MECHANISTIC APPROACH TO PLANKTON ECOLOGY

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Can we describe complex marine ecosystems in a simple manner, and in ways that make it possible to assess the effects of environmental change? Trait-based approaches have the potential to tackle the overwhelming complexity of marine ecosystems in a relatively simple way: rather than describing the many *species* and how they interact with each other and their environment, as in traditional species-centric approaches, trait ecological approaches consider interacting *individuals* characterized by a few essential traits that are interrelated through trade-offs (Anderson 2005, Litchman et al. 2013)

The overarching goal of the proposed research is to develop a mechanistically underpinned, trait-based **model of marine plankton ecosystems ranging across multiple trophic levels from bacteria to zooplankton**. The rationale, methods, and approaches have been described in a previous draft proposal to the Moore Foundation (see also Fig. 1), which we shall therefore not repeat here. Zooplankton has a key role in the model, and the themes guiding model design are trait biogeography (i.e., spatio-temporal distributions of traits) and vertical material fluxes and carbon sequestration. Here, we describe the contents of the work, and in particular describe the introduction of a **way to test the model against field observations**, using the Californian Current system as the main test bed. The Californian Current system is an upwelling system characterized by step environmental gradients and strong temporal variation, yielding a strong signal-to-noise ratio.

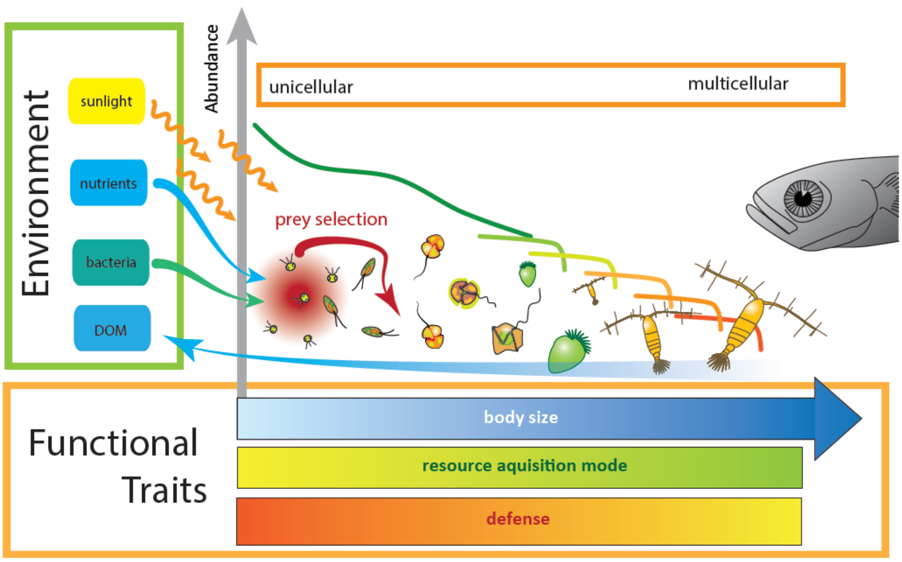

Fig. 1. Schematic of a size-resolved trait-based model of a plankton ecosystem, using only three key traits (body size, resource acquisition mode, and defense) that are interrelated through quantified tradeoffs.

The Californian Current system is in many respects representative for other major upwelling systems and therefore interesting on its own right. These upwelling systems support a large but strongly fluctuating fisheries on planktivorous fish, the composition and abundance of which are governed by the underlying plankton system and the size composition of the zooplankton food (Rykaczewski & Checkley 2008). This yields an additional perspective to our project.

The work will be organized in four interlinked work packages (WPs), each guided by a particular research question. All models will be implemented in a physical setting, and WPs 1-3 represent an increasing degree of complexity from unicellular plankton in a 0D environment toward a full size-based model in 2D environment. WP1 and 2 develop the unicellular and multicellular components, WP3 the full size based model, and WP4 sets up the model for the California Current system and tests the model against field observations collected by the *Zooglider* and through the CalCOFI monitoring program.

Each WP is the main responsibility of one post doc, although all post docs and PIs will work together as a team. The necessary combined expertise of the post docs are within the fields of Theoretical (plankton) ecology, Ecological modelling, Numerical physical oceanography, and Biological oceanography.

- **WP1:** *What is the seasonal succession and latitudinal distribution of* ***unicellular plankton*** *traits (investments in phototrophy, nutrient uptake, phagotrophy, defense, and body size)?* We develop the unicellular size-based model and solve it in 0d and 1d seasonal environments. We will initially develop an optimization model as a basis for developing a self-assembling model with population dynamics. We consider defense traits (through energy allocation) and the three resource investment traits (investments in phototrophy, nutrient uptake, phagotrophy) where the trade-offs have been calibrated by experiments on mixotrophs (Berge et al. submitted). The model is used to examine the effects of seasonality (latitude), stratification and eutrophication on trait distributions, with a specific focus on the occurrence and distribution of mixotrophy and on the vertical flux of carbon.

- **WP2:** *How do* ***multicellular zooplankton*** *trait distributions influence the biological pump?* This WP is focused on setting up a multi-cellular zooplankton model with offspring production. Technically the model is based on principles developed by our group for fish populations (Andersen et al. 2015). The main traits are defense (e.g. diurnal vertical migration), size-at-maturation, feeding mode (ambush vs. cruising), and offspring size. The food for the zooplankton is based on a simplified version of the model in WP1. The model is initially simulated in the same 0d and 1d seasonal environments as WP1 with a focus on examining how size and feeding strategy changes with latitude and during the season. The model may be extended with a description of storage/overwintering, as this is important for carbon sequestering (Jonasdottir et al. 2015). The model will then - as a test case - be set up for the California Current system. To describe the physical environment we will use an existing model, e.g., The Scripps Coupled Ocean–Atmosphere Regional (SCOAR) Model (Seo et al. 2007), and the trait-based model will then predict zooplankton traits distributions (size distribution, diurnal vertical migration, foraging mode) along transects across environmental gradients and in different seasons.

- **WP3**: *How does the* b*iogeography of the biological pump emerge from plankton traits?* In this WP we develop the full sized-based trophic model bridging from bacteria and phytoplankton to multicellular zooplankton by combining the models from WP1 and WP2. The model will be suitably simplified and use moment closure to reduce the number of state variables. The model will be implemented in the 1D environment to examine the biological pump at different seasons and latitudes, and will also allow us to examine effects of climate change. As a test case, the full model will be set up for the Californian Current System, as above, and model predictions include full plankton size spectra, distribution of resource acquisition modes, and estimates of vertical fluxes along transects across environmental gradients and in different seasons.

- **WP4:** *Field testing of model predictions*. A major focus of our proposed model is zooplankton, and the model would be able to predict trait- and size distributions of zooplankton along 2D spatial and temporal environmental gradients, as outlined above. We will collect field data for testing model predictions using the *Zooglider,* a novel instrument dedicated to quantify zooplankton. The *Zooglider* includes both a zooplankton camera and dual frequency sonar. It will be able to produce field observations of zooplankton size distribution and vertical migration and has potential to also gather some taxonomic information, thus allowing spatio-temporal mapping of the key traits considered here (body size; defense [~diel migration]; transparency; and foraging mode [can be derived from even rather coarse taxonomic resolution]). We will run Zooglider transects perpendicular to the Californian Coast in selected regions (Fig. 2) and at selected time periods to provide field data for testing the model developed in WP2. Previous work with an earlier SPRAY glider (Powell & Ohman 2015) suggests that steep horizontal gradients suitable for field testing abound in the Californian Current, where Ohman's lab has also documented horizontal gradients in zooplankton traits (Ohman & Romagnan 2016).

- Some of the specific trait-related topics we will address with *Zooglider* include: predictions of the dependence of zooplankton Diel Vertical Migration on body size and ocean optical properties (Ohman & Romagnan 2016); relationship of ambush vs. cruising zooplankton to water column stability (Mariani et al. 2013); covariation of thin layers of motile zooplankton with static stability of the water column; changes in tissue transparency with optical clarity of the water column and associated predation risk; and differential aggregation of motile and passive zooplankton at ocean front 'hot spots.'

  In addition to directed*Zooglider* sampling, we will benefit from samples taken along thetransects occupied by the CalCOFI and CCE-LTER programs (Fig. 2). These will provide additional information on the taxonomic composition and abundance of the entire plankton community. We will expand on available trait databases (Brun et al. in prep on zooplankton, and (Edwards et al. 2015) on phytoplankton) to allow us to assign traits to species (resource acquisition mode, size, defense), and thus provide field data for testing of the full, size-resolved model developed in WP3.

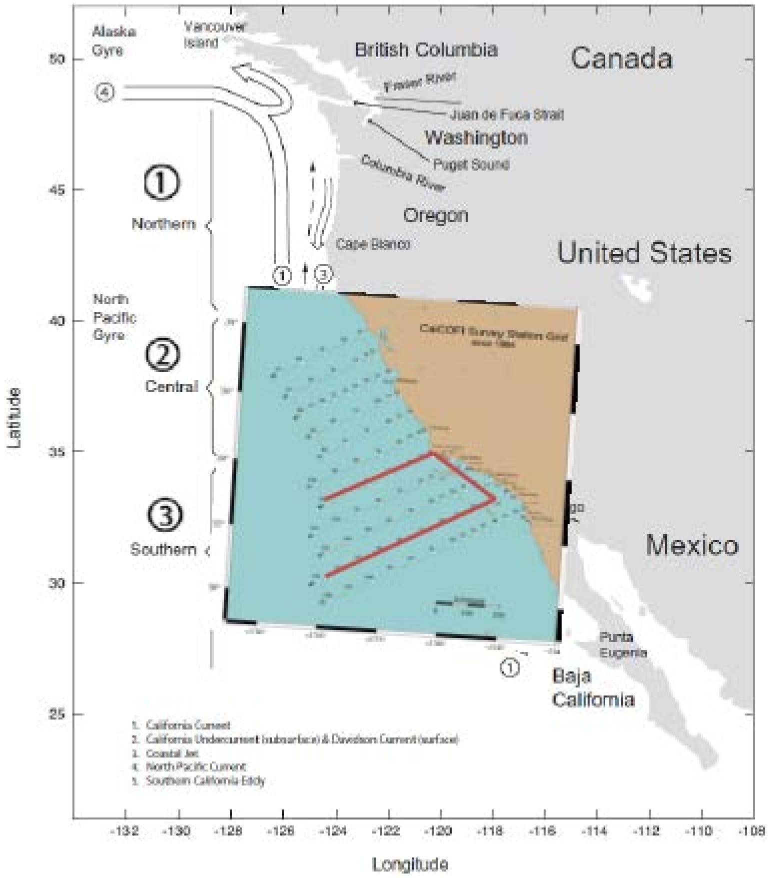

Fig. 2. The CalCOFI sampling transects in the California Current. The red transects are samples 4 times per year by CalCOFI and the California Current Ecosystem (CCE)-LTER site and provide detailed information on abundance and taxonomic composition of the entire plankton community, from bacteria to zooplankton.

WHAT IS NEW AND WHAT ARE THE RISKS?

Our vision and proposed project are bold. We have gathered a core group with very diverse expertise that allows us to attract post docs with similarly diverse backgrounds and skills. Our thesis is that only through confronting each of these specialized groups with the knowledge and technical skills of the other groups will we achieve the potential for real discovery.

While several groups worldwide work on developing trait-based descriptions and models of marine ecosystems, our project is novel in several aspects. Firstly, we develop trait-based **trophic models**, i.e., models describing several trophic levels, rather than the competition models describing single trophic level (phytoplankton) considered by most other groups. Secondly, we have developed **mechanistically underpinned tradeoffs** for the key traits of the organisms covered by our models, rather than relying on empirical or heuristic descriptions. Thirdly, trait selection in the proposed models is by **self-assembly** and not through fitness optimization (as in our current plankton models). And, finally, we propose a scheme for **testing model predictions with field observations**. While one or more of these characteristic apply to other groups' modelling activities, we are unaware of activities that simultaneously embrace them all.

The strength of the approach suggested here is that it is based on rather simple guiding principles. This implies, however, that the risk of omitting important details (e.g., effects of silica and iron dynamics). This is a classical dilemma of modelers, and the relative simplicity is a conscious choice for this 'proof of concept' project. Clearly, the implementation of the full models in a physical model of the Californian Current System is a risky step that challenges the tradeoff between simplicity and necessary detail, and the confrontation between model predictions and observations is likely to identify issues with the approach and lead to modifications. It is also not trivial to translate taxonomic information to trait information, because for many species the relevant trait values are known only with some (large?) uncertainty. However, this is a necessary step and crucial to the trait-based approach, and is indeed essential to Ecology's fundamental mission of explaining the distribution of species because the distribution of a species depends on its traits, not on its taxonomic affiliation (though often ignored or acknowledged only implicitly). While we are confident to make substantial progress in modelling and describing marine ecosystems through this project by dividing it into several parts, each with their own scientific value and outcome, the ultimate goal indeed is ambitious. However, the diverse expertise of the group and our established collaboration with relevant expert groups in the US and Europe (mainly Bruggeman in UK, Follows in USA, and Pahlow et al in Kiel) fuses realistic hope of success in meeting the ultimate goal.

IMPACT

The trait-based approach to ocean life is gaining momentum and a growing research community has developed during the past few years around a series of international workshops that our group has initiated (see the report from the last workshop in New Hampshire here: Report on the "Trait-based approaches to ocean life" scoping workshop). The suggested project is in the forefront of the development and we envisage that its results and methods will be readily picked up by this community as well as by the broader marine science community. We can also see a number of high impact publications resulting from the work, reporting both new methods as well as new fundamental understanding of marine systems, in the form of both research and synthesis or review papers.

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