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## Succession in plankton communities

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2009

### **document version**

Publisher's PDF, also known as Version of record

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### **citation for published version (APA)**

Bruggeman, J. (2009). *Succession in plankton communities: A trait-based perspective*. Gildeprint Drukkerijen.

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## Summary

This thesis addresses the general problem of describing complex natural communities with models that are necessarily simple. The work is inspired by marine plankton communities, whose influence on the global climate is large but dependent on their species composition. First, a conceptual framework for community modelling is developed, which is defined in terms of the distribution of key properties – traits – within the community. Communities are then allowed to self-assemble through competition among a large collection of virtual species, differing only in the value of one or more traits. Subsequently, a mathematical approximation is developed that reduces these large collections of species to a few key statistics, which can then be simulated with good computational efficiency. To do justice to the substantial spatial and temporal variability in the marine environment, model communities are embedded within a realistic, spatially-explicit representation of the marine water column. The resulting spatiotemporal variability allows the community models to reproduce a variety of observed patterns in aquatic systems. Finally, the abstract concept of traits is connected to actual observations: an evolution-based approach is used to identify dominant traits and trade-offs from sparse observations on natural species. These patterns in interspecific differences can directly inspire and constrain future trait-based community models.

Chapter 2 introduces a high-level conceptual approach to community modelling. This approach focuses on dominant interspecific differences (traits and trade-offs) and functional diversity, rather than on the specific properties of individual species. All species are modelled with a qualitatively identical model, and differ only in their value of one or more continuous traits. The state of the community is described by the distribution of biomass over all possible trait values. In a spatially and temporally varying environment, the dynamic behaviour of the community is then completely represented by changes in the shape of the trait distribution. This conceptual approach is tested with a simple, four-parameter phytoplankton model with two traits: the investment in light harvesting and the investment in nutrient harvesting. The distribution of these traits is modelled by discretizing both trait axes, rendering hundreds of virtual phytoplankton species that differ in light- and nutrient harvesting capability. This community model is embedded within a one-dimensional model of a turbulent water column, which explicitly resolves temporal and spatial variability in light and nutrient fields. In this setting, the model captures several well-known aquatic ecosystem features, including formation of a deep chlorophyll maximum and nutrient-driven seasonal succession.

Chapter 3 extends the conceptual, distribution-based framework by introducing a method for aggregating large numbers of virtual species. It starts with a community of species, modelled as a probability distribution of one or more continuous traits. This distribution is then characterized by a few key statistics: the distributional moments. The reduction to these statistics preserves key aspects of the community structure,

such as the typical properties of the species (the mean of the traits) and a measure of functional diversity (the variance of the traits). Instead of discretizing the trait distribution, as in chapter 2, it is now modelled by describing the dynamics of its lower moments. Spatial variability is explicitly considered: the derivation investigates the scenario where the community is transported by advection and diffusion in spatially-explicit hydrodynamic models. This turns out to pose specific requirements on the statistics that can be used to characterize the trait distribution. The final result is an approximation of community dynamics in terms of a limited number of variables. This approximation is computationally very efficient, allowing the use of this type of community model in the spatially structured environments created by one-dimensional and three-dimensional hydrodynamic models.

Chapter 4 demonstrates the capabilities of the aggregation method, by applying it to a plankton community with two traits: the investment in autotrophy and the investment in heterotrophy. This could be considered the smallest possible self-sustaining community: autotrophic machinery forms organic matter from inorganic nutrients and energy provided by light, and heterotrophic machinery breaks down organic matter into inorganic nutrients. The community structure is represented by the distribution of biomass of all possible combinations of autotrophic and heterotrophic investments. This representation is particularly appealing because it permits the existence of mixotrophs that combine autotrophic and heterotrophic feeding modes; these mixotrophs are believed to fulfil key roles in nature. The bivariate trait distribution is reduced to the total biomass, mean autotrophic and heterotrophic investments, and covariances of these investments. This renders a minimal model that does a surprisingly good job at reproducing known spatiotemporal patterns in chlorophyll, mixotrophy and phytoplankton diversity. Moreover, additional simulations with a discretized trait distribution demonstrate that the approximation in terms of distributional moments performs well: quantitative discrepancies for the total biomass and mean investments are low, while covariances show good qualitative correspondence. This indicates that it is possible to derive distribution-based community models that deliver accurate representations of natural systems without requiring a large computational effort.

Distribution-based community models suffer from an important practical problem: it is difficult to pinpoint which traits dominate interspecific differences in reality, and how these traits affect organism behaviour. To tackle this problem, chapter 5 discusses how the sparse observations can be used to estimate the trait values for any species. This is based upon a simple evolutionary model that represents the evolution of multiple traits as a correlated random walk from a single primordial species. From a set of observed trait values and the species phylogeny, the model reconstructs both the rate of evolution and the trade-offs between different traits. This information is then recombined with the original observations to produce trait value estimates for all taxa in the phylogeny.

Chapter 6 demonstrates the feasibility of the evolution-based approach to reconstructing traits and trade-offs of chapter 5 by applying it to a new, extensive database of observed phytoplankton trait values. This database comprises 7 different traits, including cell size, maximum growth rate, nutrient affinity and susceptibility to predation, and 277 phytoplankton taxa. From a limited number of observations, the method calculates point estimates for all traits of all taxa (1939 values), along with standard errors, confidence intervals and probability distributions. These estimates provide valuable information on the traits and trade-offs that dominate interspecific differences in real phytoplankton communities. Moreover, in providing estimates for a variety of traits and species, these results can contribute to most quantitative studies involving phytoplankton.

In conclusion, this thesis provides conceptual and mathematical building blocks for models that target the macroscopic behaviour of the community, rather than the details of individual species. By combining methods for the identification of traits and trade-offs, the process-based formulation of trait-based models, the reduction of complex communities to a few key statistics, and the embedding of such reduced models in a spatially explicit context, natural systems can be modelled without necessitating extreme model complexity. Application to marine plankton communities demonstrates that this produces models that maintain computational efficiency while reproducing a wealth of features of natural ecosystems.