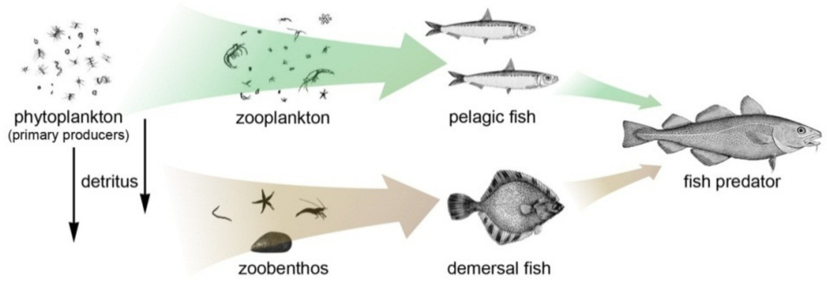


Fig. 1 Sketch of a marine food web with a pelagic (green) and benthic (brown) energy pathway. Fish predators act as couplers of both pathways.

The project will develop a simple community model of the benthic/pelagic fish community by describing fish with two traits: their asymptotic size and their feeding habitat (pelagic/benthic). The model is based on the previous fish community modelling in the Centre for Ocean Life (Andersen et al. 2016b), simplified to make it possible embed it in a Global Circulation Model (GCM). We will use the NOAA/GFDL Earth System model as the model of physics and with the COBALT primary-secondary production model (Stock, Dunne, & John, 2014). Predictions of the global distribution of benthic/pelagic species will be compared with analysis of available global catch data (Pauly and Zeller 2015).

Supervisors: Ken H Andersen, Martin Lindegren, Brian MacKenzie. Collaborators: Charlie Stock (NOAA Geophysical Fluid Dynamics Laboratory).

Project 2.5. Biomass production across trophic levels

Despite the long history and recent advances in biodiversity-ecosystem functioning research, our ability to understand and predict ecosystem functioning in nature is severely limited by a number of key shortcomings, primarily involving an inadequate consideration of food web structure and the role of species traits (Cardinale et al. 2012b; Thompson et al. 2012; Gravel et al. 2016). This project will use available global and regional data on species abundances and traits to estimate and evaluate the magnitude and variability of key ecosystem functions. We will focus on biomass production across multiple trophic levels, and its variation. We will do so by construction of algorithms for trait-based assembly of food-webs, on the basis of species traits. We will collect a set of highly resolved marine food webs for which species (nodes), their interactions (links) and traits are available across all trophic levels (Jacob et al. 2011; Eklöf et al. 2013). We will use graph-theoretic methods to transform a given food web into a weighted “trait web” where nodes represent traits and weighted links express the frequency of occurrences of interactions between species sharing a corresponding pair of interaction traits. The robustness of the configurations will be assessed by comparing trait webs derived from different locations and examining the variance with respect to link weights between trait webs. The derived knowledge on interaction traits and food web structure will be used to develop, or modify available trait-based food web models (Zhang et al. 2013, 2016) capable of predicting food web structure and functioning from multiple interaction traits.

Supervisors: Martin Lindegren, Ken H Andersen. Collaborator: Jan Baumbach (University of Odense).

Project 2.6: Macro-scale biogeochemical fluxes across trophic levels

How can macro-scale ecosystem fluxes and efficiencies be predicted from the physiological capacity and physical constraints of individual organisms? Existing theory use the size of individual organisms as the fundamental trait (Sheldon et al. 1977; Andersen and Beyer 2006). Such theory has successfully described the size structure – how biomass change with size and trophic level – of the ecosystem. What has been partly overlooked, however, is the potential to use the theory to describe ecosystem function in terms of bio-geochemical fluxes. This project will develop size-based theory to address central questions about ecosystem function:

1) What is the total respiration of CO_2 and excretion of nitrogen and phosphorus as a function of size and trophic level?
2) What is the fate of iron in the food chain – how much is concentrated at the upper trophic levels?
3) What is the loss of biomass from the pelagic zone for each trophic level, and what remains as production for higher trophic levels?
4) How does the variation in stoichiometry, i.e., C:N:P ratios, change through trophic levels by the integration of predators over prey with different C:N:P ratios?
5) How many marine mammals can the global ecosystem sustain?

The project will develop the theory on two levels. First, a complete analytically tractable theory based on existing size-spectrum theory will be created (Andersen and Beyer 2006). This extends previous work based on metabolic theory (Schramski et al. 2015), but it will not rely on assumptions about ecological transfer efficiencies – those will be predicted (Andersen et al. 2009). Second, the theory will be developed into a dynamic size-based model. The model will be based on the ideas of Banas (2011), extended to include all trophic levels, and not just plankton. This model will constitute a minimal “end-to-end” type of ecosystem model. The project will link up to projects 1.8, which provides modelling techniques to deal with the stability issues that are known to plague size-based models, and to project 1.9 which develops a more advanced model. We expect the project to provide simple predictions of the macro-ecological biogeochemical functions of all trophic levels, from bacteria to whales.

Supervisors: Ken H Andersen. Collaborator: Adam Martiny (University of California, Irvine).

Work package 3. Global change: Ecosystem responses to perturbations

This work package addresses the effects of global change using a trait-based approach. Two types of perturbations are explored: Climate change and fisheries.

Climate change will impact organisms directly by changing the trade-offs between different functions. For example, fundamental processes, such as photosynthesis, metabolism and feeding rates scale differently with temperature (Wilken et al. 2013; Toseland et al. 2013a) thus changing ecosystems in non-trivial ways in response to temperature changes though changes in the dominant type of organisms in response to changes in temperature (Projects 3.1 for microbes and 3.4 for fish). Likewise, the *interaction* between temperature and resources acquisition can lead to quantitatively and qualitatively different outcomes from those expected based on temperature and resources separately (Edwards et al. 2016, Thomas et al in press). (Project 3.2). The general warming of the oceans have already had measurable effects on the spatial distribution of species that are reported to move mainly pole-wards, but this by itself does not necessarily imply a change in ecosystem function since the trait biogeography may change (or not) independent of changes in species biogeography. Some organisms may be able to adapt to higher temperatures over multiple generations by changing their temperature reaction norms (Thomas et al. 2012; Dam 2013) preventing a geographical relocation of those organisms (Project 3.3). The understanding of how the physiological effects of climate change modify trade-offs is utilized in projects addressing the entire system by mechanistic trait-based models (3.5). Finally, the perturbations from fisheries are addressed by operationalizing our trait-based modelling framework (3.6), or by application of the fish model from WP2 in project 2.4.

Project 3.1. Temperature and the vital rates of plankton communities

It is generally understood that the pace of life increases with increasing temperature. However, for two of the central processes that govern planktonic ecosystems, namely primary production by photosynthesis and metabolism, the rate of increase is different. Temperature therefore directly shifts the balance in the trade-off between investing in light harvesting or synthesis of new biomass (Toseland et al. 2013a). This project seeks to understand the consequences of the changed trade-off for the overall structure and function of planktonic ecosystems (e.g., production, nutrient cycling, carbon sequestration) under increasing temperatures. The approach will be to develop a suite of trait-based models based on optimization, game theory, and population dynamics that will couple metabolic processes and fitness trade-offs. Our trait-based models will explicitly quantify the effects of temperature on three crucial ecosystem processes: photosynthetic carbon fixation, predation, and organic matter remineralization by extending our recent optimization model (Berge et al. 2016; Chakraborty et al. 2016b). Our model will resolve the distribution of investments into photosynthesis, phagotrophy, and organic matter acquisition within discrete size classes, allowing ecosystem level properties to emerge through the ecological interaction between different phenotypes. Ecological competition will be modelled by assuming either locally-optimal strategies for each size class or by assuming that all cells are generalists (using the resulting fluxes to determine the dominant trophic strategy in each size class), and there will be a simple coupling to biogeochemical processes resolving the cycle of carbon and a single nutrient. This will give us a mechanistic understanding of how temperature alters ecosystem processes through changes in the central trade-off between light harvesting and biomass synthesis.

Supervisors André W Visser, Ken H Andersen, Thomas Kiørboe. Collaborators: Adam Martiny (University of California, Irvine), George Hagstrom (Princeton University)

Project 3.2. Interacting effects of temperature and resources on marine phytoplankton populations and communities

Temperature and resources (such as nutrients and light) are the most fundamental drivers of biological processes. They form the core of three of ecology's most successful bodies of theory – the metabolic theory of ecology (West 1997) ecological stoichiometry (Sterner and Elser 2002), and resource competition theory (Tilman 1982).Despite their successes, these theories suffer from a major flaw: at present, they do not consider how temperature and resources *interact* to influence biological processes. Especially because both temperature and resource supply are changing globally, understanding this interaction is vital to making accurate predictions of species ranges, biodiversity, and ecosystem processes. The objective is to build an empirically grounded theoretical understanding of how temperature and resources interact to influence phytoplankton. This will involve 4 steps: (i) synthesizing and analyzing datasets from physiology experiments to shed light on the mechanisms by which temperature and resources influence population growth; (ii) developing a model describing how *population growth* is driven by interactions between temperature, light and nutrients, and testing predictions from this model using datasets of laboratory growth rate experiments and species occurrences in the oceans; (iii) developing a model describing how *communities* respond to changes in temperature and resources (based on how populations will respond and physiological trade-offs) and testing predictions from this model using existing datasets from marine field experiments; (iv) building a dynamic model of phytoplankton growth to examine how predation by zooplankton influences both *population strategies* and *community responses* across environmental resource gradients. Jointly, these activities will provide both practical results about the dependence of growth on environmental conditions that enable the accurate modelling of phytoplankton productivity, environmental nutrient concentrations and species distributions and yield theoretical insights into the resource dependence of metabolic scaling and the temperature-dependence of resource requirements that will aid the unification of distinct branches of ecological theory.

Supervisors: Thomas Kiørboe, Mark Payne. Collaborators: Elena Litchman (University of Michigan).

Project 3.3. Plasticity trade-offs of temperature adaptation in copepods

Recent work has shown that evolutionary change may occur on contemporary time scales in nature, including the adaptation of both phyto- and zooplankton to changes in temperature (Thomas et al. 2012; Dam 2013). Yet, we know very little about the capacity of individual species to respond to climate change through adaptation, the involved trade-offs, and even less about the genomic architecture underlying such response. The response to temperature will be obtained by mapping the reaction norm; i.e., how the organism performs (growth, fecundity) as a function of temperature, and the hypothesis is that the area under the reaction norm remains the same: that is, a tolerance to higher temperatures, for example, is traded off against a lower tolerance to lower temperatures. Here, we will hatch resting copepod eggs from sediment cores up to 100 years back in time to investigate if and how marine copepods have responded to past climate change in nature, and how the revived populations will respond through multiple generations to temperature change under controlled experimental conditions.. Furthermore, we will compare the response of different populations to examine the importance of genetic variation for adaptive capacity to climate change. We will use a combination of high powered genomic technology and studies of temperature dependence of life history traits to obtain simultaneous information for fitness related traits and the underlying genetic variation. These data will be essential for improving our ability to predict responses of species and systems to future changes in the marine environment (Urban et al. 2016).

Supervisors: Thomas Kiørboe, Jakob Hemmer-Hansen. Collaborators: Hans G. Dam (Univ Connecticut), Luc De Meester (University of Leuven).

Project 3.4. Response of fish physiology to climate change

Most marine organisms are ectotherms (cold-blooded) and their physiological performance is therefore directly affected by the water temperature. As a complicating factor the physiological rates also scale with body size: the standard metabolism, oxygen acquisition rates, and digestion rates all increase with size but with different scaling exponents. For fish, which have a large difference between offspring size (around 1 mg) and adult size (from 1 g to 100 kg), the interplay between how different vital rates scale with body size and temperature is pronounced and depends on how the organism invests in physiological functions, particularly oxygen acquisition and digestion (gills and gut). How does a change in temperature impact the overall function and fitness of fish species with different investment in physiological functions? Some understanding exists (Ursin 1967; Pörtner and Knust 2007; Holt and Jørgensen 2015), however, a full mechanistic understanding based on traits of investment in oxygen acquisition (gills) and digestion (stomach and intestines) is lacking. We will bring about such an understanding by meta-analyses of existing measurements of the size of gills, the digestive system, and standard metabolism supplemented with our own measurements. The empirical analysis will be used to parameterize a mechanistic model of fish physiology, described by the traits of oxygen investments, digestive investment, and maturation size. We will use the model to provide a mechanistic description of how temperature affects physiology, in particular the asymptotic size and the fitness. To predict community-level impact of temperature change, the model will be integrated in our existing size- and trait-based fish model (Andersen et al. 2016a) to simulate the community-level effects of rising temperature.

Supervisors: Ken H Andersen, Niels Gerner Andersen. Collaborators: Phil Neubauer (Dragonfly Science, New Zealand).

Project 3.5. Food-web response to climate change

Attention from the scientific community concerning climate change on marine ecosystems has focused on the impact of temperature changes on physiology (see e.g. the project description above). Such analyses rely on an assumption that the surrounding community remains unaffected, i.e., that availability of prey and risk from predation is unaffected by climate change. That assumption is, however, unlike to be true: population dynamics of species well inside their thermal niche is also determined by competitors, preys, and predators (Urban et al. 2016). This is for example evident from analyses of range shifts of species, where some move in the direction of their temperature optimum, while others move in opposite directions (Pinsky et al. 2013). The question is then which effect is most important: the direct impact of temperature on physiology, or the changes in the surrounding community? Here we will extend a trait-based food-web model developed in the first part of Center for Ocean Life (Zhang et al. 2013) to examine how the interplay between the direct physiological effects from temperature and the interactions between populations shapes the ecological consequences of climate change for populations and entire communities. Unlike other food-web models (such as Brose et al. 2006), this model has a trait-based description of organism interactions, instead of the commonly used random interactions. The model will be extended by introducing a trait to describe temperature preferences and used to make a generic assessment of the impact of climate change on a food web. Next, the model will be extended with an explicit representation of a space along a temperature gradient, to explore the range shifts of species. Finally, the model will be parameterized with a global database of temperature preference of fish (from the “Sea Around Us”) to assess global range shifts of fish species.

Supervisors: Ken H Andersen, Martin Lindegren, Mark Payne. Collaborators: Malin Pinsky (Rutgers University).

Project 3.6: Operationalize size-spectrum models of fish communities

Ecological research and science-based input to management of ecosystems rely to a high degree on model simulations. Such models are used to make impact assessments of how ecosystem function is expected to respond to perturbations such as climate change or fishing. The models are now reaching a level of complexity where individual researchers are unable to develop, implement and apply the models alone. Therefore, established model frameworks, which provide readily accessible implementations, are becoming increasingly important. Examples are the food-web framework

EcoPath with EcoSim (Christensen and Walters 2004) or the ecosystem-based management modelling framework Atlantis (Fulton et al. 2011). This development is akin to the development of models in physical oceanography. Oceanographers rely on a handful of model frameworks, many of which were initially developed in the 70ies and are being continuously supported and developed by a loosely knit modelling community. The trait-based framework of fish communities developed in the first part of Centre for Ocean Life (Andersen et al. 2016a) has the potential to become an important part of the budding family of marine ecosystem models that are sued to assess the global production of fish for consumption, and it future change. In the first part of the centre we made a simple open-source implementation available (Scott et al. 2014), and the interest and success has been overwhelming. Other groups are applying the model framework directly (e.g. Spence, Blackwell, & Blanchard, 2015; C. Zhang, Chen, & Ren, 2015) or developing it further (e.g. Jennings & Collingridge, 2015). Continued success, however, depends upon an investment in further development of the code-base, support to researchers wanting to apply the model, maintenance of the web presence, and education young researchers (PhDs and post docs). This project aims to do that. We expect that development, maintenance, and education can be supported by a part-time post doc researcher who also works on practical applications that are financed by other sources than Ocean Life, or on another Ocean Life project, such as 2.4 or 3.4.

Supervisors: Ken H Andersen. Collaborator: Julia Blanchard (Institute for Marine and Antarctic Studies, University of Tasmania).