

DynaTrait Subproject 2.13: “Modelling Seasonal Vertical Migration in Marine Zooplankton”

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In the first phase of DynaTrait (subproject 1.20) we have established the importance of top-down control and zooplankton diversity for understanding the functioning of marine plankton ecosystems. This subproject (2.13) focuses on the role of zooplankton seasonal vertical migration (SVM) behaviour and its evolution. Many zooplankton species migrate daily or seasonally between the surface ocean and depths of several hundred meters, which may be among the greatest animal mass migrations on Earth. Diel vertical migrations are understood as a means to avoid visual predators during daylight hours in the surface ocean. SVM behaviour is an overwintering strategy and forms part of the life cycle of many zooplankton species in high-latitude regions, which is thought to have evolved in response to the seasonality of primary production and as a means to avoid visual predators during times of low food availability. The sudden appearance and disappearance of a high zooplankton biomass due to SVM can affect the extent and timing of phytoplankton blooms and the associated export production. Thus, SVM behaviour can be considered one of the major traits driving marine plankton ecosystem dynamics in seasonal environments.

The main aim of subproject 2.13 is to improve our understanding of the relations of SVM to regional ecological and biogeochemical patterns and their evolution on decadal to millennial time scales. We are addressing these goals with two modelling approaches, a local (1D) model with detailed ecosystem representation and a global (3D) Earth system model (UVic Weaver et al., 2001; Keller et al., 2012) with a simplified ecosystem. Both contain optimality-based formulations of phytoplankton variable stoichiometry and zooplankton foraging.

The 1D model is the optimality-based plankton-ecosystem model (OPPLA), which has been developed in subproject 2.13. OPPLA is an off-line model and requires temperature, salinity, vertical mixing coefficients and other forcing data from a physical circulation model. We use forcing obtained from simulations with the FOCI model, which is currently developed at GEOMAR, partly also in our working group. Regional differences can be analysed with this approach by employing forcing for different locations in the ocean. The simulations can be calibrated and validated with time-series data, which are available for the Labrador Sea, the Bermuda Atlantic Time-Series (BATS) site and several other locations, so that we can contrast low- and high-latitude locations. OPPLA has a flexible ecosystem structure for simulations with various ecosystem configurations differing in the number and types of the functional groups. For example, simulations can be done with any number (including 0) of bacteria, phytoplankton, and zooplankton compartments.

We have implemented SVM behaviour in OPPLA in terms of four traits: the days of ascent and descent, and the summer- and winter-time depths. These were initially implemented as static traits (model parameters). The actual migration is represented by a high vertical velocity ($\pm 100 \text{ m s}^{-1}$) during the migration events, which last from a few days before to a few days after the days of ascent and descent. We used this configuration with forcing and data for the Labrador Sea for model calibration and analysis. The first goal was to establish under which conditions a population doing SVM can coexist with other (non-migrating) zooplankton groups. For this purpose, we have introduced also a (third) zooplankton group, which does not do SVM but is otherwise identical to the SVM group, in order to analyse the stability of the SVM behaviour in the presence of non-migrating competitors or sub-populations.

Next, we calibrated OPPLA in a configuration with one (non-migrating) microzooplankton group and one migrating mesozooplankton group. Calibrating the model proved much more challenging than anticipated, particularly regarding the selection of a suitable cost function, which is needed to

quantify the model-data discrepancy. Most existing cost functions, e.g., the root-mean-squared-error (RMSE) or likelihood-based cost functions (e.g., Chien et al., 2020), rely on the assumption that the observations are at least approximately normally or log-normally distributed. This assumption does not hold for the data from the Labrador Sea used in our sub-project, as shown for the nitrate data in Fig. 1A. The probability distribution was obtained via kernel-density estimation with adaptive bandwidth selection to account for the high density of very low nitrate concentrations in our dataset (M. Schartau, pers. comm.). Most likely for this reason, several attempts to calibrate the model with one of these cost functions failed to improve the model performance.

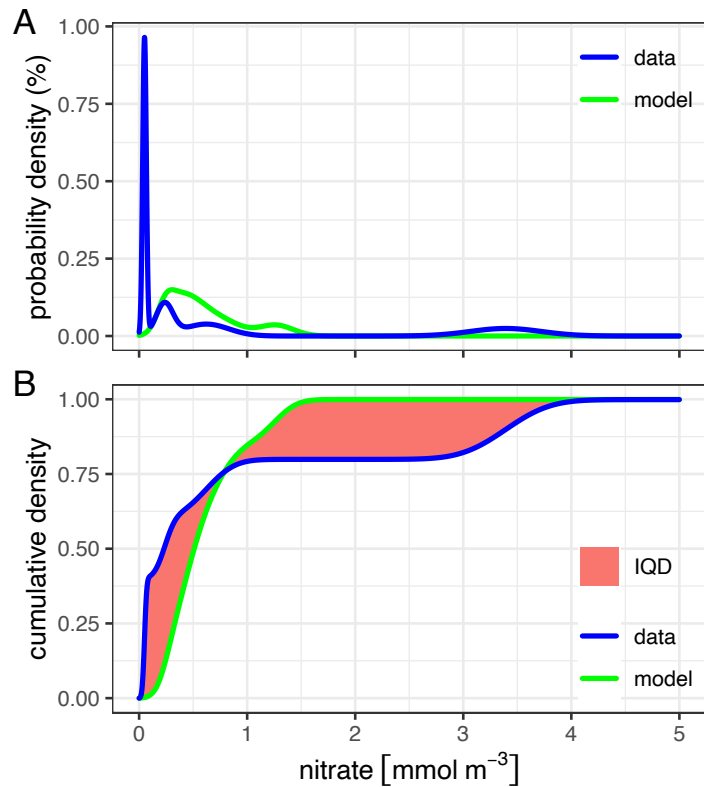


Figure 1: Integrated quadratic distance (IQD) as a measure of data-model discrepancy. (A) Probability distributions of observed nitrate concentrations (data) and corresponding predictions from the calibrated OPPLA (model). (B) The IQD is the integrated difference between the observed and predicted cumulative probability density distributions.

A cost function which is independent on the underlying probability distribution of the data is the recently-introduced integrated quadratic distance (IQD, Fig. 1B) (Thorarinsdottir et al., 2013). Formulating a cost function based on the IQD eventually enabled us to calibrate the OPPLA. For this purpose we set up two Latin-Hypercube samples of 1000 parameter sets each. We have now published the results of this study (Grossowicz & Pahlow, 2024, currently in press), where also the details of the calibration procedure can be found.

Our findings indicate that:

1. The days of ascent and descent are crucial for the long-term survival of the migrators and inter-annual variations in the timing of primary production can cause strong differences in migrator abundance between years.
2. The trophic structure must have the migrators feed more on the non-migrators than vice versa.
3. Our calibration suggests that migrators have a strong preference for carnivory, even though they act predominantly as herbivores in the plankton ecosystem.
4. SVM behaviour appears to be evolutionarily stable, i.e., the migrators compete successfully in the presence of non-migrating competitors.
5. The presence of mortality due to visual predators in the surface ocean helps the migrators but may not be necessary for their persistence.

The next step was to make two of the SVM traits, the days of ascent and descent, dynamic traits. Establishing the evolutionary stability of SVM behaviour is a prerequisite for this step because the

dynamic SVM traits would disappear on their own if they did not confer some advantage to the SVM population. The dynamics of the SVM traits are driven by generating some trait variance during the migration events and then allowing the traits to evolve as a consequence of mixing and competition. We generate trait variance via migration windows, which extend several days around the actual trait values. Within these migration windows, the migrators are assigned the current day of the year as their day of ascent/descent at which they leave their winter-/summer-time depth range. Thus, the part of the population leaving early have earlier days of ascent/descent and vice versa. When these sub-populations reach the target depth, they will mix with the population already present there, and depending on the success (previous growth) of those having arrived earlier and the size of the newly-arriving sub-population, this can change the SVM trait, eventually optimising the days of ascent and descent if the timing remains roughly constant between years. We have just started experimenting with these dynamic traits and still have to solve several technical problems. One of the open questions is currently how much trait variance we have to allow, i.e., how wide the migration windows should be to allow the migrators to respond to the inter-annual variability in the timing of primary production in the surface ocean.

We plan to do a set of simulations for different low- and high-latitude locations as mentioned above. This should tell us whether OPPLA can reproduce the regional differences, how stable the SVM behaviour is and what is its role in different seasonal regimes at different latitudes. We expect the results of these simulations to be able to guide in the implementation of SVM behaviour in the 3D (UVic) model.

We have set up the UVic model in preparation of this subproject to include the optimality-based formulations of phytoplankton variable stoichiometry and zooplankton foraging used in OPPLA and calibrated this modified UVic model (UVic-OPEM, Chien et al., 2020; Pahlow et al., 2020). We have since extended UVic-OPEM to allow simulations with two zooplankton groups in preparation for the implementation of SVM behaviour. We are currently working on allowing upward motions in UVic-OPEM, as currently only downward movements (sinking) can be handled. Based on our experience with the development of OPPLA and UVic-OPEM we plan to implement the SVM traits as dynamic traits because the static traits will only work in a specific range of latitudes, where they match the seasonality of the primary production. Since the timing of the phytoplankton blooms is opposite in northern and southern latitudes, static days of ascent and descent cannot represent SVM behaviour in a global model. Technically, dynamic traits can be implemented similarly to the variable stoichiometry of the phytoplankton in UVic-OPEM. Thus, we expect the simulations with dynamic SVM traits to provide some insight into the global distribution of SVM behaviour.

1 Bibliography

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