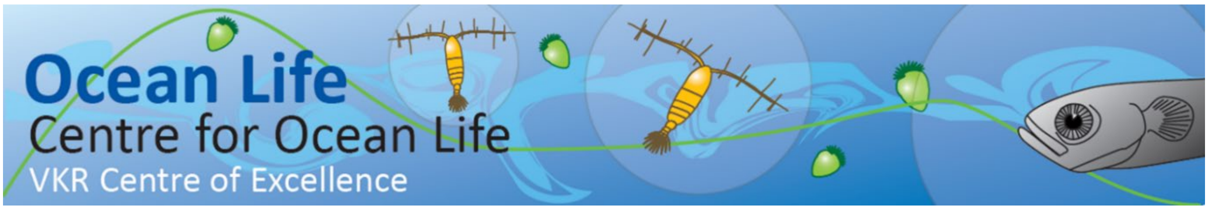

CENTRE FOR OCEAN LIFE

A VKR Centre for studies of Life in a Changing Ocean

2012-2024

FINAL REPORT

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INTRODUCTION

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

Trait-based approaches have emerged as an efficient way to describe the overwhelming complexity of marine ecosystems in a relatively simple way. The trait-based approach aims to describe how structure and function of ecological communities emerge from properties of the individual organisms. It differs fundamentally from the traditional species-centric description of ecosystems, which focuses on *differences* between *species*. In contrast, the trait-based approach focuses on *generalized* mechanistic descriptions of the challenges (feed, survive, reproduce) that all *individual* organisms face. From these descriptions of individuals, the structure and function of ecosystems emerge as different trait combinations, interrelated through trade-offs, provide greater or lesser reproductive success to their bearers in an everchanging physical environment. Notably, the trait-based approach, based on these fundamental principles, provides a framework for a predictive ecology that can map out emergent marine ecosystems in an uncertain future.

The work at the Centre has evolved along four closely related themes (work packages), where one theme feeds into the next one (Fig. 1): (i) *The individual*: identifying and mechanistically quantifying the key traits of important marine life forms (bacteria, phytoplankton, zooplankton, fish) and quantifying their associated trade-offs; (ii) *Models:* scaling of individual behaviors as described above to population and ecosystem dynamics through the development of trait-based trophic models of marine ecosystem and to predict trait distributions in nature; (iii) *Nature*: using observations from nature to describe trait distributions in the ocean and their relation to the environment and to test model predictions by comparing predicted and observed trait patterns; (iv) *Ecosystem function*: quantifying ecosystem functions (e.g., carbon sequestration and fish production) from observed and modelled trait distributions. In addition to embracing the complexity of marine ecosystems in a relatively simple way, the trait-based approach is particularly well suited to evaluate the function of an ecosystem, since ecosystem function is a result of the traits of the organisms making up the system, rather than governed by their taxonomic affiliation.

Each of the work packages has been led by a PI, and the Centre itself managed by a director and deputy director. Coherence of the work and training of young researchers in cross-disciplinary communication and understanding has been facilitated through (i) weekly mandatory meetings for all members of the Centre with presentations of ongoing work; (ii) establishment of ad hoc working groups for selected members to pursue topics of common interest (e.g., groups on modelling and biophysics); (iii) annual 2-4 day long science retreats; (iv) through joint projects and publications that have involved many or most of the member of the Centre; and (v) by all students and post docs having supervisors from complementary disciplines.

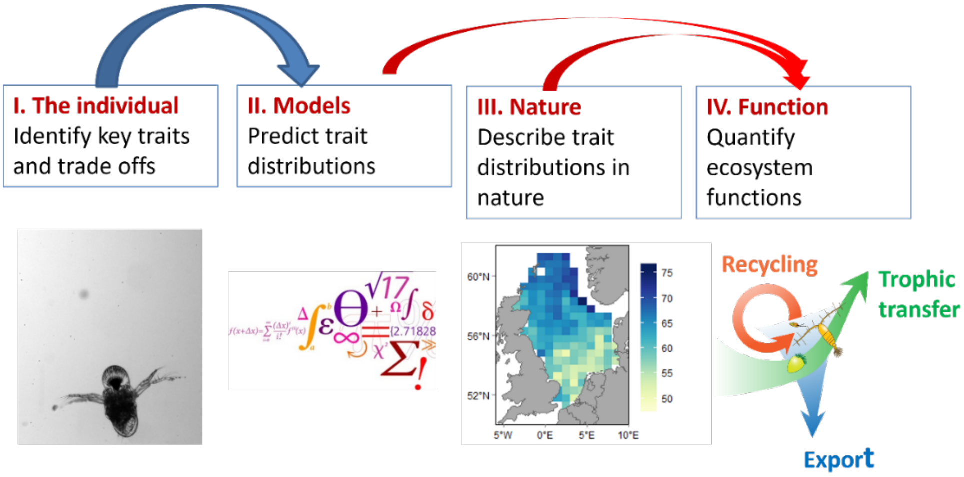

Fig. 1. *The four components of the trait-based approach as developed at the Centre for Ocean Life. From* [1]

MAIN SCIENTIFIC RESULTS

Below we describe, through a few examples, the main scientific achievements for each of the work packages defined above.

The individual: A central element in the trait-based approach is to identify the key traits associated trade-offs of the main life forms in the ocean. A key trait of an organism is a property that has a major impact on its Darwinian fitness. Therefore, key traits are related to the organism's ability to acquire resources, to survive, and to reproduce, i.e., the main components of its fitness. These activities and traits obviously materialize differently for different life forms, but useful traits transcend taxonomy within life forms. For example, the ability to do photosynthesis applies across the huge phylogenetic diversity of phytoplankton. There are inescapable trade-offs between the 3 main fitness components: no organism can simultaneously perform optimally with respect to resource acquisition, survival, and reproduction - such an organism, the Darwinian demon, would outcompete all other organisms and reduce diversity to a minimum – and the diversity, structure and function of an ecosystem is therefore governed by organismal tradeoffs (and environmental constraints).

These considerations have guided our selection of lifeforms (our focus has been on microorganisms, zooplankton, and fish) and traits for study. Our approach has been theoretical – one can rationalize some tradeoffs from physical or evolutionary constraints – and experimental. In both cases we have strived for an understanding of the underlying mechanisms. This has allowed us to (i) generalize from the few model species that we have examined, (ii) to simplify our findings in a meaningful way, and (iii) to formulate the trade-offs mathematically and in a way that they can be used for modelling (WP2).

Figures 2-3 provide examples of trade-offs related to resource acquisition and defense (survival) that we have quantified and rationalized. The first example quantifies the foraging-defense trade-off in flagellates, unicellular organisms equipped with one or a few flagella (Fig. 2). This example illustrates a fundamental dilemma for all consumers, i.e., to eat without being eaten. Gathering prey exposes the consumer to an elevated risk of being detected by a predator, something well established for large organisms in terrestrial systems, but hitherto poorly explored for microbes. Our novel contribution is to demonstrate, quantify, and mechanistically underpin the foraging-risk trade-off for pelagic microbes, and in a way that allows it to be directly implemented in our global models of pelagic microbial ecosystems.

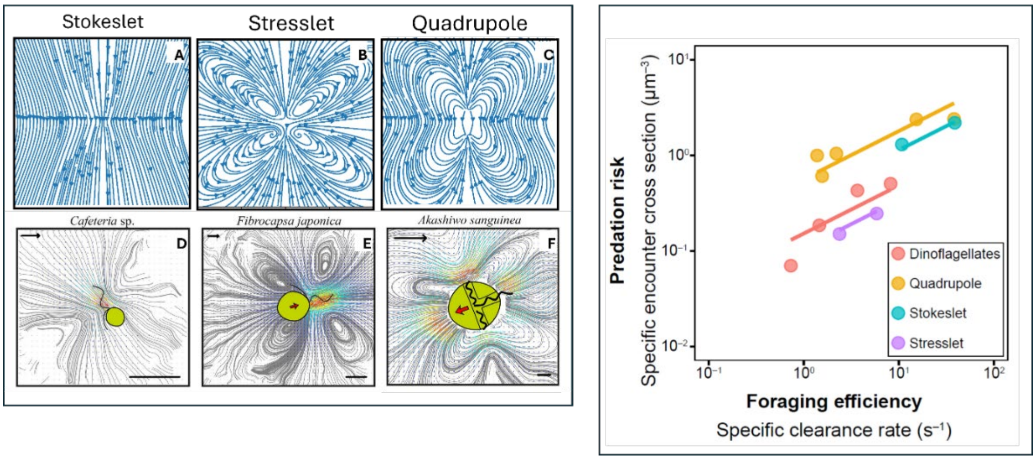

Fig. 2. *Flagellates, unicellular organisms equipped with one or a few flagella, are the most important grazers of bacteria in the ocean, and they are themselves prey to zooplankton. By the activity of their flagella, they create a feeding current from which they harvest prey. The structure of the feeding current depends on the position and activity of the flagellum, but it can be rationalized from simple fluid mechanical models (see comparison between observed and modelled flow structure in left panel; scale bar 5 µm). The feeding current, however, attracts their flow sensing predators, creating a tradeoff between foraging efficiency and predation risk (right panel). The risk/gain ratio varies with feeding flow structure, suggesting additional tradeoffs.* [2]

The next example quantifies the defense tradeoff in diatoms, a quantitatively significant group of phytoplankton that accounts for nearly half the oceanic primary production (Fig. 2). Diatoms are characterized by a silicified shell. Relative to its density, the diatom shell is the strongest natural material known. Copepods, however, are adapted to break the shell by having silicified ‘teeth’ and forceful musculature. Thus, the silicified shell provides only partial protection, but diatoms with thicker shells are deselected by the copepods. Diatoms may respond to the presence of copepods (and their diffusible cues) by increasing the thickness of their shell, but at the cost of a lower growth rate, hence a clear trade-off. The trade-offs identified here enter directly into models describing the performance of diatoms in the global ocean.

We have similarly explored and quantified organismal trade-off for other life forms, including bacteria, protists, zooplankton, and fish. The general and robust pattern that emerges from the optimization of the many different trade-offs related to resource acquisition, growth, and survival in planktonic organisms is a *slow–fast gradient in the pace-of-life.* This gradient is the result of a fundamental trade-off between current *versus* future growth and reproduction, it is expressed in different ways for different life forms, and it is the result of more specific trade-offs in each case. The gradient transcends taxonomy and life form and is found among organisms ranging from bacteria to zooplankton. It offers a way to further simplify trait-based models of complex pelagic systems.

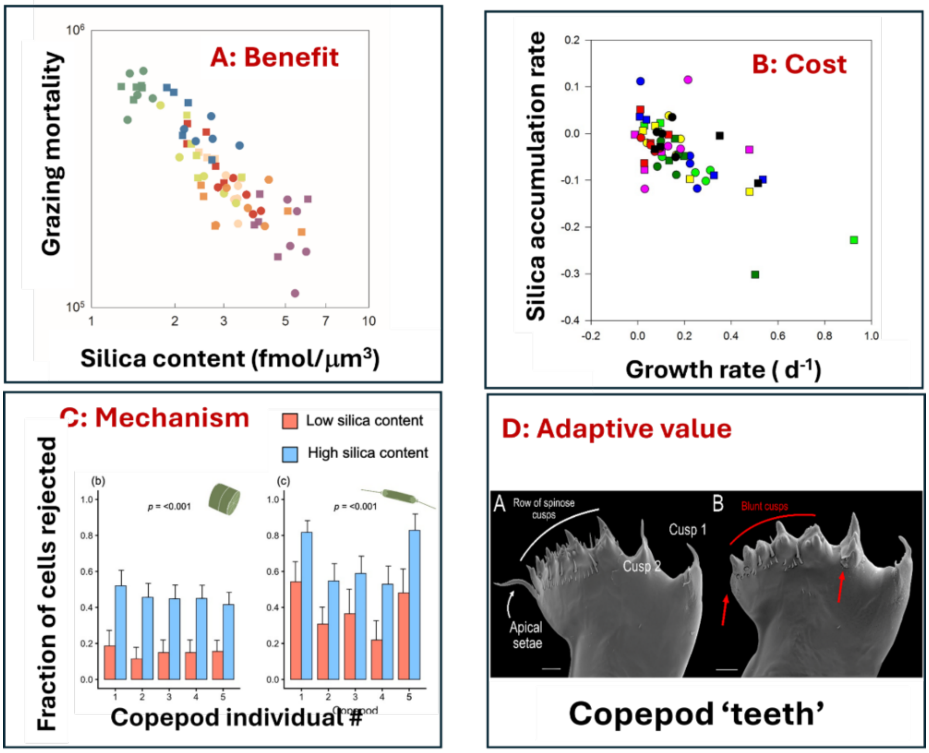

Fig. 3. *Diatoms and copepods are arguably the most important primary producers and zooplankton in the ocean. Copepods feed on diatoms, but diatoms are partly protected by their silicious 'shell', and the thicker the shell the better protected (panel A). However, this comes at a cost, because diatoms can only form a thick shell by growing slowly (panel B). The mechanism of protection is through the behaviour of the copepod: the copepod captures all cells but rejects cells with thick shells more frequently than thin-shelled cells (panel C). The copepod cracks cells before consumption by means of the 'teeth' at the base of the feeding appendages (panel D); when raised of a diet of thick-shelled diatoms, the teeth break, while they remain intack if raised on a diet of thin-shelled diatoms, illustrating the adaptive value of selectivity (left and right image in panel D). From* [3]

Models: The organismal trade-offs identified and generalized above are used to build trait-based models that describe structure and function marine ecosystems. Ecosystem structure is described by a *trait distribution*. A trait-distribution describes the number or biomass of individuals $N(\theta)$ with a given trait combination, θ, irrespective of their species. Trait distributions can be spatially explicit, i.e., describing trait biogeographies.

We have developed our own approach to trait-based modelling. The distinguishing feature of the modelling approach is that it is mechanistic, it is based upon a description of individual organisms, and the parameters are defined through the trade-offs from the "individual" theme.

The core principle is a description of individual-level processes related to acquisition of resources, allocation of resources, and mortality. Such descriptions are central to any process-oriented model; the novelty is connecting these processes to fundamental traits such that the parameters describing each process are connected via trade-offs, as quantified in the 'individual' theme. We note that trade-offs arise not only through the allocation of finite resources (energy and matter) but can appear indirectly through conflicts inherent in life tasks, e.g., foraging activity and exposure to risk (e.g., allocation of time, diurnal vertical migration, diapause, etc.). With this description the differences between individuals are represented solely by differences in trait values.

The set of traits determines the individual-level processes through the trade-offs. From the processes and the environment follow the fundamental vital rates, i.e., assimilated energy and mortality The vital rates are scaled up to community-level measures, the optimal combination of traits or the trait distribution using standard techniques from theoretical ecology.

A key step in designing a trait-based model is in the selection of traits. First, the set of traits should be small, one trait or a few, to be computationally tractable. Second, the set of traits should characterise the largest variation in the functional biodiversity. We have used “size” as a powerful “master trait” because most individual-level processes scales with body size. For the next level of traits, we have used investment in resource acquisition and the vertical position in the water column. In the following we give two examples of trait-based models on plankton and on fish.

Modelling the base of the pelagic food web has progressed on two fronts: the unicellular plankton and the multicellular plankton (copepods). In the oceans, most unicellular plankton are *mixotrophs* that combine photosynthesis with preying on smaller cells. We have developed the theoretical framework to model mixotrophy and integrated it into a size-based plankton model. The main trait here is cell size, which varies across 8 orders of mass. Further, we have used traits that represent the investment into resource harvesting: light harvesting, nutrient uptake, predation, and biomass synthesis and parameterized them using a combination of experiments and bioenergetic arguments. The result is a prediction of the emergent trophic strategies of unicellular plankton as the optimal trait combination in a particular environment (Fig. 4).

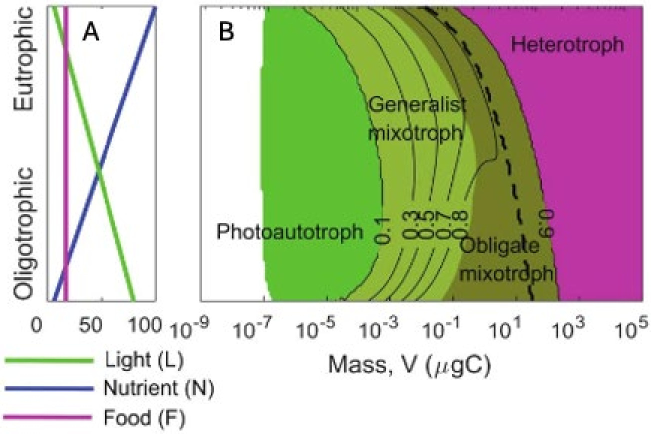

Fig. 4. *Optimal plankton traits in various environments form low productive oligotrophic (bottom) to high productive eutrophic (top). The traits are cell size (x-axis) and the resource investments into light harvesting, nutrient uptakes, and phagotrophy (predation on smaller plankton). The colors show how the optimal plankton trophic strategy varies with cell size and the environmental conditions. Generally, photoautotrophs (phytoplankton) are small, and heterotrophs (zooplankton) are large. However, in between there is a large range where a mixotrophic jack-of-all trades strategy that combines phototrophy and heterotrophy is optimal. From* [4].

We have subsequently integrated the unicellular model into a global simulation framework that forms the basis for including multicellular plankton. There was very little work on modelling multicellular plankton. This was a major gap in the understanding of the ocean ecosystem, because multicellular plankton forms the “missing link” to the higher trophic levels (e.g., fish communities). Formulating a general framework that integrates unicellular and multicellular plankton into the Nutrient-Unicellular-Multicellular NUM framework has been a major achievement of the Centre. The framework is based on two traits: adult body size and feeding strategy. The framework is based upon our large body of work on copepods and is a major legacy of the Centre. The framework has been used to calculate the carbon flux from copepods fecal pellets, and to understand the emergence of heterotrophy in the Earth’s distant past.

Modelling higher trophic levels has focused on fish and on two traits: the maximum size and the vertical position in the water column. The maximum size a fish may obtain during its life defines its physiology and ecological role: its growth and metabolic rates, its preferred prey, and the predators that may feed on it. This insight has allowed us to reformulate the classic theoretical framework for fish demography in terms of traits instead of based upon species, with big advantages for theoretical work as well as practical applications directed towards fisheries management. Important insights have been on understanding how fish populations are regulated, and why larger species of bony fish are very resilient to fishing while elasmobranchs are not. We have subsequently developed a trait-based model with a global scope: the FEISTY model. This model is unique because it makes it possible to link fish production to production of lower trophic levels as predicted from global biogeochemical models. Further, it predicts the structure of the fish food webs around the globe (Fig. 5). This model framework makes it possible to make predictions on the impact of climate change on fish and fisheries production and on carbon export.

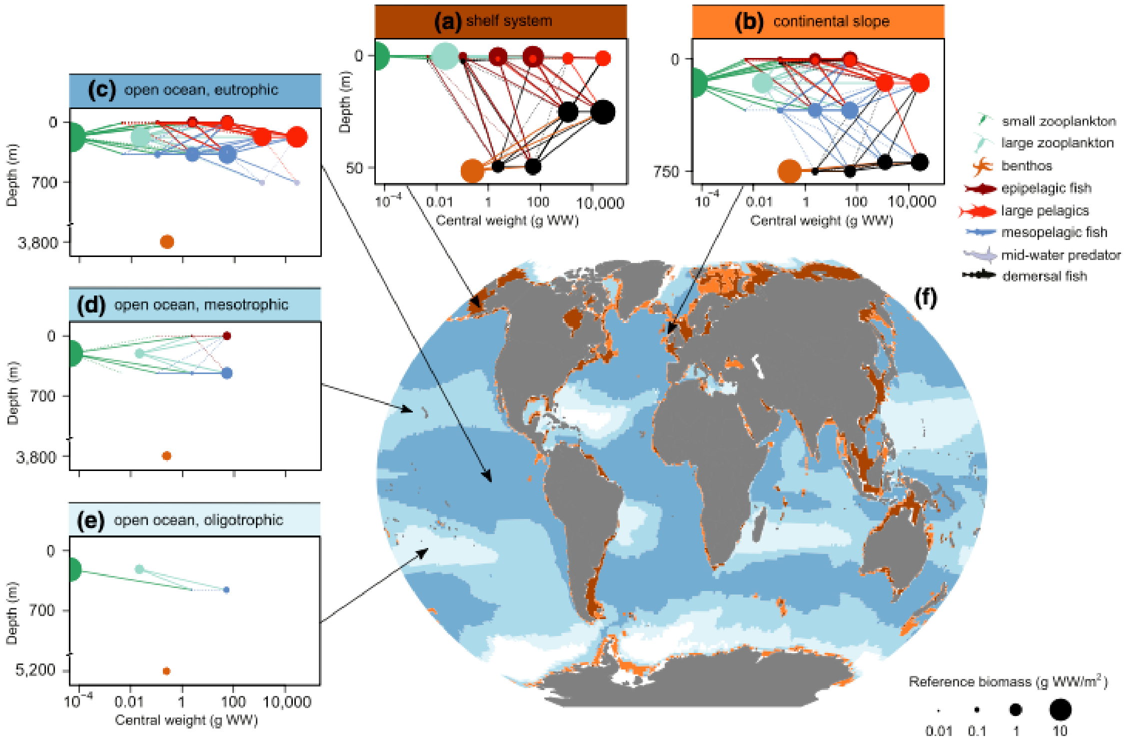

Fig. 5. *The global fish modelling framework FEISTY. The model predicts the emerging trait-based food webs (the small panels). Each panel shows 5 typical types of food webs with 5 functional groups of fish: large pelagic fish (red), small pelagic fish (dark red), mesopelagic fish (blue), bathypelagic predators (lighter blue), and demersal fish (black) as a function of their body size (x-axes) and their depth in the water (y-axes). The global map shows the global distribution of the different food web types. From the global map, we can derive the*

total biomass of fish (the global map). Further we can derive the ecosystem function of the fish community: the potential fisheries production and the benthic pelagic coupling. The estimated total fisheries production is 101 million tons per year, which corresponds well with the current global landings of 90-100 million tons per year. From [5].

Nature: The focus of this theme has been to describe trait distributions and large-scale patterns of marine biodiversity in the ocean, to understand the underlying community assembly processes, and to compare observed trait distributions with those predicted by the models developed under the 'model' theme. The first step has been the collection and standardization of trait information and available long-term monitoring data on species occurrences, abundances, and traits across multiple organism groups. Examples of such data infrastructure created within the Centre include open access trait databases of zooplankton and of marine fish. Based on the trait databases we have generated global trait distribution (trait biogeography) using advanced statistical methods and species distribution models to close gaps in the observations.

One example describes the trait biogeography of the master trait 'size' for zooplankton, both as predicted from a mechanistic trait-based model, and as derived from observations and statistical modelling (Fig. 6). Such comparisons are one way to test the validity of the mechanistic models.

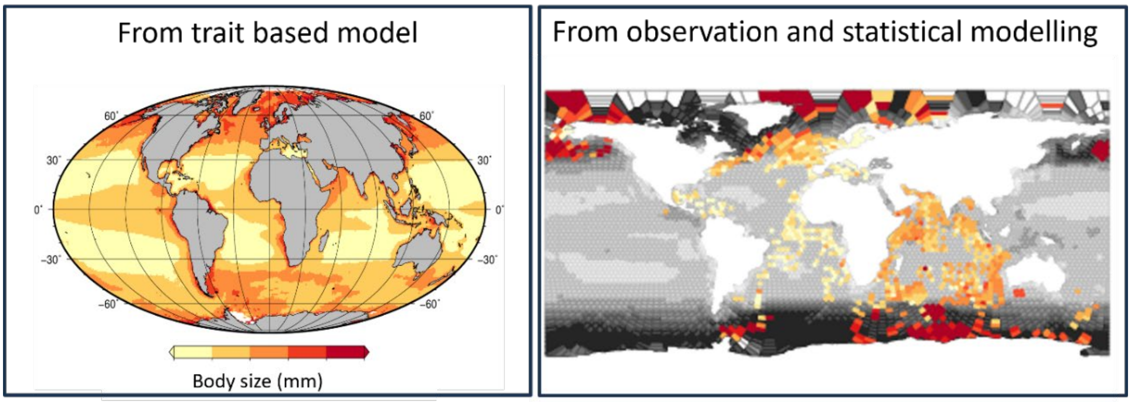

Fig 6. *Global distribution of the master trait 'size' for zooplankton, as predicted by a mechanistic trait-base model (left) and described from observations and statistical modelling.* From [1,6]

We are also using the databases to identify the processes determining the distribution and composition of marine organisms and their traits in both space and time, as well as generate large-scale patterns in biodiversity on the basis statistical species-distribution models. Recent examples of this work on marine fish community composition across the North-East Atlantic demonstrate that the composition of fish communities is governed more by species-level responses to environmental drivers than by interactions between species, and thus that 'environment filtering' is a key underlying assembly process determining fish community composition.

Large-scale patterns in biodiversity can further be derived from the databases and statistical models. These outputs can be illustrated by detailed maps of multiple taxonomic and functional (trait-based) biodiversity indicators, including both the richness and evenness of communities (Fig. 7). These models can also allow us to test scenarios aiming to maximize the protection of biodiversity, while minimizing the impacts on fisheries. As an example, we found that the current network of Marine Protected Areas (MPAs) is protecting only a small percentage of high biodiversity areas, mainly due to the small surface covered by MPAs but also because of a mismatch between the placement of MPAs and biodiversity hotspots.

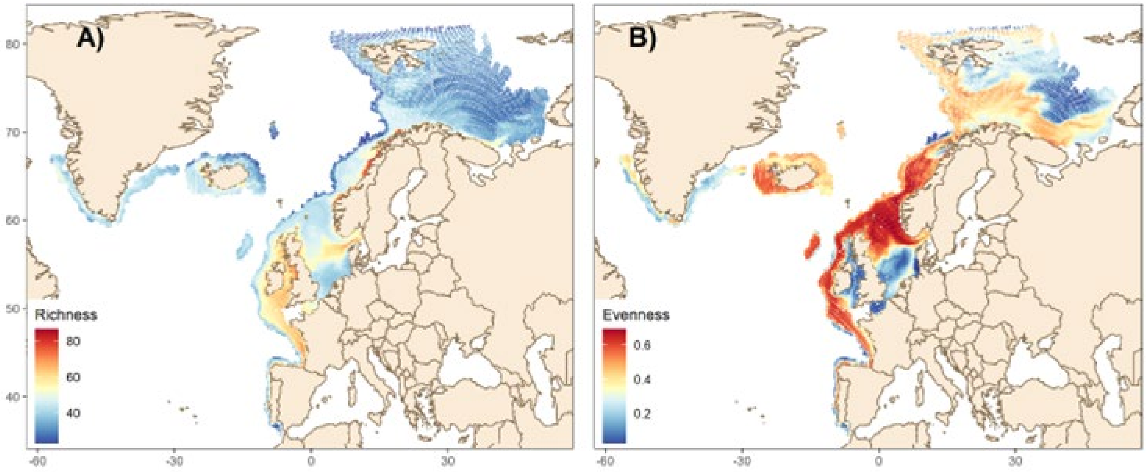

Fig 7. *Spatial patterns in two biodiversity indicators of marine fish communities for the 2000-2016 period, including the species richness (A) and evenness (B). From work in preparation.*

Ecosystem Function: A key goal of the Centre has been to develop models to predict the functioning of future oceans under climate change. How will the patterns of productivity change, how will this impact fisheries, how will the biogeochemical cycles of the ocean change, and will its ability to sequester carbon be reduced? We provide two examples of our work along these lines below.

One aspect that has received considerable focus has been the role of vertically migrating organisms in sequestering carbon through the ‘biological pump’, i.e., the biologically driven downward flux of carbon. To address this, we needed to answer 2 questions: can we mechanistically explain and quantify the cost-benefit of vertical migratory behavior and predict the consequent optimal behavior, and if so, what are the implications to ocean biogeochemistry. Starting with the assumption that vertical migration results from a trade-off between feeding opportunity and predator avoidance, we developed a game theoretic approach that could explain not only vertical migratory behavior of simple predator-prey couplets, but entire communities of trophically linked organisms. A theoretical outcome from this work was the emergence of mixed strategies – namely that even in a population of identical individuals, maximum fitness for all individuals at times is achieved if fractions of the population adopt alternate behaviors.

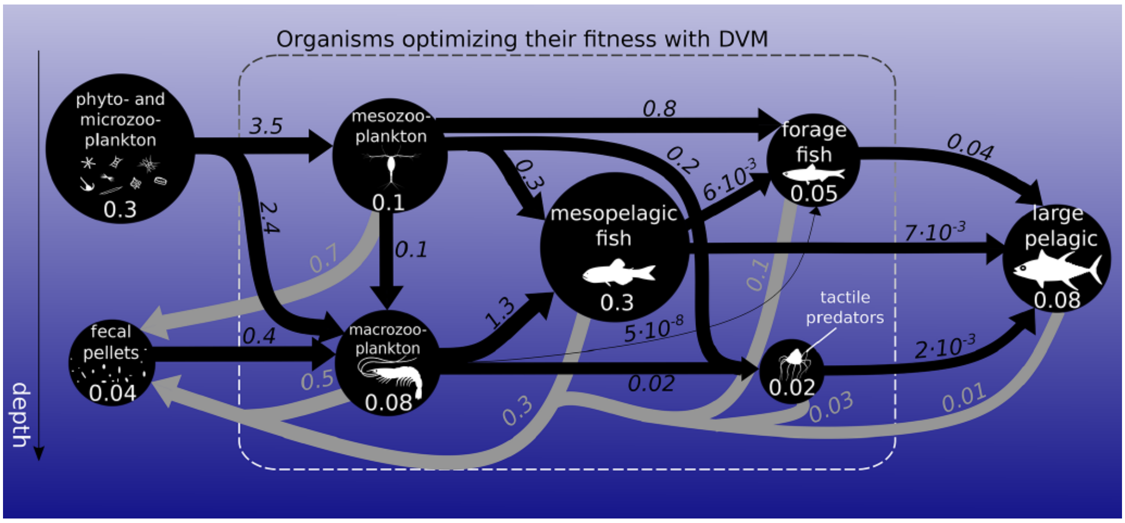

Fig 8. *Biomass (circles) and fluxes (arrows) in the food web integrated over the global ocean. Biomasses are in petagrams of carbon (PgC; white numbers). Black arrows represent ingestion, while grey arrows represent fecal-pellet excretion in PgC yr*$^{-1}$. *Arrow widths and circle diameters are proportional to the logarithm of the fluxes and biomasses they represent. Respiration losses are not represented here. The dashed box surrounds the functional groups that optimize their day and night vertical distribution with DVM. From* [7]

A major result has been to quantify the impact of metazoans (fish, zooplankton) on the biological pump. A global model, where we specifically modelled the vertical migration of major metazoan taxa, allowed us to not only quantify the trophic pathways (Figure 8) but also the impact on the ocean's biogeochemical cycles. In particular we found that of the 1300 PgC pool of biogenic dissolved inorganic carbon, about 800 PgC (i.e. over 60%) passes through metazoans (respired, fecal pellets, deadfall) before being sequestered. This is in contrast to the general paradigm, that sinking particulate organic matter (POM) is the main vector driving the biological pump. It appears that much of this POM is re-worked by metazoans in the ocean's interior, essentially transporting carbon deeper into the ocean's interior where it remains stored for longer. This work has featured in the discussion on how fisheries are impacting global carbon cycles. In a series of more targeted studies, we have focused on specific components of marine ecosystems such as the migration of copepods, Antarctic krill, squid, and whales.

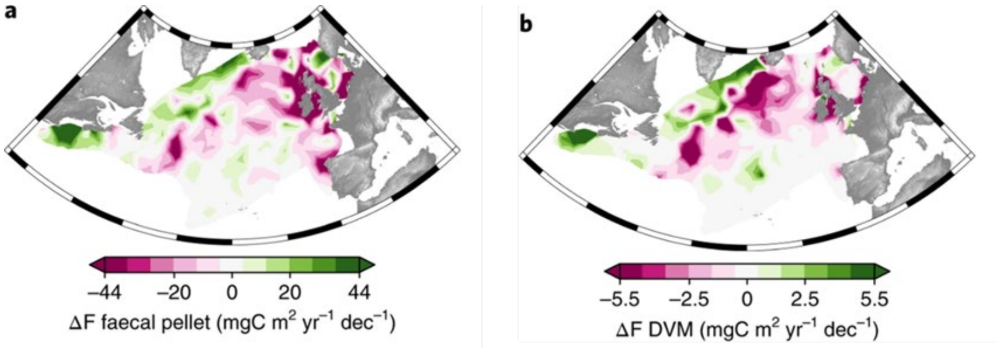

Fig 9. *Trends in (a) faecal pellet and (b) DVM fluxes at mixed layer depth from 1960 to 2014. From* [8].

Thus, we have modelled the role of marine plankton on the export of carbon from the surface mixed layer, and how this has been affected by recent climate change. Specifically, marine zooplankton show a significant spatial relocation and shift in the timing of their seasonal occurrence. We investigated how distributional and abundance changes of copepods, the dominant group of zooplankton, have affected biogenic carbon cycling. We used trait-based, mechanistic models to estimate the magnitude of carbon transported downward through sinking faecal pellets, daily vertical migration and seasonal hibernation at depth. From such estimates for over 200,000 community observations in the northern North Atlantic we found carbon flux increased along the northwestern boundary of the study area and decreased in the open northern North Atlantic during the past 55 years (Figure xx). These changes in export were primarily associated with changes in copepod biomass, driven by shifting distributions of abundant, large-bodied species. Our findings highlight how recent climate change has affected downward carbon transport by altering copepod community structure and demonstrate how carbon fluxes through plankton communities can be mechanistically implemented in next-generation biogeochemical models with size-structured representations of zooplankton communities.

These studies have coupled together observations of the abundance and distribution of specific marine populations, descriptions of their life history strategy, and transport matrix descriptions of global ocean circulation, to estimate the carbon sequestered in the oceans by these populations. For many to these populations, the residence time of carbon they sequester in the ocean is many 100s of years. An example for the "whale pump" is shown in Fix 10, while other examples have included overwintering copepods, Antarctic krill and squid.

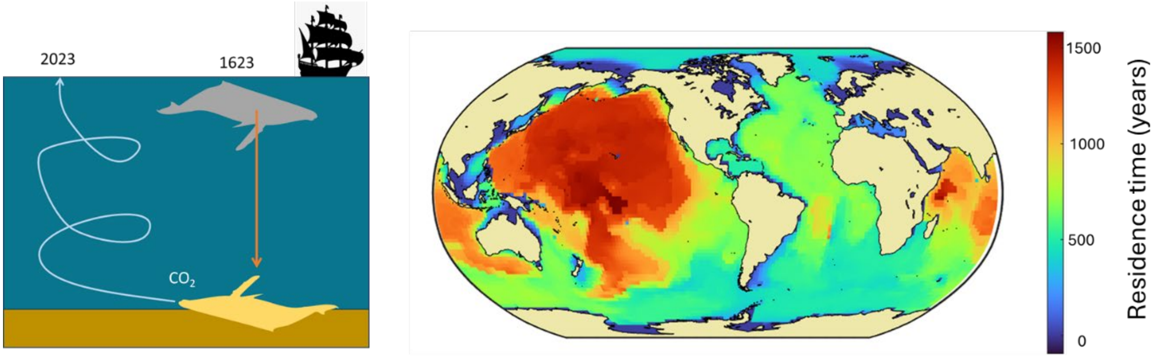

Fig. 10. *Estimated residence time for carbon injected a DIC from the deadfall of whales. Importantly, whale carbon takes on average about 700s of years to return to the surface ocean. As a consequence, the oceans are now net emitters of "whale" carbon to the atmosphere as the carbon laid down by whale populations 400 years ago is not being replaced by the decimated populations of today. From work in poreparation.*

A key concept to come out of these studies is that of legacy carbon. Specifically, the carbon capital of marine life is not in their living biomass, but rather in the legacy carbon they have laid down in the oceans as dissolved inorganic carbon (DIC). Notably, the ratio of sequestered carbon maintained by a population to its living biomass is typically several 100. For example, for mesopelagic fish, we estimate this ratio to be around 400. This means that the cost-benefit of fishing out marine resources can be couched in economic terms as carbon credits versus market value, and important consideration in developing or expanding new fisheries.

Finally, Ocean Life has contributed to the ongoing scientific debate on nature-based solutions to climate change. In particular, we make the case that marine animals and plants maintain large pools of carbon in the ocean and coastal areas that have been laid down by generations past. This legacy carbon is continuously being recycled on time scales of 100s of years. Left undisturbed, as they were for most of the last 10000 years, these carbon pools tend to equilibrium; flux in equals flux out. Human activities such as over-fishing and coastal construction, particularly in the past 75 years, have tipped these natural cycles out of balance to the extent where many pools are now net emitters of carbon. Conservation and restoration of marine habitats can bring these cycles back into balance but cannot be counted as offsetting fossil fuel emissions.

CONCLUSIONS

During its lifetime the Centre has evolved into an international hub for the development and application of trait-based approaches to describe marine ecosystems, and the Centre's interpretation and application of the approach has become known as the 'Copenhagen school'. We have reached our goal of promoting a 'fundamental understanding and predictive capacity of marine ecosystems' through the development of a suite of mechanistically underpinned models that are capable of exactly that. Our approach has been unique in the sense that probably no other group worldwide has combined experimentally derived understanding of the individual organism, with observations form nature, and models that scale up individual behaviors to population, community, ecosystem, and global level. In this, the Centre for Ocean Life has promoted a paradigm shift that now places the trait-based approach at the nexus of global ecological modelling.

Concretely, the legacy of the Centre is manifest through (i) extensive international publications (~500); (ii) through a constant flux of international scientists and students on shorter or longer (sabbatical) visits; (iii) through public outreach activities, (iv) through the establishment of an internation workshop series ('Trait-based approaches to Ocean Life') that recently returned to Copenhagen for its 6th edition and with the next workshop planned to take place in USA 2025; (v) by seeking and obtaining considerable value-added co-funding that will extend well into the future, more than tripling Villum's investment and (vi) last but not least, through the training of ~50 PhD's and ~40 Post docs, many of which now have research positions at universities and research institutions nationally and internationally.

Literature cited

[1] T. Kiørboe, A. Visser, and K. H. Andersen, A Trait-Based Approach to Ocean Ecology, ICES J Mar Science 75, 1849 (2018).

[2] L. T. Nielsen and T. Kiørboe, Foraging Trade-Offs, Flagellar Arrangements, and Flow Architecture of Planktonic Protists, PNAS 118, e2009930118 (2021).

[3] F. Ryderheim, J. Olesen, and T. Kiørboe, A Siliceous Arms Race in Pelagic Plankton, PNAS 121, (2024).

[4] S. Chakraborty, L. T. Nielsen, and K. H. Andersen, Trophic Strategies of Unicellular Plankton, Am Nat 189, E77 (2017).

[5] P. D. van Denderen, C. M. Petrik, C. A. Stock, and K. H. Andersen, Emergent Global Biogeography of Marine Fish Food Webs, Global Ecology and Biogeography 30, 1822 (2021).

[6] P. Brun, M. R. Payne, and T. Kiørboe, Trait Biogeography of Marine Copepods - an Analysis across Scales, Ecol Lett 19, 1403 (2016).

[7] J. Pinti et al., Model Estimates of Metazoans’ Contributions to the Biological Carbon Pump, Biogeosciences 20, 997 (2023).

[8] P. Brun, K. Stamieszkin, A. W. Visser, P. Licandro, M. R. Payne, and T. Kiørboe, Climate Change Has Altered Zooplankton-Fuelled Carbon Export in the North Atlantic, Nature Ecol Evol 3, (2019).