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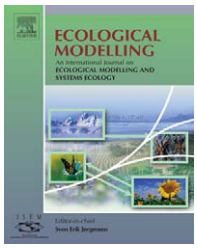

Phytoplankton co-existence: Results from an individual-based simulation model

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ABSTRACT

We have investigated phytoplankton competition in a 1D, coupled physical-biological, individual-based model, designed to simulate a size-structured phytoplankton community, whose members belong to the same functional group but differ in size (20, 40 and 60 μm ESD), and compete for two resources (light and nutrient-nitrogen) in the frame of a food-chain plankton ecosystem, forced by astronomical and climatological conditions of a subtropical site. Allometric relationships established ranked performance: small-sized individuals have higher mass-specific metabolic rates (photosynthesis, nutrient uptake and respiration) and sink more slowly than do individuals in the larger size-classes. No a priori form of niche diversification was considered. The simulation reproduced the seasonal pattern of the environmental variables and phytoplankton biomass, displayed seasonality in relative demography and sustained multi-year co-existence. Phytoplankton biomass rose during the spring bloom until nutrient depletion, decreasing afterwards due to zooplankton grazing. In the light-controlled phase of the spring bloom, the dominance ranking in the mixed layer was consistent with the allometric ranking of energetics; small, middle and large-sized phytoplankton accounted for 77.2%, 22.4% and 0.4% of total biomass (ca. 5 gC m^{-2}). Vernal subduction into the seasonal thermocline shaped a summer nutricline at ca. 30 m depth, below which reproduction generated a deep chlorophyll maximum. During summer, zooplankton diel vertical migration, foraging and excretion, and microbial remineralisation of detritus produced a feeble and declining source of ammonium in the oligotrophic layer. Differential subduction into the seasonal thermocline and nutrient stress promoted the dominance of small phytoplankton in this layer. By the end of summer, the survivors of the three size-classes lay at different depths, which provides a mechanism to relax competition: small cells survived in the mixed layer, the middle-sized in the seasonal thermocline, and the largest in both the seasonal and permanent thermoclines. Large phytoplankton survived longer in the eutrophic but poorly lit environment due to their lower mass-specific respiration. Oligotrophy lasted until the mixed layer reached the nutricline in autumn. Those cells in the seasonal and permanent thermoclines were entrained into the mixed layer as it deepened, seeding the growing season next year. The numbers of plankton in the three seed populations depended critically on their reproduction during summer. In winter, growth was accelerated by the re-establishment of the diurnal thermocline. From year-to-year, the

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relative demographic success (the annual competitive advantage, ACA) of the competing populations depends critically of their relative energetics and the biomasses in the seed populations. Taken together, these two factors yielded negligible ranking among the size-classes, and thus co-existence was achieved over three simulated years despite substantial seasonal variation in competitive advantage.

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1. Introduction

The study of the mechanisms that control and maintain species diversity in natural ecosystems is one of the key areas of research in modern ecology (Flöder and Sommer, 1999). Species diversity should be added to species composition, disturbance, nutrient supply and climate as a major controller of population and ecosystem dynamics and structure (Tilman, 1999). There is an apparent conflict between the competition theory (Hardin, 1960), which predicts that the number of co-existing species cannot exceed the number of limiting resources (competitive exclusion principle), and the high species diversity observed in natural ecosystems (e.g. Harris, 1986). In the pelagic, where only few resources are potentially limiting, this phenomenon is known as the "Hutchinson's paradox of the plankton" (Hutchinson, 1961). The wealth of community theories developed to address this paradox follow two different lines of thought (Wilson, 1990). Equilibrium theories assume the existence of stable equilibria in natural systems, and the control and maintenance of species diversity is explained by mechanisms such as niche differentiation, which often takes the form of resource partitioning (Tilman, 1977) or selective grazing (Amstrong, 1994). Non-equilibrium theories reject the steady-state assumption and focus instead in transient dynamics and stochastic descriptions, and propose that environmental changes prevent competitive exclusion to occur by relaxing or reversing competitive hierarchies before competition fully developed (Hutchinson, 1961; Reynolds, 1993; Sommer et al., 1993; Nogueira et al., 2000; Nogueira and Figueiras, 2005).

Simulation models provide a valuable tool to investigate the mechanisms that control and maintain species diversity. Until recently, most of them kept the formulation based on a three-stage food-chain (Riley et al., 1949): limiting nutrient–phytoplankton–zooplankton (NPZ model). The objective of realism forces model formulations towards increasing complexity, in terms of the number of state variables and processes included, and higher resolution, taking into account interactions that occur over a wide range of spatio-temporal scales (e.g. models listed by Totterdell, 1993; Jørgensen et al., 1995; Evans and Garçon, 1997). The increment of the number of functional groups (i.e. model components that share the same process functions) is commonly based on trophic and/or taxonomic considerations. Biodiversity in such models is related to the processes that promote and maintain the co-existence of different functional groups (e.g. Evans, 1988; Fasham et al., 1990; Fennel and Neumann, 2004). It is desirable to increase complexity further to take into account the variability of the parameters of the process functions within the functional-group level. Although the consequences of aggregation are poorly investigated (Ebenhöh, 1994), it is recognised that lumping multiple species having disparate process rates into a single functional group could result in a poor parameterisation. This increases the distortion in modelling transfers among ecosystem components (Evans and Fasham, 1993) and hinders the analysis of important ecosystem features such as competition. In an extreme case, it is possible to develop a dynamic simulation model from a specific data set (e.g. Andersen et al., 1987), but as the number of species could be considerable, the model becomes complex to handle and the estimation of the parameters very difficult. An alternative approach is to define the structure of the model based on general properties of the ecosystem (Platt et al., 1981), which has the advantage of constraining the number of parameters to be estimated. The most generalised applicable property of the plankton ecosystem is size, which influences the rates of metabolic processes, the interactions among planktonic (and other) organisms and the structure and function of the ecosystem (Peters, 1983; Dickie et al., 1987; Cushing, 1989; Chisholm, 1992; Kiørboe, 1995; Legendre and Rassoulzadegan, 1996). Size-based models (e.g. Moloney and Field, 1991; Moloney et al., 1991; Gin et al., 1998; Baird et al., 2004) make use of allometric relationships to estimate the parameters of the biological process functions for each of the size-classes of organism that integrate each functional group.

The maintenance of biodiversity in plankton ecosystem models is difficult to achieve, even when the competing species belong to different functional groups. It generally requires the prescription of some form of niche diversification, such as resource partitioning (Dippner, 1998; Huisman and Weissing, 1999), selective grazing (Moloney and Field, 1991; Amstrong, 1994), different behaviour (Broekhuizen, 1999) or the introduction of trade-off conditions (Evans, 1988) among the competing plankton. A general assumption in these models is that the competing species must be sufficiently ecologically distinct in order to co-exist (Chesson, 1991). Co-existence is more difficult to achieve when the competing species belong to the same functional group and a competitive hierarchy exists among them (Ebenhöh, 1994).

Despite the multiplicity of formulations and spatio-temporal scales considered in plankton simulation models (e.g. Jørgensen et al., 1995), they can be classified in three types according to the way they aggregate the plankton (Woods, 2005): (1) box, (2) field and (3) individual-based models. The first two treat the components of the plankton ecosystem as continuum fields, integrating in an Eulerian frame the set of differential equations that describe the physical, chemical and biological processes. The application of the Eulerian-continuum method has a relatively easy computer implementation, and therefore has usually been the method adopted (e.g. models listed in Totterdell, 1993; Jørgensen et al., 1995;

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